

# Adult body length and sexual size dimorphism in *Lacerta agilis boemica* (Reptilia, Lacertidae): between-year and interlocality variation

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*Lacerta agilis boemica* occupies a wide range of altitudes in the eastern North Caucasus (Russia). Snout-vent length (SVL) of 713 individuals of *L. a. boemica* from 9 localities was studied for inter-annual and microgeographic variation in adult body size and sexual size dimorphism (SSD). Means and 80th percentiles of SVL distributions were used in our comparisons and showed strongly correlated patterns of interlocality variation. The largest differences between samples from different years within populations were comparable in magnitude with those among localities. Among localities, adult SVL of males and females exhibited no increase with altitude. Moreover, males from the lowland localities reach a larger body length than those from the other sites. SSD was strongly associated with altitude, with the SSD index of Lovich & Gibbons (1992) varying from  $-0.07$ – $-0.09$  in the lowland sites to  $-0.03$ / $0.02$  in the mountains. Higher growth costs of reproduction in females and a stronger intrasexual selection in males in the lowland sites relative to their counterparts from higher elevations were proposed to explain the altitudinal variation in SSD in *L. a. boemica*.

Keywords: *Lacerta agilis boemica*, lizards, sexual size dimorphism, altitudinal variation.

## INTRODUCTION

Differences between males and females in characteristic body size, so-called Sexual Size Dimorphism (SSD), are widespread among reptiles. During last decades, SSD has been a target of many herpetological studies dealing with ecological morphol-

ogy, life-history, and behaviour (*e.g.*, Braña 1996, Stamps *et al.* 1997, Wikelski & Trillmich 1997, Butler *et al.* 2000, Rutherford 2004). The primary adaptive hypotheses for the ultimate causes of SSD in lizards are (1) sexual selection for large male size (success in male combat) and (2) natural selection for large female size (advantage in fecundity) (see Cox *et al.* 2003 for a review). Both hypotheses were supported in quite many studies involving different lizard *taxa* (*e.g.*, Anderson & Vitt 1990, Olson 1992, Wikelski & Trillmich 1997). However, recent comparative phylogenetic analysis by Cox *et al.* (2003) found only a weak support for these two hypotheses as general explanations of SSD in lizards. The authors noted the importance of investigating proximate causation as had been previously stressed by other SSD students (*e.g.*, Shine 1990, Stamps 1993, Watkins 1996).

Lacertid lizards exhibit noticeable variation in the extent and direction of SSD (Fitch 1981). However, only few papers addressed this variation, mostly at the level of inter-specific differences (Braña 1996, Gvozdik & Boukal 1998, Molina-Borja 2003, Molina-Borja & Rodríguez-Domínguez 2004).

Recently we have initiated a study of intraspecific variation in SSD in the sand lizard, *Lacerta agilis* which occupies a larger part of the temperate Palearctic from southern England and the Pyrenees in the west to the Baikal Lake in the east (Bischoff 1988).

Centre of the origin and diversification of *L. agilis* is the Caucasus region where five of the nine broadly recognized subspecies occur (Darevsky *et al.* 1976, Kalyabina-Hauf 2003). The south-eastern North Caucasus (Russia) is occupied by *L. a. boemica* (Suchow 1929). This subspecies occurs in a wide range of altitudes from 0-2000 m above sea level, often in high population densities (Roitberg *et al.* 2000). Such a distribution provides an opportunity to comparatively study populations from geographically proximate but climatically contrasting localities. The present paper addresses the variation of adult body size and SSD in *L. a. boemica* on the temporal (over years within populations) and microgeographic scale. This report supplements our previous paper (Roitberg & Smirina 2006) in that it includes much larger study material and operates with traditional (rather than growth-based) estimates of body size. Our aims were (1) to present extensive body size data for this particular subspecies; (2) to estimate the extent of variation of adult body length and SSD in a large data set in which the effect of phylogeny is obviously negligible; (3) to test concordance of different statistics for adult body size and SSD. The latter two points were particularly important for future analysis of the macrogeographic variation in adult body length and SSD in *L. agilis*.

## MATERIALS AND METHODS

*Study material*

The study material – total of 713 presumably adult individuals – originates from nine localities (sites) which are mostly concentrated in the south-eastern half of the *L. a. boemica* range (Table 1). These include four lowland sites (up to 250 m above sea level), three submontane sites (550-600 m a.s.l.), and two mountain sites (960, 1900 m a.s.l.). All but one site were repeatedly sampled in different years. In Site 4, which was sampled most intensively, the lizards captured in 1982-1984 were examined alive and then released in the capture site. In the other study sites the collected lizards were preserved and subsequently examined for many different aspects of morphological variation (Roitberg 1982, 1991, 1994; Roitberg & Rostova 1999) and skeletochronology (Roitberg & Smirina 1995, 2005). No animals were sacrificed for the present study.

