Sex, Size, and Gender Roles

Evolutionary Studies of Sexual Size Dimorphism

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CHAPTER 14

Variation in sexual size dimorphism within a widespread lizard species

Evgeny S. Roitberg

14.1 Introduction

Lizards exhibit pronounced variation in the extent and direction of sexual size dimorphism (SSD; Fitch 1981; Cox *et al.* 2003; see Chapters 4 and 15 in this volume), and in recent decades they have been among the model groups for studying this phenomenon (Blanckenhorn 2005, p. 981). Most papers on SSD in lizards present either broad comparisons across species (e.g. Braña 1996; Chapters 4 and 15) or detailed analyses of individual populations (e.g. Watkins 1996; Rutherford 2004). Studies of patterns of intraspecific variation in SSD are less numerous and generally involve only few study populations (regional samples), or the study populations come from a small geographic area (Jenssen *et al.* 1995; Censky 1996; Wikelski and Trillmich 1997; Lappin and Swinney 1999; Flemming and Mouton 2001; Hasegawa 2003; Molina Borja 2003; Roitberg and Smirina 2006a). Only few studies (Parker and Pianka 1975; Fitch 1981; Zamudio 1998) provide more extensive data on geographic variation in SSD. Even for animals in general, extensive studies of geographic variation in SSD within species are quite rare (Rising 1987; Storz *et al.* 2001; Pearson *et al.* 2002; Fairbairn 2005; Tamate and Maekawa 2006). However, intraspecific variation is particularly promising for testing adaptive hypotheses (and other hypotheses related to current environmental conditions) because at this level the effect of phylogenetic conservatism is very small (Shine and Fitzgerald 1995; McCoy *et al.* 2003).

This chapter considers geographic variation in SSD for a widespread Eurasian lizard species, *Lacerta agilis*. First I document the variation in SSD across a large part of the species' range, examine its major trends, and check for correlations of this variation with morphology (body size), environment (climate), and phylogeny. Then, using samples of aged individuals, I evaluate the relative contribution of sex differences in growth trajectories and adult mortality in shaping adult SSD. Finally, I put my findings into the context of recent discussions on ultimate and proximate determinants of variation in SSD.

14.2 Study species

Lacerta agilis is a small to medium-sized lacertid lizard that occupies much of the temperate Palaearctic from the Pyrenees in Western Europe to the Baikal Lake in Siberia (Figure 14.1). This species is often abundant, easy to catch, and highly polymorphic, and has become a model species for comprehensive microevolutionary studies (Yablokov *et al.* 1980). Recent studies have provided an intraspecific phylogeny (Kalyabina *et al.* 2001; Kalyabina-Hauf and Ananjeva 2004) and detailed life-history data for several populations (Strijbosch and Creemers 1988; Olsson 1992, 1993; Olsson and Shine 1996; Gullberg *et al.* 1997). Together, these characteristics make *L. agilis* a particularly suitable subject for studying intraspecific variation in SSD.

14.3 Methods

14.3.1 Study samples and estimating adult body size

I collected original and published data on snout–vent length (SVL) from 52 local or regional samples

