



# Age and growth of the common wall lizard, *Podarcis muralis* (Laurenti, 1768)

## Ali İhsan Eroğlu, Ufuk Bülbül\*, Muammer Kurnaz and Yasemin Odabaş

Karadeniz Technical University, Faculty of Sciences, Department of Biology, 61080 Trabzon, Turkey

Submitted: February 23, 2017. Final revision received: March 7, 2018. Accepted: March 14, 2018

#### Abstract

The present study was designed to compare the life history traits of two *Podarcis muralis* populations located at sites of different elevation. The age at maturity was similar in both populations, whereas longevity was found to be lower in the lowland one (Dereköy). The males and females of both populations had a similar snout-vent length (SVL) and mean age. Sexual size dimorphism (SSD) was weak in the highland population, males being slightly larger than females, whereas a strong male-biased SSD was observed in the lowland one. The growth coefficient (*k*) and growth rates were similar in both populations. This study indicates that the age at maturation (2-3 years) and growth rates (2.37 mm/year) are similar in two populations of *P. muralis* exposed to different climatic and environmental conditions. Longevity was slightly higher in the highland population (16 years) compared to the lowland one (14 years).

#### Keywords

growth rate; longevity; sexual size dimorphism; skeletochronology; SVL

# Introduction

The common wall lizard, *Podarcis muralis* (Laurenti, 1768) is widely distributed in the southern, western and central part of Europe and in northwestern Turkey, and it was introduced in the United States of America (Böhme et al., 2009; Sillero et al., 2014). *Podarcis muralis* populations can be found from sea level to 2500 m a.s.l. The IUCN Red List of Threatened Animals classifies *P. muralis* as LC (Least Concern) (Böhme et al., 2009). Although there are some reports concerning the size (Vogrin, 1999) and population dynamics (Strijbosch et al., 1980; Barbault & Mou, 1988; Allan et al., 2006) of *P. muralis*, age estimation by skeletochronology was

<sup>\*)</sup> Corresponding author; e-mail: ufukb@ktu.edu.tr

only performed by Castanet & Roche (1981) and Vollono & Guarino (2002), the former being from France and the latter from Matese Regional Park, Italy.

Age and growth are two important parameters used to characterize the population dynamics of a given species (Halliday & Verrell, 1988; Rahman & Tachihara, 2005; Tao et al., 2012). Two important methods (mark-recapture and skeletochronology) are used to estimate age and growth in ectotherms (Halliday & Verrell, 1988; Gül et al., 2014; Sinsch, 2015). The mark-recapture method provides the most robust information, but it is also time-consuming. Skeletochronology is an alternative way to estimate an individual's age by observing the presence of growth layers in the bone tissue and by counting the lines of arrested growth (Castanet & Smirina, 1990; Castanet, 1994). Both the age structure and the growth rate provide important data concerning the persistence and survival rate, as well as the reproductive potential of a certain population (Newman & Dunk, 2002).

Previous studies (Wapstra et al., 2001; Roitberg & Smirina, 2006a; Guarino et al., 2010) indicate that lizard populations inhabiting lower elevation sites are smaller (i.e., mean snout-vent length, SVL) compared to those from high elevations. On the other hand, body size variation is not shaped by geographical gradients only (latitude and altitude) (Sinsch et al., 2015). Growth rates depend on food availability and the thermal environment (Adolph & Porter, 1993). Previous examples of growth rate variation throughout bioclimatic gradients in lizards support the hypothesis that populations living in cooler sites should either grow faster (Caley & Schwarzkopf, 2004; Conover et al., 2009) or compensate their slower growth rate with larger eggs and hatchlings and delayed sexual maturity (Bülbül et al., 2016a). Therefore, the main purpose of the present study was to determine and compare the age structure and growth parameters in two populations of *P. muralis* inhabiting contrasting altitudes and habitats in Turkey. We also aimed to assess the relationships of longevity and age at sexual maturity with sexual size dimorphism (SSD) and growth rates.

## Material and methods

A total of 93 *Podarcis muralis* individuals (43  $\sigma$   $\sigma$  and 50  $\varphi\varphi$ ) were caught in the present study. Lizards were collected from two populations: 53 individuals (21  $\sigma$   $\sigma$  and 32  $\varphi\varphi$ ) from Dereköy, Kırklareli Province (June 18, 2016), and 40 (22  $\sigma$   $\sigma$  and 18  $\varphi\varphi$ ) from the Kazdağı, Balıkesir Province (June 20-21, 2016), during the breeding season. The Kazdağı population (39°42′190″N, 26°51′569″E) is located in a highland area at an altitude of 1646 m a.s.l. The habitat consists of a rocky area in the alpine zone. The lizards were caught on rock surfaces of the slope on the Babadağ highland way. *P. muralis* lives in sympatry with *Lacerta viridis* in this area. The Dereköy population (41°53′845″N, 27°21′554″E) is located in a lowland area at an altitude of 475 m a.s.l. The lizards were caught on a rocky slope on the edge of the Kırklareli-Bulgaria highway. The common wall lizard lives in sympatry with *Testudo graeca*, *Ablepharus kitaibellii*, *L. trilineata*, *L. viridis*, *Dolichophis caspius* and *Vipera ammodytes* in this area.