In each study site, all specimens were caught from an area of a few dozen hectares. The only exception was Site 2 where we pooled small samples collected in several sites in and around Groznyy (these data are courtesy of K.Yu. Lotiev).

Snout-vent length (SVL), used as conventional measure of overall body size, was measured to the nearest 1 mm.

*Definition of adult samples*

In a sample collected in the first half of the activity season the SVL distribution is clearly bimodal. The smaller-size class is represented by yearlings – individuals experienced one hibernation only, while the larger-size class is built by older animals experienced two or more hibernations (Roitberg & Smirina 1995, 2006). These classes

Table 1. Geographic characteristics of the study sites.

| Locality       | Geographical coordinates | Altitude, m |
|----------------|--------------------------|-------------|
| 1. Novokurskiy | 43°39'N, 43°54'E         | 240         |
| 2. Grosnyy     | 43°15'N, 45°41'E         | 200         |
| 3. Kostek      | 43°20'N, 46°46'E         | 50          |
| 4. Makhachkala | 42°59'N, 47°30'E         | - 10        |
| 5. Buinaksk    | 42°45'N, 47°04'E         | 600         |
| 6. Termenlik   | 42°25'N, 47°00'E         | 960         |
| 7. Sergokala   | 42°28'N, 47°42'E         | 550         |
| 8. Khuchni     | 41°57'N, 47°57'E         | 600         |
| 9. Kuli        | 42°01'N, 47°15'E         | 1900        |

generally correspond to subadults and adults. The yearlings tend to grow much faster than the adults, and later in the season their size distributions can overlap. In this study we treated as adults all animals with SVL > 70 mm. Following considerations led us to this criterion. 1. In virtually all investigated lizard species the onset of maturity is size- rather than age-dependent (*e.g.*, Galán 1996, Tracy 1999). 2. Females with SVL of 71-75 mm quite often had oviductal eggs, whereas those of 66-70 mm wore eggs exceptionally rare (no direct data were available for the breeding state of the males). 3. In most study samples, the SVL of 71 mm fall in the gap between body length distributions of adults and subadults; so a shift of the separation point from 70 to 73 mm resulted in only minor (if any) changes of our sample statistics, with the pattern of variation remaining virtually the same.

### *Estimating characteristic body size*

An important methodological problem in comparative studies is the choice of appropriate statistics for adult body size. Average and extreme values are the most widely used statistics and they are often the only parameters available in publications. The average size is statistically powerful thus providing reasonable estimates even by small sample sizes. However, in animals which exhibit substantial postmaturation growth, the mean adult size can be influenced by plenty of proximate factors affecting the size distribution. These are local and temporal variation in size at maturity, growth rates, adult mortality, and so forth (Stamps & Andrews 1992, Stamps 1993, Watkins 1996).

In lizards and other ectotherms, body growth after maturity is usually asymptotic. That is, it slows progressively with size and virtually ceases at advanced size and age (see *e.g.*, Olsson & Shine 1996 for *L. agilis* growth curves). The mean (typical) growth curve and its asymptote (*A*) can be developed from individual growth increments or body sizes of aged individuals (*e.g.*, Andrews 1982, Brown *et al.* 1999). For comparative studies focusing on differences among populations or between sexes, asymptotic size (*A*) is a preferable statistic because it is affected by a much shorter list of proximate factors than average size (Stamps & Andrews 1992, Stamps 1993, Brown *et al.* 1999). As growth curves are often not available, some other simple statistics were suggested to estimate asymptotic size. Largest individual method (Stamps & Andrews 1992) clearly overestimates *A* and it is highly dependent on sample size (Brown *et al.* 1999). Instead, the 80th or other higher percentiles have been recommended for theoretical reasons (Brown *et al.* 1999) and exhibited a good conformity with the growth-based estimates in several sets of lizard data (Brown *et al.* 1999, Kratochvíl & Frynta 2002, Roitberg & Smirina 2006). Both the means and 80th percentiles of adult samples were used in this study.

