

Skeletochronology uncovers population- and sex-dependent growth trajectories in the sand lizards of Western Poland

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Obtaining population demography metrics in a non-lethal way is essential for the evidence-based management of reptiles that are declining in increasingly degraded European landscapes. Here, we quantified life-history traits of the sand lizard *Lacerta agilis argus* in Western Poland and tested whether they varied by sex and locality. Using skeletochronology, we aged 177 individuals from three populations inhabiting different habitats. The lizards reached sexual maturity after their second hibernation; and the mean adult age was 4.6 ± 1.9 years (range 2-8). The annual survival rate was 0.80 and the adult life expectancy was 5.25 years. The Sexual Dimorphism Index (SDI) was female-biased but small (SDI = 0.04). Linear modelling showed that the snout-vent length increased with age, yet the age-size slope differed between sexes and among populations: females and lizards from the two warmer, drier sites grew faster and attained a larger body size than males or lizards from the cooler forest site. Sex had no main effect on the size once age was accounted for. These results demonstrate that even over short geographic distances, habitat thermal conditions modulate the growth trajectories in this ecologically flexible species. Our study highlights the value of skeletochronology for rapid, non-lethal assessments of the population demography in temperate lizards.

Key words: age, life expectancy, survival rate, body size, life-history variation, population demography, *Lacerta agilis*.

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The growth of lizards is indeterminate and heavily depends on environmental factors; hence, they are used as model organisms in exploring macroecological patterns (e.g. Altunışık *et al.* 2024; Ağdağ *et al.* 2025; Kara *et al.* 2025). Nevertheless, although they have been gaining attention and impetus in recent years (Bülbül *et al.* 2023), demographic studies on the *Lacerta* genus are still scarce (Altunışık *et al.* 2022).

The advent of skeletochronology has shifted the paradigm in studying the life-history traits of ectotherms, as this method is much more time efficient than the

only viable alternative, namely the capture-mark-recapture method (Smirina 1974; Castanet & Smirina 1990; Altunışık *et al.* 2022). Skeletochronology allows for obtaining time-dependent population demography data like the growth rate, age of reaching sexual maturity, duration of sexual activity period and the longevity. An age estimation is performed by counting the lines of arrested growth (LAGs), which reflect periods of slowed or arrested bone deposition. While in temperate ectotherms such periods usually coincide with the annual hibernation, similar marks



can also arise from aestivation or resource scarcity (Castanet & Smirina 1990; Sinsch *et al.* 2007; Altunışık *et al.* 2022). In addition to providing age estimates, the spacing of successive LAGs carries biological information: narrower distances between outer growth marks typically indicate reduced somatic growth, following the onset of reproduction (Wapstra *et al.* 2001). Even though the skeletochronology approach entails the possibility of missing LAGs due to endosteal resorption, this issue is not prominent when using phalanges (e.g. Quiroga *et al.* 2015), and can be corrected by comparing the diameter of a juvenile bone with the size of the medullary cavity of adults (Lyapkov 2025).

The sand lizard (*Lacerta agilis* Linnaeus, 1759) is a diurnal, ground-dwelling species with a broad latitudinal and vertical distribution over vast areas of Eurasia (Blanke & Fearnley 2015). Within the species, the sexes differ in terms of their colouration, pattern, head and limb length (Majláth *et al.* 1997), home range (Wieczorek *et al.* 2020), digit ratio (Kaczmarski *et al.* 2020), and size, even though within lacertids in general, there is no clear pattern of sexual size dimorphism (SSD) (Cox *et al.* 2007). Interestingly, as a polytypic species, *Lacerta agilis* shows a spectrum of SSD patterns that are aligned with the oviparity-viviparity continuum (Roitberg *et al.* 2015). In the *agilis* clade sensu Andres *et al.* 2014, the SSD is female-biased (larger females), and for *L. agilis boemica* it is the opposite, whereas the remaining clades show intermediate SSD patterns (Roitberg *et al.* 2015). The *Lacerta a. argus* inhabiting Poland are recognised to belong to the *agilis* clade (Roitberg *et al.* 2015) and have a female-biased SSD (Juszczyk 1974), with females and males reaching on average a 7.35 and 6.55 cm snout-vent length (SVL), respectively (Ekner *et al.* 2008).