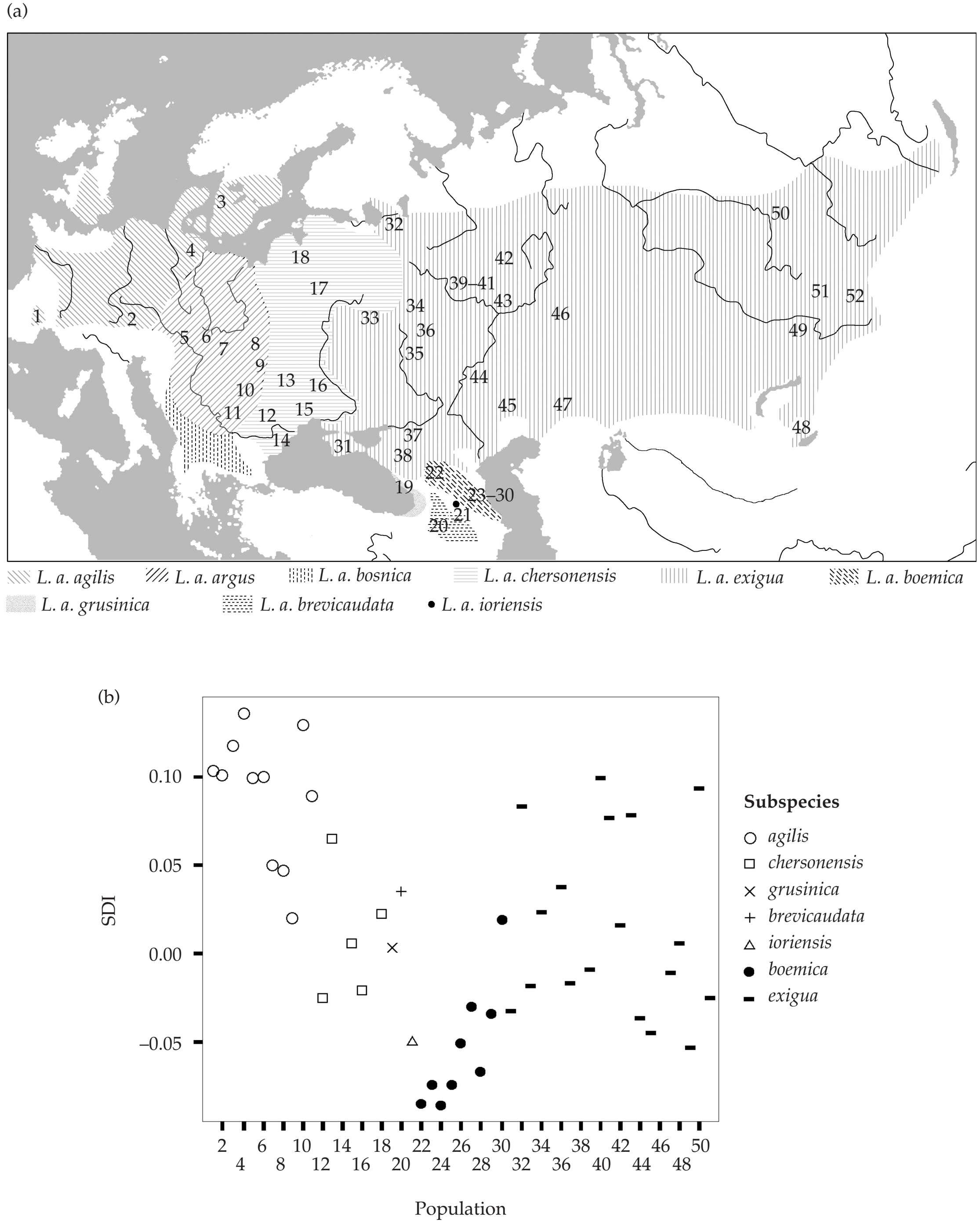

Figure 14.1 Geographic distribution of different subspecies of *L. agilis* (after Kalyabina *et al.* 2001, with modifications), study samples (a), and their variation for SSD (b). Following Rahmel (1988) I consider *L. a. argus* as a synonym of *L. a. agilis* in all analyses. SSD is estimated using the index of Lovich and Gibbons (1992): SDI = (size of larger sex/size of smaller sex)−1, set as negative if males are the larger sex and positive if females are the larger sex (see text for further explanation).

across the species range (Figure 14.1a; see Appendix, Table A14.1). Each sample included at least 10 individuals of each sex (median sample size was 33 for males and 34 for females). A few samples were excluded from analyses for means because they exhibited unusually high variances and obviously included immature animals. Even for the rest of the data, criteria for including an individual in the sample may not have been identical among researchers. Moreover, in animals with substantial postmaturation growth, the size distribution of adults in a particular sample can be affected by proximate factors such as local and temporal variation in the proportion of newly matured animals, size at maturity, growth rates, and adult mortality (Stamps and Andrews 1992; Stamps 1993; Watkins 1996). The choice of an appropriate statistic for estimating adult body size is therefore an important methodological problem. Average and extreme values are the most widely used statistics, and they are often the only parameters available in publications. Average size is statistically powerful and provides reasonable estimates even for small sample sizes. However, the mean is particularly sensitive to the confounding factors mentioned above (Stamps and Andrews 1992; Stamps 1993). The maximum value and the higher percentiles are less powerful than the mean, but they are more resistant to any variation outside the upper area of the character distribution. These statistics have been proposed as estimators of the typical asymptotic size (the size of full-grown animals) in the population (Box 14.1).

To validate the use of means in my study, I repeated some analyses using maximum values and (whenever individual SVL data were available) the 80th percentiles of the size distributions. Estimates of SSD (see Section 14.3.2) based on these three statistics for characteristic body size showed very concordant variation (Table 14.1), validating the use of means in this study.

14.3.2 Estimating SSD

I quantified SSD with the sexual dimorphism index, SDI, equal to (size of the larger sex/size of the smaller sex) − 1, arbitrarily expressed as positive if females are larger and negative if males are larger (Lovich and Gibbons 1992). I chose this index because it generates values that are intuitive, directional, properly scaled, and symmetrical around 0 (Lovich and Gibbons 1992).

Table 14.1 Spearman rank correlations (r_s) between SSD calculated from different estimators of adult body length. The sexual dimorphism index, SDI = (size of larger sex/size of smaller sex) − 1, is arbitrarily expressed as positive if females are larger and negative if males are larger (Lovich and Gibbons 1992).

	SDI for 80th percentiles	SDI for maximum values
SDI for means	0.968 ($P < 0.01$, $N = 20$)	0.747 ($P < 0.01$, $N = 39$)
SDI for 80th percentiles		0.846 ($P < 0.01$, $N = 19$)

Box 14.1 Estimators of asymptotic size

In lizards and most other ectotherms, linear growth after maturity is usually asymptotic; that is, it slows progressively with size and virtually ceases at advanced size and age. The mean (typical) growth curve and its asymptote (*A*) can be developed from individual growth increments or body sizes of aged individuals (e.g. 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 and Andrews 1992; Stamps 1993; Brown *et al.* 1999). As growth curves are often not available, some other simple statistics have been proposed as estimates of asymptotic size. Use of the maximum value (the largest-individual method, Stamps and 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 have been shown to conform to the growth-based estimates in several sets of lizard data (Brown *et al.* 1999; Kratochvil and Frynta 2002; Roitberg and Smirina 2006b).

Whenever possible, three SDI values, based on means (SDI_X), maximum values (SDI_{MAX}), and the 80th percentiles (SDI_{P80}) were computed for each study sample.

14.3.3 Estimating allometry of SSD

Following Fairbairn (1997) the slope of major-axis regression (model II) of log(male SVL) on log (female SVL) was used to quantify the allometry of SSD. The slopes (β) and their 95% confidence intervals were computed with a program designed by P. Legendre (available at www.fas.umontreal.ca/biol/legendre). They were tested against the null hypothesis of $\beta = 1$ (isometry). The pattern with $\beta > 1$ is most common and referred to as Rensch's rule (Fairbairn 1997; Chapters 3 and 6).