*Estimating sexual size dimorphism*

We quantified SSD with the index:  $SSD = (\text{size of larger sex} / \text{size of smaller sex}) - 1$ , arbitrarily expressed as positive if females are larger and negative if males are larger (Lovich & Gibbons 1992). We chose this index because it generates values that are intuitive, directional, properly scaled, and symmetrical around zero (Lovich & Gibbons 1992, Smith 1999). For each study sample, two SSD values, one based on means ( $SSD_x$ ) and the other on 80th percentiles ( $SSD_{p80}$ ), were computed.

*Statistical analysis*

For analysis of interannual variation, operational units of statistical comparisons were samples of specimens of the same sex, collected from the same locality in the same year. The interannual variation was not examined for localities where the operational units were too small ( $n < 10$ ). For analyses of interlocality variation, samples of different years were pooled for each combination of sex and locality. As the assumptions of normality (Shapiro-Wilk  $W$ -test test) or homogeneity of variances (Levene test, Liliefors) were often violated in our study samples, even if SVL was log-transformed, we used only nonparametric tests. By multiple comparisons, we considered only those individual differences, which remained significant ( $P < 0.05$ ) after the sequential Bonferroni adjustment (Rice 1989).

We used SPSS 11.5 for all the analyses.

## RESULTS

*Temporal variation in adult SVL and sexual size dimorphism*

Summary statistics for male and female adult SVL and SSD in our study samples are given in Table 2 (rows with single years). A Kruskal-Wallis test was made for each of the 10 sex  $\times$  locality combinations with adequate sample sizes. The following interannual differences for mean SVL remained significant after the sequential Bonferroni adjustment: Site 4, males ( $\chi^2_{\Lambda} = 24.9$ , d.f. = 4,  $P < 0.001$ ); Site 5, females ( $\chi^2_{\Lambda} = 10.5$ , d.f. = 2,  $P = 0.005$ ). We could reveal no regular trend in this variation. In Site 4, the males collected in 1970 were clearly larger (means, 80th percentiles) than those of 1980, 1982, and 1983, but the males of 1984 were nearly as large as the males of 1970. In Site 5, females of 1982 were larger than those collected in 1970 and 1979 (Table 2). One regular trend was found in the temporal dynamics of SSD. In sites 4, 5, and 7, each of which provided samples of 1970, 1979 (1980), and 1982, the SSD for means was stronger in the samples of 1970 than in the samples of the other years (Table 2). This has a  $(1/3)^3 \approx 0.0027$  chance of occurring at random that significantly differs

Table 2. Male and female SVL and sexual size dimorphism (SSD) in adult samples of *Lacerta agilis boemica*. N – sample size; Min, Max – extreme values; X – mean; SD – standard deviation; P80 – 80th percentile;  $SSD_x$  and  $SSD_{P80}$  – Lovich & Gibbons (1992) SSD index calculated for means and percentiles, correspondingly. See Table 1 for geographic characteristics of the study sites.