A system of interacting intrinsic (genetic) and extrinsic (environmental) factors is known to shape morphological traits and subsequent population demographics. The observed phenotypes and characteristics of a particular population result from trade-offs encompassing both their physiology and ecology. Likewise, the lizards inhabiting higher altitudes and latitudes are known to reach sexual maturity later and show a greater longevity (Wapstra *et al.* 2001; Roitberg & Smirina 2006a; Roitberg *et al.* 2015; but see: Guarino *et al.* 2010; Gül *et al.* 2014), which is mediated by, among other things, their growth rate, which is in turn influenced by the length of the activity period. Yet, despite these life-history patterns, the adult SVL shows no universal altitudinal or latitudinal trend across lizard taxa, suggesting that the body-size responses are modulated by lineage-specific constraints. Moreover, ecological interactions,

thermal conditions and other aspects of the habitat quality are known to affect a population's growth rate, survival rate, age of attaining sexual maturity, longevity, life expectancy, age structure, skeletogram patterns and fertility (Augert & Joly 1993; Wapstra *et al.* 2001; Atkins *et al.* 2020; Altunışık *et al.* 2022; Ma *et al.* 2022), which explains the disparate results of sand lizard demographic studies. Therefore, we might expect the demographic characteristics of populations living in habitats with varying thermal conditions to differ. Age also affects the growth rate, which is highest in the first year of life (Szafrńska 1978; Roitberg & Smirina 2006b; Kurczewski 2014). Kurczewski (2014) attributes this pattern to intense foraging, combined with longer daily and annual activity periods.

The aim of our work is to describe the life-history traits of three sand lizard populations and investigate how age, sex, population and their interactions shape the growth patterns. By comparing sexes and populations, we hope to determine whether the growth trajectories differ intersexually and geographically.

Materials and Methods

This study was approved by the Regional Directorate for Environmental Protection (Permit No. WPN-I.6401.206.2015.JK) and the Local Ethics Committee for Animal Experiments (Resolution No. 70/2016).

Study sites and fieldwork

Fieldwork was conducted in Lubusz Voivodeship at three sites characterised by different environmental conditions: Zielona Góra County (cca. 51°52'N, 15°27'E), Żary County (cca. 51°37'N, 15°05'E) and Nowa Sól County (cca. 51°43'N, 15°43'E). The sampling took place from September 2016 to September 2017, with a great majority of the captures made in May 2017 at all three sites. The location of the sand lizard populations we studied places them in the *agilis* clade sensu Andres *et al.* 2014.

The Zielona Góra sampling site covered an area of 30 ha and was undergoing a conversion from intensively farmed land into a suburban neighbourhood with low-rise buildings. Agricultural land, wasteland and a mosaic of *Arrhenatheretalia elatioris* grassland constituted the largest share of the land cover, accounting for 80.4% of the area. Riparian forest (Alno-Ulmion) made up 13.3% of the site, while buildings covered 6.3%. The local herbaceous vegetation was dominated by *Agrostis capillaris*, *Arrhenatherum elatius*, *Poa pratensis*, *Bromus*

hordeaceus, *Calamagrostis epigejos* and *Festuca pallens*. Bushes were made up of *Crataegus* spp., *Rosa canina*, *Sambucus nigra* and *Rubus* spp., while trees were represented by *Alnus glutinosa* and *Betula pendula*.

The study site in Żary was a post-excavation site with an area of 12.7 ha. Young forest (mainly small *Pinus sylvestris*, *Betula pendula* and *Populus tremula*) made up the biggest share of the land cover (42%). Grassland dominated by *Calamagrostis epigejos* covered 30% of the area. Marshes made up 24%, and a few small ephemeral water bodies accounted for the remaining 4%.

The Nowa Sól study site, with a 2.9 ha surface area, was a very arid post-excavation site heavily transformed by human activities. Steep slopes that had been created due to sand mining were covered with psammophilous grassland (83% of the land cover). Shrubs and foliage made up 12% of the land cover, and a water body covered 5%. The most abundant plants at that site were *Corynephorus canescens*, *Silene* spp., *Koeleria macrantha* and *Astragalus arenarius*.