The activity periods for lizards ranges from early May to early September in Kazdağı and from early April to late October in Dereköy (according to our observations and climate data including temperature, rainfall and moisture supported by the 11th Trabzon Meteorology Regional Directorate). In 2016, the mean annual temperature, precipitation, and humidity at the Kazdağı site were 7.7°C, 108.80 mm, and 48.80%, respectively. During the activity period of the lizards, the mean temperature, precipitation, and humidity were 15.1°C, 41.04 mm, and 41.12%, respectively. In the same year, the mean annual temperature, precipitation, and humidity at Dereköy were 13.7°C, 52.40 mm, and 71.90%, respectively. During the activity period of the lizards, the mean temperature, precipitation, and humidity at 20.04 mm, and 71.90%, respectively.

The lizards were caught by hand and the sex of the animals was determined by applying pressure to the base of the tail to force eversion of the hemipenes of males. Snout-vent length was measured with a digital caliper (0.1 mm precision). For subsequent histological analyses, the second phalanges from the longest toe of the hind limb of the lizards were clipped and preserved in 10% formalin solution. After measuring SVL and toe-clipping, the lizards were released back into their natural habitats. The animals were treated in accordance with the guidelines of the local ethics committee (KTÜ.53488718-651/2014/56).

The toes were first preserved in a 10% solution of formaldehyde, followed by peeling, and subsequently were kept in 5% nitric acid solution for 2.5 hours to decalcify the bone tissue. Later, all toe samples were loaded into a tissue processing system (Leica TP1020 tissue processor, Germany). The skeletochronology protocol lasted 16 hours with 80 minute periods (change time of solution) using solutions of alcohol (eight times), xylene (two times) and paraffin (two times), respectively. Then, all tissue samples were embedded in paraffin with a tissue embedding device (Thermo Scientific, UK). The cross-sections (8  $\mu$ m) were obtained from embedded phalanges with a rotary microtome, they were then stained using hematoxylin (Non-Acidified type, Thermo Scientific<sup>TM</sup> Shandon<sup>TM</sup> Harris Hematoxylin, UK) for 2 minutes. Entellan ("Entellan<sup>®</sup> new", rapid mounting medium for microscopy, Merck, Germany) was used for mounting the stained cross-sections on microscope slides. Finally, the cross-sections were observed under a light microscope.

We assessed endosteal resorption of the first lines of arrested growth (LAGs) by comparing the diameters of eroded marrow cavities with the diameters of noneroded marrow cavities in sections from the youngest specimens.

Age determination was estimated by following the standard protocol proposed by Castanet and Smirina (1990) and Castanet (1994). LAGs on the cross-sections were independently counted by three observers (A.İ. Eroğlu, M. Kurnaz and U. Bülbül) and results were compared. Observed double lines were considered as one LAG for age determination. The distance between two adjacent LAGs is a good indicator of individual growth in a given year (Kleinenberg & Smirina, 1969; Bülbül et al., 2016a). The point where an obvious decrease in spacing between two subsequent

LAGs was observed, was taken to mark the age when sexual maturity was achieved (Ryser, 1988; Bülbül et al., 2016a).

In order to determine whether the age and SVL differed between males and females, we used a general linear model (GLM) and employed multivariate analysis of covariance (MANCOVA). Pearson's Correlations Test (P < 0.01) was applied to measure the strength of the relationship between age and SVL. In the MANCOVA, sex and population (location) were used as fixed factors and SVL and age were used as dependent variables. All statistical tests were carried out with IBM SPSS 21.0 for Windows and the level of significance chosen was P < 0.05.

Sexual Size Dimorphism (SSD) was quantified with the Lovich & Gibbons (1992) size dimorphism index (SDI) according to the following formula:

 $SDI = (mean length of the larger sex/mean length of the smaller sex) \pm 1$ .

In this formula, +1 is used if males are larger than females and defined as negative, or -1 if females are larger than males and arbitrarily defined as positive.