| Sites          | Years | Males      |           |            |             |              |              | Females    |           |            |             |             |             | SSD_m | SSD_p80 |
|----------------|-------|------------|-----------|------------|-------------|--------------|--------------|------------|-----------|------------|-------------|-------------|-------------|-------|---------|
|                |       | N          | Min       | Max        | X           | SD           | P80          | N          | Min       | Max        | X           | SD          | P80         |       |         |
| 1. Novokurskiy | 1970  | <b>34</b>  | <b>73</b> | <b>106</b> | <b>92.5</b> | <b>7.39</b>  | <b>100.0</b> | <b>34</b>  | <b>74</b> | <b>98</b>  | <b>85.2</b> | <b>6.63</b> | <b>92.0</b> | -0.09 | -0.09   |
| 2. Groznyy     | total | <b>14</b>  | <b>77</b> | <b>114</b> | <b>93.7</b> | <b>10.84</b> | <b>101.0</b> | <b>14</b>  | <b>73</b> | <b>104</b> | <b>87.2</b> | <b>9.28</b> | <b>96.0</b> | -0.07 | -0.05   |
| 3. Kostek      | 1984  | 14         | 71        | 103        | 88.9        | 10.55        | 100.0        | 10         | 71        | 95         | 84.8        | 6.97        | 88.8        | -0.05 | -0.13   |
|                | 1985  | 11         | 71        | 106        | 88.5        | 11.89        | 100.2        | 18         | 71        | 90         | 79.8        | 5.38        | 84.2        | -0.11 | -0.19   |
| 3. Kostek      | total | <b>25</b>  | <b>71</b> | <b>106</b> | <b>88.7</b> | <b>10.92</b> | <b>99.8</b>  | <b>28</b>  | <b>71</b> | <b>95</b>  | <b>81.6</b> | <b>6.35</b> | <b>87.2</b> | -0.08 | -0.14   |
| 4. Makhachkala | 1970  | 36         | 80        | 109        | 94.0        | 7.15         | 100.0        | 24         | 71        | 95         | 83.8        | 6.44        | 90.0        | -0.12 | -0.11   |
|                | 1980  | 25         | 71        | 102        | 83.8        | 9.47         | 96.6         | 24         | 73        | 97         | 81.1        | 6.48        | 86.0        | -0.03 | -0.12   |
|                | 1982  | 18         | 71        | 99         | 86.1        | 7.53         | 91.6         | 23         | 72        | 97         | 83.3        | 6.79        | 90.4        | -0.03 | -0.01   |
|                | 1983  | 14         | 72        | 104        | 82.9        | 10.08        | 95.0         | 20         | 73        | 97         | 80.3        | 6.37        | 86.6        | -0.03 | -0.10   |
|                | 1984  | 13         | 76        | 106        | 90.5        | 10.85        | 102.0        | 17         | 75        | 95         | 82.2        | 6.73        | 90.0        | -0.10 | -0.13   |
| 4. Makhachkala | total | <b>108</b> | <b>71</b> | <b>109</b> | <b>88.3</b> | <b>9.89</b>  | <b>98.0</b>  | <b>108</b> | <b>71</b> | <b>97</b>  | <b>82.2</b> | <b>6.57</b> | <b>88.0</b> | -0.07 | -0.11   |
| 5. Bulnask     | 1970  | 27         | 72        | 97         | 85.8        | 6.83         | 93.4         | 26         | 72        | 88         | 79.4        | 4.78        | 86.0        | -0.08 | -0.09   |
|                | 1979  | 18         | 73        | 97         | 81.9        | 7.43         | 90.0         | 23         | 71        | 88         | 78.8        | 4.83        | 83.4        | -0.04 | -0.08   |
|                | 1982  | 16         | 75        | 99         | 85.3        | 6.27         | 90.0         | 16         | 76        | 92         | 84.4        | 5.45        | 90.6        | -0.01 | 0.01    |
| 5. Bulnask     | total | <b>61</b>  | <b>72</b> | <b>99</b>  | <b>84.5</b> | <b>6.97</b>  | <b>91.0</b>  | <b>65</b>  | <b>71</b> | <b>92</b>  | <b>80.4</b> | <b>5.42</b> | <b>86.0</b> | -0.05 | -0.06   |
| 6. Termenlik   | total | <b>14</b>  | <b>79</b> | <b>100</b> | <b>90.4</b> | <b>7.02</b>  | <b>97.0</b>  | <b>16</b>  | <b>75</b> | <b>99</b>  | <b>87.7</b> | <b>6.55</b> | <b>93.4</b> | -0.03 | -0.04   |
| 7. Sergokala   | 1970  | 20         | 78        | 94         | 85.2        | 4.87         | 89.8         | 21         | 71        | 87         | 77.8        | 4.81        | 83.2        | -0.09 | -0.08   |
|                | 1979  | 21         | 72        | 96         | 84.0        | 7.36         | 92.6         | 23         | 71        | 90         | 79.3        | 5.98        | 85.4        | -0.06 | -0.08   |
|                | 1982  | 17         | 75        | 97         | 84.2        | 5.80         | 90.0         | 16         | 76        | 88         | 80.9        | 3.57        | 83.8        | -0.04 | -0.07   |
| 7. Sergokala   | total | <b>58</b>  | <b>72</b> | <b>97</b>  | <b>84.5</b> | <b>6.06</b>  | <b>90.0</b>  | <b>60</b>  | <b>71</b> | <b>90</b>  | <b>79.2</b> | <b>5.09</b> | <b>84.0</b> | -0.07 | -0.07   |
| 8. Khuchni     | 1985  | 12         | 73        | 94         | 83.9        | 8.02         | 92.2         | 17         | 71        | 96         | 80.2        | 8.21        | 89.4        | -0.05 | -0.03   |
|                | 1986  | 13         | 76        | 103        | 87.3        | 7.78         | 94.6         | 12         | 77        | 91         | 86.5        | 4.58        | 91.0        | -0.01 | -0.04   |
| 8. Khuchni     | total | <b>25</b>  | <b>73</b> | <b>103</b> | <b>85.7</b> | <b>7.92</b>  | <b>93.4</b>  | <b>29</b>  | <b>71</b> | <b>98</b>  | <b>82.8</b> | <b>7.53</b> | <b>90.0</b> | -0.03 | -0.04   |
| 9. Kull        | total | 11         | 73        | 100        | 89.9        | 8.07         | 97.0         | 11         | 78        | 100        | 91.6        | 6.96        | 97.0        | 0.02  | 0.00    |

from 0.5 (binomial test,  $P < 0.001$ ). For comparisons between 1970 and 1982, the SSD for 80th percentiles showed a similar pattern (Table 2).