The sand lizards were captured by pitfall traps combined with drift fences. Their sex was then determined on the basis of the overall body shape, size, pattern, colouration and shape of the cloacal region. Individuals which lacked visible secondary sex characteristics were classified as juveniles. The SVL of each individual was measured with a precision of 0.1 mm. For the subsequent skeletochronological analyses, a portion of the second digit of the right hind limb was collected from each specimen. Then, until the time of the analysis, the samples were stored at -20°C . In total 177 individuals were analysed, including 41 from Zielona Góra County (16 males, 18 females and 7 juveniles), 59 from Żary County (23, 23 and 13, respectively) and 77 from Nowa Sól County (32, 32 and 13, respectively).

Skeletochronological procedures

To obtain the age, we performed skeletochronological analyses. We followed the standard skeletochronological procedures after Castanet and Smirina (1990), Smirina (1994), Andreone and Guarino (2003), Rozenblut and Ogielska (2005). Phalanges were manually cleaned of the soft tissue and preserved in 70% ethanol until processing. Depending on the bone size, the samples were decalcified in a 1:1 solution of 10% formic acid and 4% formaldehyde for 0.5–1.5 h, then rinsed four times in distilled water (15 min each) and stored again in 70% ethanol. After air-drying, the bones were embedded in

a tissue freezing medium and sectioned at -24°C into multiple 10 μm transverse slices using a freezing microtome (Leica CM 1850 UV). Sections were stained with an aqueous solution of 0.05% cresyl violet (Sigma) applied directly onto the slide for 5 min, after which the stain was drained on absorbent paper. This procedure enhanced the visibility of the lines of arrested growth (LAGs), which were separated by zones of annual bone deposition. The slides were scanned using a NanoZoomer2.ORS Hamamatsu scanner, and the images were analysed and archived with the NanoZoomer Digital Pathology software.

Despite careful preparation, the quality of the cross-sections varied among the samples, with 35–60% being of a sufficient quality for a reliable interpretation. No consistent differences in the LAG visibility or spacing were detected between males and females, or across the three populations examined. Endosteal resorption was occasionally observed, occurring more often in older individuals, but its prevalence also did not differ among the sexes or populations, and therefore did not compromise the analyses. Representative cross-sections illustrating the LAG patterns in individuals after their first, second, fifth and seventh hibernations are provided in Supplementary Material Figure S1.

Statistical analyses

For all three populations pooled together, the annual survival rate (Svr) was estimated with the Robson and Chapman method (1961), Seber's method (1973) was used to assess the adult life expectancy (ESP), while Sexual Dimorphism Index (Lovich and Gibbons 1992) was utilised to quantify size differences between the sexes. These approaches are commonly used in studies on lizard population demographics (Altunışık *et al.* 2022, 2024; Kara *et al.* 2025).

To investigate the influence of age, sex and population on the body size, we fitted a linear model with the snout-vent length (SVL, in cm) as the dependent variable. The primary predictors included the age (in years, by a proxy of LAGs), sex (male or female) and population (Zielona Góra, Nowa Sól, Żary). Moreover, interaction terms between the age and both the sex and population were included to account for potential intersexual and inter-locality differences.

Before the model fitting, we evaluated whether the relationship between SVL and age followed a logarithmic pattern. A visual inspection and model comparison indicated that a logarithmic transformation did not improve the model fit; thus, the untransformed linear relationship was retained. Although classical

nonlinear growth models such as von Bertalanffy or Gompertz are used in ectotherm growth studies, we did not apply them here because our data showed an approximately linear growth trajectory within the sampled ages, and a simpler linear model was sufficient for testing the sex and population effects. Residuals were checked for normality and homoscedasticity using Q-Q plots and residual vs fitted plots, confirming that the model assumptions were met. The final model was specified as: Snout-Vent Length \sim age * sex + age * population. Pairwise comparisons among the population effects were conducted using estimated marginal means (emmeans package), with the Sidak correction for multiple testing. Model terms were evaluated using likelihood ratio tests (drop1 function), with Chi-squared statistics used to assess the contribution of interaction terms. The model showed a strong overall fit (adjusted $R^2 = 0.905$), and significant interaction effects were observed between the age and both the sex and population ($p < 0.01$). All statistical analyses were performed in R, version 4.1.3 (R Core Team 2022).