The growth patterns were estimated following von Bertalanffy's growth model, as previous studies have shown that it decribes the relationship between body size and age better (James, 1991; Wapstra et al., 2001; Roitberg & Smirina, 2006b; Guarino et al., 2010). The general form of von Bertalanffy's growth equation used is  $L_t = L_{\infty}(1 - e^{-k(t-t_0)})$ , where  $L_t$  is length at age t,  $L_{\infty}$  is a parameter depicting average asymptotic length, e is the base of the natural logarithm, k is a growth interval presently under study. As applied in the study of Guarino et al., 2010, we used as size at hatching ( $L_{t_0} = 24.1 \text{ mm}$ ) the mean value provided by In den Bosh & Bout (1998). The parameters  $L_{\infty}$  (asymptotic SVL) and k, and their asymptotic confidence intervals (*CI*), were estimated by means of a non-linear regression procedure using the IBM SPSS 21.0 software program. Then, the growth rates were calculated as  $R = k(L_{\infty} - L_t)$  (Bülbül et al., 2016a; Lu et al., 2017). The growth curves were considered to be significantly different if the 95% confidence intervals of the growth coefficient k did not overlap (James, 1991; Wapstra et al., 2001).

## Results

The resorption zone reached the first LAG in 12 specimens (22.60%) from the Dereköy population and in 16 specimens (40%) from the Kazdağı population without creating any difficulty in terms of age determination. Double lines were observed in 17 (32.10%) specimens from Dereköy and in 7 specimens (17.50%) from Kazdağı.

The oldest females and males in the Dereköy population were found to be 12 and 14 years old, whereas they were 13 and 16 years old, respectively, in the Kazdağı population (fig. 1). The age at maturity was two years in four individuals, and three years in 49 individuals in the Dereköy population while it was three years in all individuals of the Kazdağı population.



Figure 1. Age distributions for male and female *P. muralis* from the Dereköy (A) and Kazdağı (B) populations.

#### Lowland population

In the Dereköy population, age ranged from 3 to 12 years in females and 3 to 14 years in males. The mean age of the specimens was found to be significantly different between the sexes (MANCOVA; F = 4.979, df = 51, P < 0.05). Intersexual differences in body size (length) were male-biased (SDI = -0.047). The mean SVL was found to be significantly different between the sexes (MANCOVA; F = 4.527, df = 51, P < 0.05). A positive correlation was observed (Pearson's correlation) between SVL and age for males (r = 0.647, P < 0.01) and females (r = 0.708, P < 0.01). The growth pattern estimated following von Bertalanffy is given in fig. 2A. For both sexes, the estimated asymptotic SVL was smaller than the maximum SVL recorded (SVL<sub>asym</sub>  $\pm$  SE, males: 57.61  $\pm$  9.70 mm; females: 55.67  $\pm$ 6.86 mm). CI ranges for SVLasym were 38.60-76.62 for males and 42.22-69.12 for females. The growth coefficient was found to be similar between the sexes ( $k \pm SE$ , males:  $0.50 \pm 0.17$ ; females:  $0.36 \pm 0.13$ ). CI ranges for k were 0.17-0.83 for males and 0.11-0.61 for females. The growth rates of the specimens were not significantly different (independent-samples t-test; t = -0.773, df = 13, P > 0.05) between the sexes.

#### Highland population

Age ranged from 4 to13 years in females and from 6 to 16 years in males from the Kazdağı population. The mean age was significantly different between the sexes (MANCOVA; F = 4.784, df = 38, P < 0.05). Intersexual differences in body size (length) were male-biased (SDI = -0.025). The mean SVL was not different between the sexes (MANCOVA; F = 1.015, df = 38, P = 0.320). A positive correlation was observed (Pearson's correlation) between SVL and age for males (r = 0.857, P < 0.01) and females (r = 0.875, P < 0.01). The growth pattern estimated following von Bertalanffy is given in fig. 2B. For both sexes, the estimated asymptotic SVL was smaller than the maximum SVL recorded (SVL<sub>asym</sub> ± SE



**Figure 2.** Von Bertalanffy growth curves for males (open circles, solid line) and females (solid circles, dashed line) of *P. muralis* from the Dereköy (A) and Kazdağı (B) populations. The open square shows snout-vent length mean of the lizards at hatching as reported by In den Bosch & Bout (1998). Growth parameters are given in the text.

males:  $62.68 \pm 6.80$  mm; females:  $63.30 \pm 6.89$  mm). CI ranges for SVL<sub>asym</sub> were 49.36-76 for males and -49.8-76.8 for females. The growth coefficient was found to be similar between the sexes ( $k \pm$  SE, males:  $0.19 \pm 0.11$ ; females:  $0.20 \pm 0.12$ ). CI ranges for k were 0.02-0.42 for males and -0.3-0.43 for females. The growth rates of the specimens were not found to be significantly different between the sexes (independent-samples *t*-test; t = -2.002, df = 16, P > 0.05).