### Interlocality variation in adult SVL and sexual size dimorphism

Summary statistics for male and female adult SVL and SSD in 9 localities (years combined) are given in Table 2 (bold figures). Interlocality variation was highly significant in both sexes (Kruskal-Wallis test: males,  $\chi^2 = 35.2$ , d.f. = 8,  $P < 0.001$ ; females,  $\chi^2 = 49.1$ , d.f. = 8,  $P < 0.001$ ). Population means ranged from 85–93 mm in males and 79–92 mm in females (Table 2). In nearly all localities, sex differences were male-biased (males were the larger sex, SSD index negative), being significant for sites 1, 3–5, 7 ( $P < 0.001$ –0.01).

Table 3 shows geographic co-variation among the different statistics for male and female SVL, SSD, and altitude. Strong correlations were found within each pair of different statistics of the same biological variables: the mean and the 80th percentile of adult SVL in males ( $r_s = 0.86$ ,  $P < 0.003$ ) and females ( $r_s = 0.98$ ,  $P < 0.001$ ) as well as the figures of the SSD index calculated for the two SVL statistics ( $r_s = 0.92$ ,  $P <$

Table 3. Spearman rank correlation coefficients ( $r_s$ ) between different statistics for male and female SVL, sexual size dimorphism, and altitude. Interlocality variation. Statistics:  $X_m$  and  $X_f$  – sample means,  $P80_m$  and  $P80_f$  – 80th percentiles for males and females;  $SSD_x$  and  $SSD_{P80}$  – sexual size dimorphism index of Lovich & Gibbons (1992) calculated for means and 80th percentiles, correspondingly. Bold figures designate  $r_s$  values with  $P < 0.05$ .

| Variables   |       | $SSD_x$      | $SSD_{P80}$  | $X_m$  | $P80_m$      | $X_f$        | $P80_f$      |
|-------------|-------|--------------|--------------|--------|--------------|--------------|--------------|
| Elevation   | $r_s$ | <b>0.812</b> | <b>0.795</b> | -0.326 | -0.664       | 0.176        | 0.142        |
|             | $P$   | 0.008        | 0.010        | 0.391  | 0.051        | 0.651        | 0.715        |
| $SSD_x$     | $r_s$ |              | <b>0.917</b> | -0.133 | -0.561       | 0.450        | 0.383        |
|             | $P$   |              | 0.001        | 0.732  | 0.116        | 0.224        | 0.308        |
| $SSD_{P80}$ | $r_s$ |              |              | 0.117  | -0.301       | 0.617        | 0.600        |
|             | $P$   |              |              | 0.765  | 0.431        | 0.077        | 0.088        |
| $X_m$       | $r_s$ |              |              |        | <b>0.862</b> | <b>0.783</b> | <b>0.817</b> |
|             | $P$   |              |              |        | 0.003        | 0.013        | 0.007        |
| $P80_m$     | $r_s$ |              |              |        |              | 0.460        | 0.536        |
|             | $P$   |              |              |        |              | 0.213        | 0.137        |
| $X_f$       | $r_s$ |              |              |        |              |              | <b>0.983</b> |
|             | $P$   |              |              |        |              |              | 0.000        |

0.001). The SSD figures calculated for the means and 80th percentiles were also similar in their absolute values: the average difference was  $0.013 \pm 0.023$  ( $n = 9$ ).

Both SSD indices exhibited a strong positive correlation with altitude ( $r_s = 0.80$ – $0.81$ ,  $P < 0.01$ ). In contrast, among the SVL statistics for single sexes, only the 80th percentiles of male SVL showed a marginally significant correlation with altitude (Table 3). The two statistics of male SVL correlated moderately with those of females: only two of the four correlations were significant (Table 3).