14.3.4 Estimating sex differences in body growth and survival

As male and female lizards rarely differ in terms of hatchling size, the primary proximate mechanisms to shape adult SSD are sex differences in (1) postnatal growth trajectories (e.g. Chapter 19) and (2) survival schedules. The corresponding patterns that can be revealed in cross-sectional samples from populations are sex differences in (1) age-specific SVLs and (2) age compositions. Data available for two populations of *L. a. agilis* (Strijbosch and Creemers 1988; Olsson and Shine 1996) and five populations of *L. a. boemica* (Roitberg and Smirina 2006b) have been extracted from published figures and summarized in Figures 14.2 and 14.3.

Although the age at sexual maturation is likely to differ among these populations (and between males and females within some populations), in all cases, all or the vast majority of yearlings are juveniles or subadults, and virtually all 2-years-olds are adults or at least subadults. In my analyses, I have therefore considered all animals of 2 or more years of age to be adults.

14.4 Results

14.4.1 Geographic patterns

The main geographic pattern in SSD is a contrast between the Western European *L. a. agilis* and the

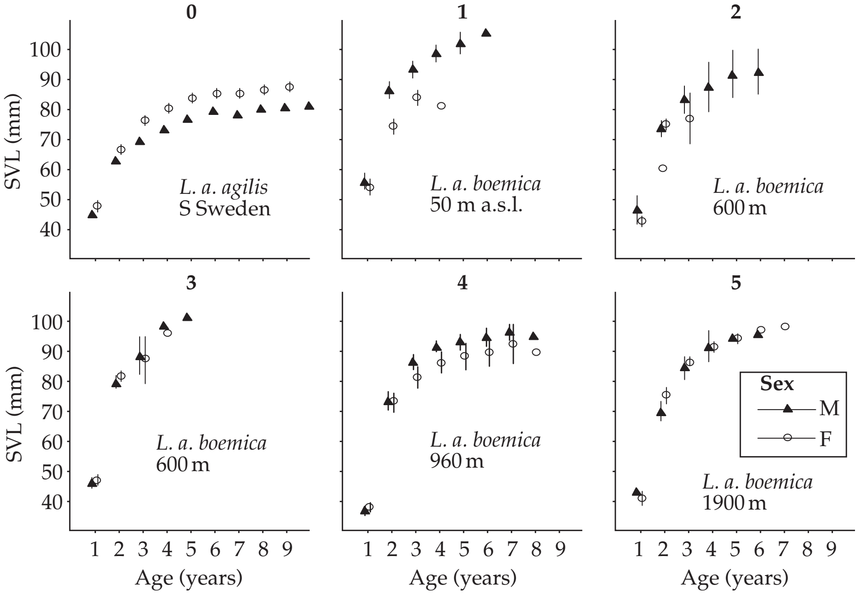

Figure 14.2 Age-specific SVLs (mean ± 2 SE) in different *L. agilis* populations. Data from: Olsson and Shine (1996) for South Sweden; Roitberg and Smirina (2006) for *L. a. boemica* (shown with elevations above sea level, a.s.l.).

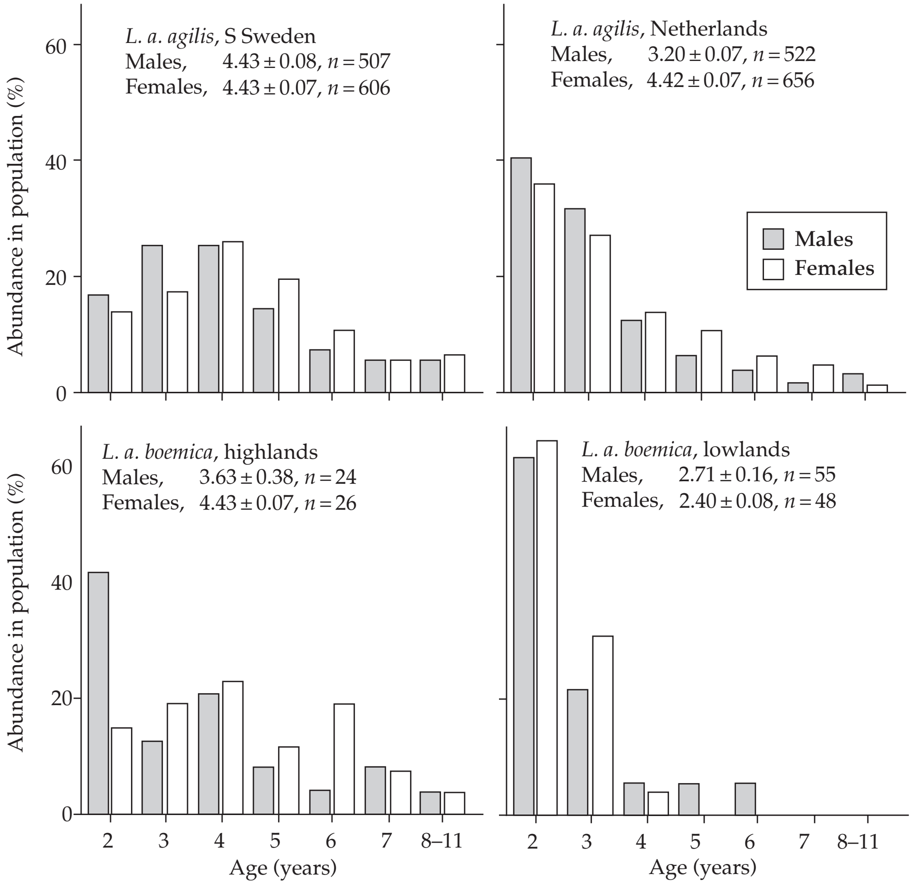

Figure 14.3 Age compositions of individuals of 2 or more years old in different *L. agilis* populations. Means ± SE are also given. Data from: Olsson and Shine (1996) for South Sweden; Strijbosch and Creemers (1988) for Netherlands; Roitberg and Smirina (2006b), for *L. a. boemica*.