Results

The juveniles ($N = 33$) were several days to two years old. The adults ($N = 144$) were two to eight years old, with the majority (54.9%) being 5–6 years old. Both males and females attained sexual maturity roughly after their second hibernation, as every lizard showing secondary sex characteristics was at

least two years old. Fig. 1 illustrates the mean SVL (\pm SE) by age (in LAGs) for juveniles and adults of each sex, confirming a linear increase in body size with age.

While the annual survival rate was estimated to be 0.80, adult lizards had a mean age of 4.58 ± 1.89 years and an estimated life expectancy of 5.25 years. The Sexual Dimorphism Index was female-biased and equal to 0.04, suggesting modest sex differences in the size of the lizards. The oldest lizard was an eight-year-old female from Nowa Sól County.

The linear model explained a substantial proportion of variation in the SVL (adjusted $R^2 = 0.905$; $F_{7,136} = 194.7$; $p < 0.001$). Age had a strong positive effect on the SVL ($p < 0.001$), while no sex differences in the SVL were found ($p = 0.075$). For full model parameter estimates, see Supplementary Material Table S1. Pairwise comparisons showed that the lizards from Żary were significantly smaller than those from Nowa Sól ($p < 0.001$) and Zielona Góra ($p < 0.001$), while no significant difference was found between the Nowa Sól and Zielona Góra populations ($p = 0.918$).

Significant interactions were found between the age and both the sex ($p = 0.006$) and population ($p < 0.001$), indicating that the relationship between age and SVL varied between sexes and populations (Table 1). Specifically, the age-growth relationship was weaker in males, while females exhibited a steeper growth trajectory, indicating their faster growth after attaining three years of age (Fig. 2A). Although