## DISCUSSION

### *Temporal variation in adult SVL and sexual size dimorphism*

The largest of the interannual differences in adult SVL and SSD revealed in the study sites were comparable in magnitude with those among localities. One regular trend, a stronger male-biased SSD in the samples of 1970 relative to the samples of 1979–82 within three study sites, was revealed. Along with temporal, environmentally induced variation in maturation pattern, growth rates, and adult mortality (Stamps 1993 and references therein), seasonal changes in proportion of younger (newly matured) adults and behavioural exclusion (Andrews & Stamps 1994, Watkins 1996) can affect the size distribution of males and/or females and SSD in a particular sample. Lack of detailed data on population dynamics, environmental fluctuations, and spatial distribution of old and younger adults makes it difficult to identify sources of the revealed interannual variation in adult SVL and sexual size dimorphism in *L. a.*

*boemica*. In any event, the presented data show that differences in adult SVL or SSD observed between single-year samples from few localities may be irrelevant to geographic variation, and samples of several years and/or a considerable number of the study sites are necessary to discover the actual geographic or altitudinal pattern.

### *Patterns of altitudinal variation in adult SVL in lizards*

Unlike comparable studies on three Australian skink species (Rohr 1997, Qualls & Shine 1998, Wapstra *et al.* 2001) which showed a pronounced increase in maximum, asymptotic and mean adult SVL (along with a higher longevity) at high elevations, our study revealed no clear trend for adult SVL in males or females. This is despite the facts that the altitudinal range of our study sites (over 1900 m, Table 1) was even higher than in the investigations cited above, and the adult lizards from higher altitudes (960, 1900 m) exhibited clearly higher mean and maximum ages than those from elevations of 50-600 m (Roitberg & Smirina 1995, 2006). A comparison between a low-elevation (Ararat valley, 850 m a.s.l.) and a high-elevation (Sevan coast, 1900 m) populations of *L. strigata* in Armenia (Melkumyan 1983) exhibited the same pattern as *L. a. boemica*: relatively small difference in mean adult SVL (91.9 mm and 93.8 mm) and substantial difference in longevity (3-4 years *vs* 6-7 years) (Melkumyan 1983). Even related species from the same mountain system can have quite different patterns of altitudinal variation for adult SVL: in the Chiricahua Mountains (Arizona), reproducing females of *Sceloporus jarrovi* from a high elevation were larger than their lower-elevation counterparts (Ballinger 1979), while the opposite pattern was reported for *S. scalaris* (Mathies & Andrews 1995). Both patterns were, however, not as strong as those by skinks and did not involve substantial differences in maximum SVL (fig. 1 in: Ballinger 1979; fig. 5 in: Mathies & Andrews 1995). Further data on conspecific populations from geographically proximate but climatically contrasting localities, involving various lizard *taxa* and different environmental gradients should help to interpret the observed diversity of patterns of geographic variation in adult body length.

### *Altitudinal variation in sexual size dimorphism in L. a. boemica*

SSD in *L. a. boemica* is predominantly male-biased (Table 2). Interlocality variation of this SSD exhibited a strong correlation with altitude (Table 3), varying from -0.07/-0.09 in the lowland localities to -0.03/-0.02 in the mountain sites (Table 2). Our skeletochronological investigation of 5 of the 9 populations of this study (Roitberg & Smirina 2006) provided some insight to proximate causation of the observed SSD pattern. Sex-biased adult mortality does not seem to be an important factor as we did not find any consistent sex differences in the age composition of adults (*op. cit.*).



Instead, the SSD in *L. a. boemica* apparently results from sex differences in growth trajectories, mainly due to reduced growth in females in the year of their first reproduction (op. cit.). Based on the models by Adolph & Porter (1993, 1996) and some original data we hypothesized that the growth costs of reproduction should be higher in the lowland females than in females from higher elevations because the former are expected to mature at earlier age and smaller size, and produce more eggs per year. Thus we viewed the higher male-biased SSD in the lowland populations as a by-product of the interaction between the growth and maturation patterns (Roitberg & Smirina 2006). Sex differences in growth curves were reported as the primary proximate factor of SSD in some other lizard species (Watkins 1996, Rutherford 2004).