North Caucasian *L. a. boemica*. Whereas SSD was consistently female-biased in *L. a. agilis, L. a. boemica* exhibited either no sex differences or a clearly male-biased SSD (Figure 14.1b). The other subspecies tend to occupy intermediate positions along the SSD axis (Figure 14.1b).

SSD also varied within subspecies (Figure 14.1b). In *L. a. exigua* and *L. a. boemica,* this variation is apparently related to climate. In *L. a. exigua* the SDI exhibited a positive correlation with the latitude (Figure 14.4a) and in *L. a. boemica* with the altitude (Figure 14.4b). That is, in both subspecies, the male-biased SSD is associated with low latitudes and altitudes.

14.4.2 Allometry

Despite marked geographic variation in SSD, patterns of geographic variation in body length were highly concordant between the sexes both within and across subspecies (Table 14.2). For the whole data-set, the major-axis regression slope of log (male SVL) on log(female SVL) was significantly greater than 1 (Figure 14.5; Table 14.2), which is consistent with Rensch's rule. However, this pattern is shaped solely by the contrast between the small-sized and female-larger *L. a. agilis* and the large-sized and male-larger *L. a. boemica* (Figure 14.5). If these two forms are excluded from

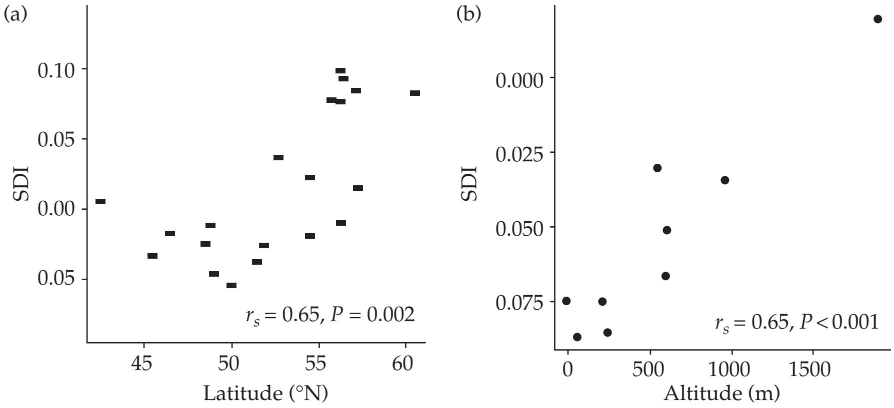

Figure 14.4 Spearman rank correlation (r_s) between the SSD index (SDI) and latitude or altitude within subspecies. (a) *L. a. exigua*; (b) *L. a. boemica.*

Table 14.2 Major-axis regression slopes of male size on female size (log-transformed mean SVL) among populations within and across subspecies of *L. agilis*.

Data-set	**Slope estimate (95% CI)**	**Pearson correlation coefficient (*r*) between male and female SVL**
All samples, $n = 47$	1.48 (1.17–1.91)	$0.78^{\dagger}$
All, without *L. a. agilis* and *L. a. boemica*, $n = 27$	0.83 (0.56–1.21)	$0.73^{\dagger}$
L. a. agilis, $n = 11$	0.94 (0.69–1.27)	$0.90^{\dagger}$
L. a. chersonensis, $n = 5$	0.57 (0.34–0.85)	0.95*
L. a. boemica, $n = 9$	0.73 (0.21–1.74)	0.72*
L. a. exigua, $n = 19$	0.85 (0.44–1.54)	$0.66^{\dagger}$

$*P < 0.05$; $^{\dagger}P < 0.01$.

analysis, the remaining variation across subspecies and the variation within subspecies actually exhibit a weak tendency toward the converse of Rensch's rule (Table 14.2).

14.4.3 Relative impact of sex differences in growth and survival

Figure 14.2 summarizes data on age-specific body length in males and females in a Swedish population (*L. a. agilis*) and five populations from the southeastern North Caucasus (*L. a. boemica*). In the Swedish population, mean SVL of females was consistently higher than that of the same-age males (see also Olsson and Shine 1996). In contrast, populations of *L. a. boemica* exhibited either no consistent differences in average growth curves of males and females or age-specific SVLs were clearly larger in males. The latter pattern occurred in the lowland population whose SSD was strongly male-biased. Thus, sex differences in averaged growth trajectories correspond well to the patterns of adult SSD: the larger sex (females in *L. a. agilis* and males in the lowland *L. a. boemica*) grow faster than the smaller sex.

Figure 14.3 shows age compositions of adult males and females for the two contrasting subspecies. For *L. a. boemica*, I pooled three samples from the lowland and submontane sites and two samples from the mountain sites because there were only small differences within these groups. Both Northern European populations showed a high longevity (mean adult age was 3.3–4.4 years), with females being slightly older than males (Mann–Whitney U test: $Z = -3.45$, $P < 0.001$ for Sweden; $Z = -2.76$, $P = 0.006$ for The Netherlands). Noteworthy, the mountain *L. a. boemica* were comparable to the Swedish and Dutch *L. a. agilis* for their mean adult age and the pattern

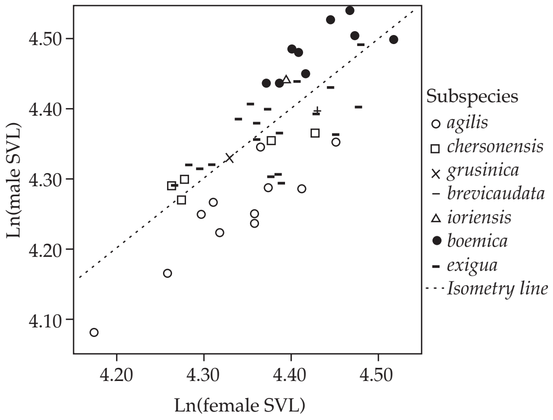

Figure 14.5 Plot of log-transformed male size on log-transformed female size for 52 study samples of *L. agilis*.

of female-biased survival (Figure 14.3), although in *L. a. boemica* this bias was not statistically significant ($Z = -1.69$, $P = 0.09$). In contrast, the lowland *L. a. boemica* showed a much younger mean adult age than both the mountain *L. a. boemica* and the North European *L. a. agilis*, and exhibited no signs of female-biased survival (Figure 14.3). The variation in age structure thus tends to conform to the variation in SSD, but the sex differences in age composition are minor as compared to the differences in growth curves.