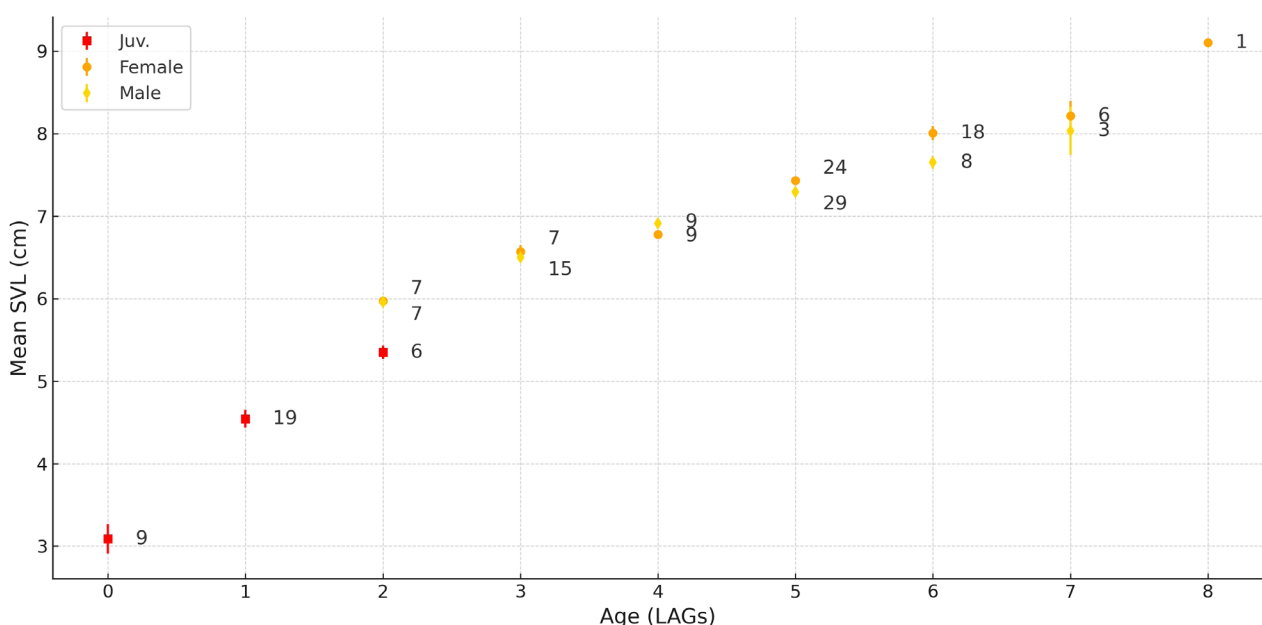


Fig. 1. Mean snout-vent length (SVL; cm) of *Lacerta agilis* by age (number of LAGs) for juveniles, adult females and adult males. Points show group means and vertical bars represent standard errors. The sample size for each age group is indicated next to its symbol.

Table 1

Likelihood-ratio tests assessing whether interaction terms improve the fit of the full linear model of the lizard snout-vent length (SVL). Each interaction was removed in turn (using drop1) and the reduced model compared with the full model containing the main effects of Age, Sex and Population. Columns show the change in the degrees of freedom (ΔDf), change in deviance / sum of squares (ΔSS), residual sum of the squares of the reduced model (RSS) and the resulting Akaike Information Criterion (AIC). Significance codes: ** $p < 0.01$; *** $p < 0.001$

Term	ΔDf	ΔSS	RSS	AIC	p-value	Significance
Age \times Sex	1	0.35	6.83	-425.02	0.006	**
Age \times Population	2	1.83	8.31	-398.83	<0.001	***



Fig. 2. Relationship between the snout-vent length (SVL; cm) and years of age (number of LAGs) in *Lacerta agilis*. A. Growth trajectories by sex. Females showed a steeper increase in the SVL with age than males, indicating sex-specific growth patterns. B. Growth trajectories by population. Lizards from Żary exhibited slower growth compared to those from Nowa Sól and Zielona Góra, highlighting population-level differences in the growth dynamics. Shaded areas represent 95% confidence intervals. Individual data points are shown with a slight random scatter (jitter) to improve the readability and reduce overplotting.

the age-population interaction for the Zielona Góra population was non-significant ($p = 0.151$; Supplementary Material Table S1), the lizards from Żary nonetheless had a markedly shallower growth trend than those from Zielona Góra or Nowa Sól, indicating slower growth in that population (Fig. 2B).

Discussion

Our finding that, on average, *L. agilis* reaches sexual maturity in the second year of life is comparable to the results of other studies, according to which this species reaches sexual maturity between the second and fifth year of age (Guarino *et al.* 2015), or in the second and third years of life in males and females, respectively (Candan 2021).

We estimated the annual survival rate for the three populations altogether at 80% (0.80), which is a surprisingly high figure and might be indicative of an overrepresentation of adults in our study, which showed a higher survival rate (69.4%) compared to both subadults (61.4%) and juveniles (38.4%) (Berglind 2004).

Regarding the estimated adult life expectancy (5.25 years) and the average age of an adult individual (4.58 ± 1.89 years), our results differed markedly from those of Guarino *et al.* 2010, which obtained a mean age of 2.3 ± 0.2 for males and 2.59 ± 0.5 for females. These authors, however, acknowledged the peculiarity of their studied population with regard to that aspect.

Our oldest lizard was an eight year-old female, like in Kidov *et al.* (2014), while in other studies the maximum longevity for a female of this species has been estimated to be 12 years (Sweden, Olsson & Shine 1996), six years (Dagestan, Roitberg & Smirina 2006a) and three years (Italy, Guarino *et al.* 2010). The maximum age reported for this species by Strijbosch and Creemers (1988), who used the capture-mark-recapture method, was 12 years (male),

while some individuals in the southern part of the species' range (central Europe) have been reported to live up to about 15 years (Axelsson *et al.* 2020). However, we cannot exclude the possibility that the maximum age we obtained was underestimated due to the progressive narrowing of LAGs near the bone periphery, which may cause some lines to become indistinguishable in older specimens. This phenomenon has been noted in previous skeletochronological studies (e.g. Hemelaar 1985; Sagor *et al.* 1998).