Unlike the interannual differences which should mainly reflect the proximate level processes (phenotypic plasticity or demographic dynamics), the geographic variation in adult body length and SSD can also involve a genetic component. The 80th percentiles of the SVL distributions of adult males showed a marginally significant negative correlation with altitude (Table 3). Moreover, for this statistic, as well as for maximum values, the males from four lowland localities are clearly larger than those from the higher elevation sites (Mann-Whitney U test,  $Z = -2.46$ ,  $P < 0.01$ ). We hypothesize the larger male size (and partly the stronger sexual size dimorphism) in the lowland populations of *L. a. boemica* to result from a stronger intrasexual selection due to a high population density (Stamps *et al.* 1997). Indeed, whereas in our lowland and submontane localities an observer could meet several dozen individuals during 3-5 hours, at most 10-15 animals were recorded during a comparable excursion in the mountain study sites (E.S. Roitberg unpublished data). Furthermore, the lowland populations of *L. a. boemica*, at least in the eastern part of its distribution, are rather dense but spatially limited (Roitberg *et al.* 2000). That is, in some respects these populations are comparable with the populations of small islands. A tendency of island populations to exhibit a stronger male-biased SSD as compared to their mainland relatives is widespread in reptiles (Fitch 1981). For lacertid lizards, a rather strong male-biased SSD was also reported just for the island forms with high population densities (Salvador 1984, Pérez-Mellado & Salvador 1988). Further studies should test our hypotheses on proximate and ultimate factors of variation in adult body size and sexual size dimorphism in *L. a. boemica*.

## FINAL COMMENTS

The mean and 80th percentile, two different summary statistics for adult body length, exhibited closely concordant patterns of geographic variation. Even stronger interlocality correlation was found between the figures of the Lovich & Gibbons

(1992) SSD index calculated for the two statistics; the figures were also similar in their absolute values. These findings provide support for an analysis of geographic variation of SSD in *L. agilis* by use of numerous published data on mean SVL. Such a study is now in progress (Roitberg 2005).

A comparison of mean and maximum values of adult body length in the study populations with those for the other *L. agilis* populations suggest that *L. a. boemica* belongs to the largest forms of this species. The largest male of the Site 2 was 114 mm SVL (Table 2). Like another *L. a. boemica* male individual of unknown origin which SVL was 115 mm (Warnecke 2000) it equals the maximum body length thus far reported for *L. agilis* (Blanke 2004).

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Author's postprint appendix: Table 2 repeated (this table appeared in low quality on p. 180)