14.5 Discussion

14.5.1 Comparing variation in SSD within and between subspecies

SSD in *L. agilis* exhibits a pronounced geographic variation. For mean adult SVL, SSD ranges from 7–9% in favor of males to 10–13% in favor of females. A comparable magnitude of divergence in SSD has been documented among related lizard species (Lappin and Swinney 1999; Chapter 19) but not within a single species. In snakes, a unique case of a much more dramatic geographic variation in SSD was found in the python, *Morelia spilota* (Pearson *et al.* 2002). In other vertebrates, SSD varying from male-biased to female-biased in different geographic populations within a species has been reported for only few species (e.g. Storz *et al.* 2001; Tamate and Maekawa 2006).

My study revealed two robust patterns of geographic variation in SSD: a clear contrast between *L. a. agilis* and *L. a. boemica* (pattern 1) and ecogeographical clines within subspecies (latitudinal in *L. a. exigua* and altitudinal in *L. a. boemica*) with more male-biased SSD in warmer climates (pattern 2). Pattern 1 is consistent with the temperature-mediated clines (i.e. summer is cooler in Western Europe than in the North Caucasus), but it is likely that the two patterns have at least partly different causation. Pattern 1 is greater in magnitude and is shaped primarily by divergence in male size (Rensch's rule), whereas female size variation contributes equally or more than male size variation to pattern 2. Further, phylogeographic studies reveal pronounced genetic divergence between *L. a. agilis* and *L. a. boemica*, but no substantial substructure within either subspecies (Kalyabina *et al.* 2001; Kalyabina-Hauf and Ananjeva 2004). Thus, pattern 1 is associated with substantial genetic divergence whereas pattern 2 is not.

14.5.2 Possible determinants of the SSD divergence between *L. a. agilis* and *L. a. boemica*

The patterns described above suggest that the divergence in SSD between subspecies (pattern 1) includes an adaptive component related to geographic differences in patterns of sexual selection. A basal position of *L. a. boemica* in the species phylogeny (Kalyabina *et al.* 2001; Kalyabina-Hauf and Ananjeva 2004) suggests that the small male size and female-biased SSD of *L. a. agilis* is a derived state. An adaptive shift to a smaller male size and female-biased SSD can be predicted by the so-called small-male-advantage hypothesis (Zamudio 1998; Cox *et al.* 2003). Let us assume that the formation of the nominate subspecies in Western Europe was accompanied by a shift to a social system with lower male aggression and higher rate of promiscuity. Such a shift in social behavior and SSD in regions with cooler climate and lower population density as compared to conspecifics from densely populated regions with warmer climates has been reported for another widespread lizard (an iguanid, *Uta stansburiana*; Tinkle 1969; Parker and Pianka 1975; Fitch 1981) and a snake (a python, *Morelia spilota*; Pearson *et al.* 2002). The SSD variation among populations of horned lizards (*Phrynosoma*) has occurred primarily by changes in male size arguing for the small-male-advantage hypothesis (Zamudio 1998).

The available evidence suggests that in Western Europe, *L. agilis* generally occurs at much lower population densities than in the North Caucasus. In many Western European territories this species is classified as endangered (Blanke 2004 and references therein), whereas in the forest-steppe and steppe zone of Eurasia, including North Caucasus, *L. agilis* is often very abundant, its density reaching up to 1000 individuals per hectare (Baranov and Yablokov 1976). There is also anecdotal supportive evidence from animals kept in terraria that *L. a. boemica* is more aggressive than *L. a. agilis* (Hemmerling and Obst 1967). Also, the prevalence of bite scars, which is often used as a proxy of the intensity of male–male agonistic encounters in snakes and lizards (e.g. Shine and Fitzgerald 1995; Hasegawa 2003), is significantly higher in *L. a. boemica* (23.1%, $N = 78$) than in *L. a. agilis* (0.0%, $N = 46$; E.S. Roitberg, unpublished work).

Although male–male sexual aggression appears to be lower in *L. a. agilis* than in *L. a. boemica*, larger male *L. a. agilis* are more successful in agonistic interactions than smaller males (Olsson 1992). Nevertheless, the rate of agonistic encounters and their contribution to male mating success in *L. a. agilis* may well be lower than in *L. a. boemica*. Competition for access to mates is only one component of sexual selection; others include mate searching and the postcopulatory phase (Blanckenhorn 2005). In mate searching, which seems to increase at low population density, small males should have advantage due to their higher mobility and earlier maturation (Blanckenhorn 2005 and references therein). Interestingly, a trade-off between fighting capacities and mobility among individual males has been recently demonstrated for another lacertid lizard, *Lacerta monticola* (López and Martín 2002).

Another possible explanation for pattern 1 involves geographic differences in growth constraints (Chapter 19) or viability selection for small body size (Blanckenhorn 2000). Cool and humid summer climates in most of the species' range in Western Europe should reduce activity and energy acquisition opportunities relative to those in more continental Eurasia. This might constrain body growth in a similar way as resource limitation (Congdon 1989). Under such conditions, environmental constraints for growth and viability selection for small body size are expected to be strong in both sexes, but in females these forces can be partly counterbalanced by fecundity selection (Kratochvíl and Frynta 2002). Indeed, the correlation between female size and clutch size (egg number) is quite high in *L. a. agilis* (Olsson 1993; Amat *et al*. 2000). Moreover, the available data, limited to a few females from single localities, suggest that *L. a. agilis* is characterized by higher relative clutch mass and smaller egg and hatchling size than the more eastern forms, including *L. a. boemica* (Rykena 1988; Warnecke 2000). The above points argue for a high potential for fecundity selection in the Western European populations.