The Sexual Dimorphism Index calculated for the three populations altogether was equal to 0.04, with females being larger, thus aligning with the findings of Ekner *et al.* 2008 for a population from another part of Poland.

To the best of our knowledge, age and its relationship to size in Polish sand lizards has so far been examined only by Borczyk and Paško (2011). Using skeletochronology, they analysed 187 individuals (122 adult females, 52 adult males and 13 juveniles) from eight lowland and montane populations. The oldest male and female were estimated to be five and six years old, respectively, and age was strongly correlated with the SVL ($r = 0.82$). However, the regression of age on the SVL yielded a standard error of ± 1.36 years, showing that size alone is an imprecise age proxy. For our three lowland populations, a multivariate model predicting SVL from the age, sex and population accounted for 90.5 % of the variance (adjusted $R^2 = 0.905$). Because we modelled the SVL as a function of age (rather than age from the SVL), a direct numerical comparison of standard errors would require re-fitting a univariate age-on-SVL regression to our data. Nevertheless, the much higher R^2 in our lowland sample supports the idea that pooling ecologically distinct montane and lowland lizards in Borczyk and Paško's dataset inflated their age-estimation error. With regard to the snout-vent length, our model showed significant effects of the age and population, whereas the sex was not significant. Lizards from the Żary population were the smallest and grew the slowest; this site is a cool, young post-excavation forest where closed stands of pine, birch and poplar, interspersed with marshy and grassland patches, provide a relatively shaded, humid microclimate that is sub-optimal for the species. In contrast, the Zielona Góra population occupies a disturbed but warmer suburban mosaic, in which grasslands dominate between low-rise buildings and riparian woodland; despite the human alteration, the more open, well-insolated conditions favour faster growth and a larger size. The third population, at Nowa Sól, lives in an even more arid post-mining sand pit. Steep, sparsely vegetated slopes of psam-

mophilous grassland create the driest and warmest microhabitat among the three sites. Thus, the two more xerothermic localities – disturbed Zielona Góra and post-extraction Nowa Sól – offer thermal environments that promote greater body size and growth, whereas the cooler, shaded Żary forest constrains the lizards' growth, leading to the pronounced size differences detected by the model. Moreover, we found differences in growth between the sexes, with females growing faster. Interestingly, the opposite pattern was found for populations living in Dagestan (Roitberg & Smirina 2006a) and the Alps (Guarino *et al.* 2010). The cause of these contrasting findings probably rests in distinct breeding ecologies shaped by environmental conditions and warrants further investigation.

Future demographic work on lowland sand-lizard populations should couple skeletochronology with fine-scale measurements of the microclimatic and habitat variables that could shape the age structure – such as the temperature, vegetation openness, prey availability and predation pressure – and include those covariates explicitly in statistical models. Crucially, such studies should also examine how these drivers interact over time, factoring in habitat changes (e.g. early-to-late successional stages) to reveal the processes that generate population-level variations in growth and survival.

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Conflict of Interest

The authors declare no conflict of interest.

Author Contributions

Research concept and design: M.W., B.N.; Collection and/or assembly of data: M.W., B.N.; Data analysis and interpretation: M.W., B.N., F.M., M.S.; Writing the article: M.S.; Critical revision of the article: M.W., B.N., F.M., M.S.; Final approval of article: M.W., B.N., F.M., M.S.

Supplementary Materials

Supplementary Materials to this article can be found online at:

<http://www.isez.pan.krakow.pl/en/fovia-biologica.html>
Supplementary files:

SM.01. Figure S1. Representative phalangeal cross-sections of sand lizard (*Lacerta agilis*) stained with cresyl violet, showing the lines of arrested growth (LAGs) at different ages: (A) after the first hibernation; (B) after the second hibernation; (C) after the fifth hibernation; and (D) after the seventh hibernation.

SM.02. Table S1. Linear model results for the snout–vent length (SVL) in relation to age, sex and population. Significant results are marked in bold. ** denotes $p < 0.01$; *** denotes $p < 0.001$.

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