| Sites                 | Years        | Males      |           |            |             |              |              | Females    |           |            |             |             |             | SSD_m        | SSD_p80      |
|-----------------------|--------------|------------|-----------|------------|-------------|--------------|--------------|------------|-----------|------------|-------------|-------------|-------------|--------------|--------------|
|                       |              | N          | Min       | Max        | X           | SD           | P80          | N          | Min       | Max        | X           | SD          | P80         |              |              |
| <b>1. Novokurskiy</b> | <b>1970</b>  | <b>34</b>  | <b>73</b> | <b>106</b> | <b>92,5</b> | <b>7,39</b>  | <b>100,0</b> | <b>34</b>  | <b>74</b> | <b>98</b>  | <b>85,2</b> | <b>6,63</b> | <b>92,0</b> | <b>-0,09</b> | <b>-0,09</b> |
| <b>2. Groznyy</b>     | <b>total</b> | <b>14</b>  | <b>77</b> | <b>114</b> | <b>93,7</b> | <b>10,84</b> | <b>101,0</b> | <b>14</b>  | <b>73</b> | <b>104</b> | <b>87,2</b> | <b>9,28</b> | <b>96,0</b> | <b>-0,07</b> | <b>-0,05</b> |
| 3. Kostek             | 1984         | 14         | 71        | 103        | 88,9        | 10,55        | 100,0        | 10         | 71        | 95         | 84,8        | 6,97        | 88,8        | -0,05        | -0,13        |
|                       | 1985         | 11         | 71        | 106        | 88,5        | 11,89        | 100,2        | 18         | 71        | 90         | 79,8        | 5,38        | 84,2        | -0,11        | -0,19        |
| <b>3. Kostek</b>      | <b>total</b> | <b>25</b>  | <b>71</b> | <b>106</b> | <b>88,7</b> | <b>10,92</b> | <b>99,8</b>  | <b>28</b>  | <b>71</b> | <b>95</b>  | <b>81,6</b> | <b>6,35</b> | <b>87,2</b> | <b>-0,09</b> | <b>-0,14</b> |
| 4. Makhachkala        | 1970         | 36         | 80        | 109        | 94,0        | 7,15         | 100,0        | 24         | 71        | 95         | 83,8        | 6,44        | 90,0        | -0,12        | -0,11        |
|                       | 1980         | 25         | 71        | 102        | 83,8        | 9,47         | 96,6         | 24         | 73        | 97         | 81,1        | 6,48        | 86,0        | -0,03        | -0,12        |
|                       | 1982         | 18         | 71        | 99         | 86,1        | 7,53         | 91,6         | 23         | 72        | 97         | 83,3        | 6,79        | 90,4        | -0,03        | -0,01        |
|                       | 1983         | 14         | 72        | 104        | 82,9        | 10,08        | 95,0         | 20         | 73        | 97         | 80,3        | 6,37        | 86,6        | -0,03        | -0,10        |
|                       | 1984         | 13         | 76        | 106        | 90,5        | 10,85        | 102,0        | 17         | 75        | 95         | 82,2        | 6,73        | 90,0        | -0,10        | -0,13        |
| <b>4. Makhachkala</b> | <b>total</b> | <b>106</b> | <b>71</b> | <b>109</b> | <b>88,3</b> | <b>9,69</b>  | <b>98,0</b>  | <b>108</b> | <b>71</b> | <b>97</b>  | <b>82,2</b> | <b>6,57</b> | <b>88,0</b> | <b>-0,07</b> | <b>-0,11</b> |
| 5. Buinaksk           | 1970         | 27         | 72        | 97         | 85,8        | 6,83         | 93,4         | 26         | 72        | 88         | 79,4        | 4,78        | 86,0        | -0,08        | -0,09        |
|                       | 1979         | 18         | 73        | 97         | 81,9        | 7,43         | 90,0         | 23         | 71        | 88         | 78,8        | 4,83        | 83,4        | -0,04        | -0,08        |
|                       | 1982         | 16         | 75        | 99         | 85,3        | 6,27         | 90,0         | 16         | 76        | 92         | 84,4        | 5,45        | 90,6        | -0,01        | 0,01         |
| <b>5. Buinaksk</b>    | <b>total</b> | <b>61</b>  | <b>72</b> | <b>99</b>  | <b>84,5</b> | <b>6,97</b>  | <b>91,0</b>  | <b>65</b>  | <b>71</b> | <b>92</b>  | <b>80,4</b> | <b>5,42</b> | <b>86,0</b> | <b>-0,05</b> | <b>-0,06</b> |
| <b>6. Termenlik</b>   | <b>total</b> | <b>14</b>  | <b>79</b> | <b>100</b> | <b>90,4</b> | <b>7,02</b>  | <b>97,0</b>  | <b>16</b>  | <b>75</b> | <b>99</b>  | <b>87,7</b> | <b>6,55</b> | <b>93,4</b> | <b>-0,03</b> | <b>-0,04</b> |
| 7. Sergokala          | 1970         | 20         | 78        | 94         | 85,2        | 4,87         | 89,8         | 21         | 71        | 87         | 77,8        | 4,81        | 83,2        | -0,09        | -0,08        |
|                       | 1979         | 21         | 72        | 96         | 84,0        | 7,36         | 92,6         | 23         | 71        | 90         | 79,3        | 5,98        | 85,4        | -0,06        | -0,08        |
|                       | 1982         | 17         | 75        | 97         | 84,2        | 5,80         | 90,0         | 16         | 76        | 88         | 80,9        | 3,57        | 83,8        | -0,04        | -0,07        |
| <b>7. Sergokala</b>   | <b>total</b> | <b>58</b>  | <b>72</b> | <b>97</b>  | <b>84,5</b> | <b>6,06</b>  | <b>90,0</b>  | <b>60</b>  | <b>71</b> | <b>90</b>  | <b>79,2</b> | <b>5,09</b> | <b>84,0</b> | <b>-0,07</b> | <b>-0,07</b> |
| 8. Khuchni            | 1985         | 12         | 73        | 94         | 83,9        | 8,02         | 92,2         | 17         | 71        | 98         | 80,2        | 8,21        | 89,4        | -0,05        | -0,03        |
|                       | 1986         | 13         | 76        | 103        | 87,3        | 7,78         | 94,6         | 12         | 77        | 91         | 86,5        | 4,58        | 91,0        | -0,01        | -0,04        |
| <b>8. Khuchni</b>     | <b>total</b> | <b>25</b>  | <b>73</b> | <b>103</b> | <b>85,7</b> | <b>7,92</b>  | <b>93,4</b>  | <b>29</b>  | <b>71</b> | <b>98</b>  | <b>82,8</b> | <b>7,53</b> | <b>90,0</b> | <b>-0,03</b> | <b>-0,04</b> |
| <b>9. Kuli</b>        | <b>total</b> | <b>11</b>  | <b>73</b> | <b>100</b> | <b>89,9</b> | <b>8,07</b>  | <b>97,0</b>  | <b>11</b>  | <b>78</b> | <b>100</b> | <b>91,6</b> | <b>6,96</b> | <b>97,0</b> | <b>0,02</b>  | <b>0,00</b>  |