A third hypothesis for pattern 1 is that the SSD difference between the two genetically diverged subspecies is at least partly caused by evolutionary lag in the response of *L. a. agilis* to anthropogenic changes in habitat availability. Before the Middle Ages, low population densities might have been even more characteristic for *L. a. agilis* than in later times, because the natural deficiency of steppe and forest-steppe landscapes in Western Europe had not yet been mitigated by human deforestation activity (see Bischoff 1984). Anthropogenic changes in habitat availability and hence lizard density may favor increased male size, but the SSD has not yet reached evolutionary equilibrium. The virtual lack of overlap between the SDI values for the two taxa (Figure 14.1b), in spite of obviously overlapping density levels, offers some support for this hypothesis.

14.5.3 Possible determinants of eco-geographic clines within subspecies

Geographic differences in patterns of sexual selection might also contribute to pattern 2 because the northern *L. a. exigua* (Peters 1959; Bulakhova 2005) and the high-elevation *L. a. boemica* (Roitberg and Smirina 2006a) populations generally exhibit relatively low densities. However, the variation in SSD within subspecies appears not to be genetically based (i.e. does not reflect genetic divergence among populations) and is strongly influenced by variation in female as well as male size (see Section 14.4.2). This clinal variation can be most parsimoniously addressed in terms of differential tradeoffs between growth and reproduction (proximate causation, the nonadaptive hypotheses of Cox *et al*. 2003). Based on the model of Adolph and Porter (1996) and growth data for five populations of *L. a. boemica* (Roitberg and Smirina 2006b), I propose the following explanation. In warm climates of lowland and southern localities, juveniles grow sufficiently to reach their maturation size by late May or early June of their second year, and to reproduce as yearlings. For females, this means a substantial allocation of energy to egg production, possibly at the expense of body growth. In cooler climates, the yearling females do not reach the maturation size until mid-summer (when it is too late for reproduction) and continue to invest energy in body growth. They start reproduction 1 year later but at a larger mean size than lowland females. As established for many lizard species, size at maturity strongly correlates with final size (Stamps *et al*. 1998). Thus, early maturation might be responsible for smaller mean body length of adult females in the lowland populations. Another possible reason for smaller female size in warmer climates may be higher annual reproductive expenditures because many females there make two clutches per season. Thus, the clinal variation in SSD within subspecies might be partly an epiphenomenon of selection on life-history variables, with no adaptive significance in terms of SSD per se (Roitberg and Smirina 2006b). Similar proximate factors might also contribute to pattern 1. However, in this case some additional forces related to male size must have contributed to the observed divergence.

14.5.4 Sex differences in growth, survival, and maturation time

My analyses of published data on age-specific SVLs and age composition in several populations of *L. a. agilis* and *L. a. boemica* (Figures 14.4 and 14.5) suggest sex differences in growth trajectories to be the major proximate determinant of adult SSD. The larger sex also tends to have higher survival and that may contribute to SSD as well, but this bias in age composition is generally small compared to sex differences in growth curves. In other lizard studies, differential growth was also more important in shaping SSD than differential survival (Watkins 1996; Rutherford 2004).

An additional related mechanism is sexual bimaturation (i.e. later maturation of the larger sex; Stamps and Krishnan 1997). Female *L. a. agilis* do appear to mature a year later than the males in some populations (Rahmel and Meyer 1988; Strijbosch and Creemers 1988) but no bimaturation was found for another *L. a. agilis* population with a strongly female-biased SSD (Nöllert 1989). Thus, the possible contribution of sexual bimaturation to adult SSD in this species remains to be determined.

14.6 Final remarks

Although numerous factors unrelated to geographic variation could affect SSD in particular study samples, these effects are unlikely to create a strong and regular pattern shaped by a large number of independently collected data units. With no doubt, both patterns revealed in the geographic variation of SSD of *L. agilis*—pronounced differences between *L. a. agilis* and *L. a. boemica,* and eco-geographic clines within subspecies—are biologically relevant. Another firm conclusion is that female-biased SSD of *L. a. agilis* and male-biased SSD of the lowland *L. a. boemica* result primarily from differential growth, the larger sex exhibiting higher growth rate. However, within a correlational study it was impossible to reliably differentiate between the different hypotheses that predict similar geographic patterns of variation in SSD.

14.7 Future research

Along with general body size (SVL), absolute and relative size of particular body segments related to female fecundity (abdomen length) or male fighting capacity (head dimensions) should be examined for variation in sexual dimorphism among populations (see Braña 1996; Chapters 4 and 15). Such data coupled with comparative data on different aspects of reproductive output (particularly the slope of the regression of fecundity on female size; see Braña 1996; Cox *et al*. 2003) could help to assess applicability of the sexual-selection and fecundity-advantage hypotheses for the revealed SSD patterns. Intensive mark–recapture or skeletochronological studies on northern (female-larger) and southern (male-larger) populations of *L. a. exigua* would estimate whether this divergence arose through the same proximate mechanisms as a parallel but stronger divergence between *L. a. agilis* and *L. a. boemica*.

Common-garden experiments involving populations that exhibit contrasting SSD patterns could determine whether observed growth differences between the sexes (and those between males of *L. a. agilis* and *L. a. boemica*) are genetically fixed or constrained by environment at the proximate level (see John-Alder and Cox, this volume for relevant experiments with *Sceloporus* species). Behavioral studies of *L. a. agilis* and *L. a. boemica* in the field and laboratory (cf. Tinkle 1969; Shine and Fitzgerald 1995; McCoy et al. 2003; Hasegawa 2003; chapter 15) could additionally address the sexual selection hypothesis. The use of paternity analysis to assay sexual and fecundity selection on body size would be a powerful tool. Such investigations have been made for a Swedish population of *L. a. agilis* (e.g. Gullberg *et al*. 1997), and it would be of great interest to similarly investigate a conspecific population that exhibits an opposite, male biased SSD.

14.8 Summary

The sand lizard, *Lacerta agilis* occupies a large part of temperate Eurasia from the Pyrenees to the Baikal Lake. This chapter presents an analysis of geographic variation in SSD within this species based on original and published data on SVL of adult males and females in 52 local or regional samples. The major pattern, distinctive differences between the consistently female-larger *L. a. agilis* (West Europe) and the predominantly male-larger *L. a. boemica* (the south-eastern North Caucasus), is primarily determined by divergence in male size (Rensch’s rule). The other subspecies (*L. a. chersonensis, L. a. exigua*, and the three Transcaucasian forms) tend to occupy intermediate positions along the SSD axis. Within subspecies, the variation in SSD is characterized by latitudinal (*L. a. exigua*) and altitudinal (*L. a. boemica*) clines towards a male-biased SSD in warmer climates, with female size varying as much or more than male size.

Data on age-specific SVLs and age compositions for *L. a. agilis* and *L. a. boemica* show that sex differences in body growth are the major proximate determinant of adult SSD, the sex-biased adult survival being of minor importance. Selective and proximate-level factors are discussed as possible determinants of the geographic patterns in SSD. These include sexual, fecundity and viability selection; growth limitations by environmental constraints for energy intake; and a trade-off between growth and egg production in females. The available correlational data are not sufficient to permit adequate evaluation of these hypotheses, but future directions for research are proposed.

14.9 Acknowledgments

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14.10 Suggested readings

Cox, R.M., Skelly, S.L., and John-Alder, H.B. (2003) A comparative test of adaptive hypotheses for sexual size dimorphism in lizards. *Evolution* **57**, 1653–1669.

Pearson, D., Shine, R., and Williams, A. (2002) Geographic variation in sexual size dimorphism within a single snake species (*Morelia spilota*, Pythonidae). *Oecologia* **131**, 418–426.

Roitberg, E.S. and Smirina, E.M. (2006) Age, body size and growth of *Lacerta agilis boemica* and *L. strigata* (Reptilia, Lacertidae): a comparative study of two closely related lizard species based on skeletochronology. *Herpetological Journal* **16**, 133–148.

Roitberg, E.S. and Smirina, E.M. (2006) Adult body length and sexual size dimorphism in *Lacerta agilis boemica* (Reptilia, Lacertidae): between-year and interlocality variation. In *Mainland and Insular Lizards. A Mediterranean Perspective* (Corti, C., Lo Cascio, P., and Biaggini, M., eds). Florence University Press, Florence, Italy, 175–187.

Storz, J.F., Balasingh, J., Bhat, H.R., Nathan, P.T., Doss, D.P.S., Prakash, A.A., and Kunz, T.H. (2001) Clinal variation in body size and sexual dimorphism in an Indian fruit bat, *Cynopterus sphinx* (Chiroptera: Pteropodidae). *Biological Journal of the Linnean Society* **72**, 17–31.

Zamudio, K.R. (1998) The evolution of female-biased sexual size dimorphism: a population-level comparative study in horned lizards (*Phrynosoma*). *Evolution* **52**, 1821–1833.

Table A14.1 Summary statistics for adult SVL of male and female *L. agilis* in 52 local and regional samples. See Figure 14.1a for geographic locations, and Figure 14.1b for the SDI for means. Means of samples 17, 35, 38, and 46 were excluded from analyses (see Section 14.3.1) because they exhibit unusually high standard deviations (SDs) and obviously include immature animals. No published data included 80th percentiles (P80): these were computed from histograms or scatter plots. If only total sample size was available (study samples 8 and 17), *N*/2 was assumed for male and female sample sizes.

	Study sample	Males						Females						Data source
		n	Min	Max	Mean	SD	P80	n	Min	Max	Mean	SD	P80	
1	Pyrenees	41			77.70	4.03		70			85.74	6.69		Amat *et al.* (2000)
2	Switzerland	30	63	78	68.18	3.35	70.6	28	68	83	75.05	4.02	78.4	Helfenberger and Bendel (1994)
3	South Sweden	44			70.00	5.97	77.5	45			78.20	4.70	85.0	Olsson (1988)
4	NE Germany	28	64	79	72.60	4.03		28	65	98	82.46	7.14		Nöllert (1988)
5	Lower Austria	41	48	74	59.21	8.30		41	49	85	65.09	9.26		Rahmel and Meyer (1987)
6	Moravia	17	48	82	64.30	7.42		17	61	80	70.70	5.77		Gvozdik and Boukal (1998)
7	East Slovakia	57	58	97	77.20	10.14		54	61	100	78.70	12.20		Majlath *et al.* (1997)
8	W Ukraine, Carpathians	55	61	85	71.24	1.93		55	62	91	74.57	1.19		Shcherbak and Shcherban' (1980)
9	Romania, E Carpathians	68	50	86	69.20	8.61		73	65	98	78.10	8.62		Fuhn and Vancea (1964)
10	Romania, S Carpathians	11	66	78	72.80	9.38		18	70	92	79.30	6.24		Fuhn and Vancea (1964)
11	Romania, Oltenia	28	50	81	70.00	4.20		22	50	93	73.50	6.18		Fuhn and Vancea (1964)
12	Romania,Valakhia	23	64	82	72.90	5.06		25	64	84	71.10	5.13		Fuhn and Vancea (1964)
13	Romania, Moldova	47	68	91	78.70	5.17		31	70	94	83.80	5.89		Fuhn and Vancea (1964)
14	SE Romania	20	44	91				18	54	90				Fuhn and Vancea (1964)
15	SW Ukraine	39	61	84	71.49			59	62	85	71.88			Kotenko and Tarashchuk (1982)
16	Ukraine, Uman'	18	59	86	73.62	6.46	79.0	24	56	84	72.10	7.59	78.0	E.M. Smirina, unpublished data
17	Belorussia	280		87	60.76	54.22		280		90	63.50	43.84		Pikulik *et al.* (1988)
18	Latvia, Daugavpils	20	68	90	77.90	5.61	83.6	26	72	90	79.65	4.8	83.8	E.S. Roitberg, unpublished data
19	Abkhasia	28	57	92	75.80	1.32		21	59	105	76.00	1.10		Darevsky *et al.* (1976)
20	Armenia	110	76	93	81.20	12.48		151	82	96	84.00	15.11		Darevsky *et al.* (1976)
21	East Georgia, Tianeti	37	74	91	85.00	4.87		22	74	89	81.00	4.69		Muskhelishvili (1970)
22	N Caucasus, Novokurskiy	34	73	106	92.50	7.39	100.0	34	74	98	85.24	6.63	92.0	E.S. Roitberg, unpublished data
23	N Caucasus, Groznyy	14	77	114	93.71	10.84	101.0	14	73	104	87.21	9.28	96.0	K.Yu. Lotiev, unpublished data
24	N Caucasus, Kostek	25	71	106	88.68	10.92	99.8	28	71	95	81.61	6.35	87.2	E.S. Roitberg, unpublished data
25	N Caucasus, Makhachkala	106	71	109	88.34	9.69	98.0	108	71	97	82.20	6.57	88.0	E.S. Roitberg, unpublished data
26	N Caucasus, Buinaksk	61	72	99	84.51	6.97	91.0	65	71	92	80.42	5.42	86.0	E.S. Roitberg, unpublished data
27	N Caucasus, Termenlik	14	79	100	90.36	7.02	97.0	16	75	99	87.69	6.55	93.4	E.S. Roitberg, unpublished data

28	N Caucasus, Sergokala	58	72	97	84.48	6.06	90.0	60	71	90	79.20	5.09	84.0	E.S. Roitberg, unpublished data
29	N Caucasus, Khuchni	25	73	103	85.68	7.92	93.4	29	71	98	82.83	7.53	90.0	E.S. Roitberg, unpublished data
30	N Caucasus, Kuli	11	73	100	89.91	8.07	97.0	11	78	100	91.64	6.96	97.0	E.S. Roitberg, unpublished data
31	Crimea	87	60	108	84.70	11.00	93.0	70	64	114	82.00	10.10	90.0	Shcherbak (1966)
32	Leningrad region	34	61	87	74.17			24	68	90	80.35			Peters (1959)
33	Kaluga region	18	63	84	74.80	6.23		32	61	99	73.40	8.37		Strel'tsov and Voronin (1973)
34	Ryazan region	333	60	112	78.64	12.69	88.4	380	60	112	80.43	13.96	94.0	Zharkova (1973)
35	Lipetsk region	136			72.02	36.15		197			72.80	39.30		Klimov *et al.* (1999)
36	Tambov region	18			80.90	7.64		42			83.90	8.42		Korneva and Yatsenko (1989)
37	W Cis-Caucasia	302	63	111	79.73	10.56	90.0	296	63	108	78.37	10.12	87.0	Lukina (1966)
38	Stavropol region	470	75	110	91.59	26.45		470	75	110	85.07	34.69		Tertyshnikov (2002)
39	Middle Volga, locality 1	30			75.20	4.05		63			74.48	6.03		Darevsky *et al.* (1976)
40	Middle Volga, locality 2	32			73.31	7.41		87			80.55	7.83		Darevsky *et al.* (1976)
41	Middle Volga, locality 3	36			73.92	8.58		80			79.59	9.30		Darevsky *et al.* (1976)
42	Vyatka region	21	74	91	83.52	4.55	87.6	30	74	98	85.30	5.21	89.8	E.S. Roitberg, unpublished data
43	Tatarstan	115	65	105	81.70	8.20	89.5	30	70	105	88.10	9.06	92.0	Garanin (1983)
44	Saratov region	56	62	98	75.20	15.19		68	57	94	72.50	15.59		Zavialov *et al.* (2000)
45	Volga-Ural	26			80.30	19.38		26			76.80	18.87		Darevsky *et al.* (1976)
46	S Ural, Bashkiria	33	33	91	69.00	88.12		40	54	98	76.90	67.36		Khabibullin (2001)
47	NW Kazakhstan, Emba	27	78	103	89.33	7.03	97.4	50	75	100	88.32	6.01	94.6	E.S. Roitberg, unpublished data
48	Kirgizia	17	71	87	77.93	4.58		15	68	88	78.37	6.51		Yakovleva (1964)
49	East Kazakhstan	13	67	97	82.00	7.93		20	65	86	77.80	6.26		Berdibayeva (1989)
50	S Siberia, Tomsk				78.50						85.80			Bulakhova (2005)
51	S Siberia, Altai	34	68	95	81.38	7.34	89.0	52	67	97	79.37	7.98	86.4	V.A. Yakovlev, unpublished data
52	Mongolia	10	56	85	73.00	9.17		10	50	80	71.30	9.17		Munkhbayar *et al.* (1998)

E, East; N, North; NE, Northeast; NW, Northwest; S, South; SE, Southeast; SW, Southwest; W, West.