### Comparison of both populations

A growth zone and thin basophilic outer line corresponding to a winter line of arrested growth were present in cross sections of the phalanges in all individuals of both populations (fig. 3). Males of the highland population had significantly different SVL (MANCOVA; F = 10.235, df = 41, P < 0.05) and age (MANCOVA; F = 9.741, df = 41, P < 0.05) than males from the lowland, although there was no difference in growth rate (independent-samples *t*-test; t = 0.173, df = 16, P > 0.05). Similar results were found for SVL (MANCOVA; F = 10.482, df = 48, P < 0.05), age (MANCOVA; F = 14.885, df = 48, P < 0.05) and growth rate (independent-samples *t*-test; *t* = -0.220, df = 13, P > 0.05) analyses performed for females from both populations. Descriptive statistics of age, snout-vent length (SVL) and growth rates for both populations are given in table 1.

## Discussion

We estimated and compared age and growth parameters in two Turkish populations of *P. muralis* from contrasting altitudes. The age at maturity was similar in both populations, while mean lifespan and longevity were lower in the lowland population.

Altitudinal variations may influence the life-history traits of reptiles. As a rule, individuals inhabiting higher elevation sites are older than those from the lower ones

152



**Figure 3.** Hematoxylin sections (8 µm thick) through phalanges of male (A) and female (B) *P. muralis.* (A) Five-year-old male (57.8 mm SVL) from the Dereköy population. (B) Eight-year-old female specimen (60.0 mm SVL) from the Kazdağı population. Abbreviations: MC, marrow cavity; EB, endosteal bone; RL, resorption line; P, periphery.

(Wapstra et al., 2001; Roitberg & Smirina, 2006b; Guarino et al., 2010; Bülbül et al., 2016a). In addition, lizards in cooler areas show a larger body size than those from warmer areas (Roitberg & Smirina, 2006a).

## Longevity and age at maturity

Castanet & Roche (1981) found specimens of maximally five years old (longevity was five years in males and four in females) of the common wall lizard and reported that longevity would be at least six years for *P. muralis*. Similarly, Vollono & Guarino (2002) reported the longevity of the species as five years. Compared to these results, we found higher longevity in both populations (14 years in the low-land and 16 years in the highland). Boretto et al. (2015) studied age and growth in an endemic Argentinian lizard species (*Phymaturus punea*) from 3100-4200 m a.s.l where the longevity was 18 years in males and 20 years in females.

Some lizards from colder climates delay age at which maturity is reached, investing prematuration energy into their growth and maintenance, presumably to maximize future reproduction (Tinkle et al., 1970; Wapstra et al., 2001; Roitberg

#### Table 1.

Descriptive statistics of age, snout-vent length (SVL) and growth rates for both populations. Abbre-
viations: CI, confidence intervals; GR, growth rate; k, growth coefficient; n, number of samples; SE,
standard error.

Characters	Sex	Dereköy					Kazdağı			
		n	Mean	Range	SE	n	Mean	Range	SE	
SVL	ೆರೆ	21	56.6*	45.1-60.4	0.83	22	60.1	54.1-64.9	0.75	
Age		21	6.95*	3-14	0.52	22	9.63*	6-16	0.65	
GR		8	1.95*	0.03-6.41	0.78	10	1.81*	0.57-3.81	0.35	
SVL	QQ	32	54.0*	44.4-63.5	0.80	18	58.9	50.8-65.5	0.89	
Age		32	5.66*	3-12	0.32	18	7.67*	4-13	0.60	
GR		7	2.85*	0.28-6.81	0.86	8	3.08*	0.95-5.68	0.56	
SVL		53	55.0*	44.4-63.5	0.61	40	59.5*	50.8-65.5	0.57	
Age	♂♂ + çç	53	6.17*	3-14	0.29	40	8.75*	4-16	0.47	
GR		15	2.37	0.03-6.81	0.58	18	2.37	0.57-5.68	0.34	
Characters	Sex	п	Mean	95% CI	SE	n	Mean	95% CI	SE	
k	ೆರೆ	8	0.50	0.17-0.83	0.17	10	0.19	0.02-0.42	0.11	
SVLasym		21	57.61	38.60-76.62	9.70	22	62.68	49.36-76	6.80	
k	φç	7	0.36	0.11-0.61	0.13	8	0.20	-0.3 - 0.43	0.12	
SVLasym		32	55.67	42.22-69.12	6.86	18	63.30	49.8-76.8	6.89	

& Smirina, 2006b). In our study, the highland population (Kazdağı) was exposed to colder climatic conditions than the lowland one (Dereköy). Accordingly, age at maturity and longevity were found slightly higher (two to three years in the lowland population and three years in the highland population) in the Kazdağı population. Similar to our results, Castanet & Roche (1981) reported an age of sexual maturity of two to three years in a population of *P. muralis*.

## Mean age and age distribution

The highland population had a significantly higher mean age than the lowland one. Similarly, lizards were older in highland populations of *Darevskia parvula*, *D. clarkorum, Lacerta agilis* and *L. strigiata* (Bülbül et al., 2016a, b; Roitberg & Smirina, 2006a). Contrarily, a few reports indicated that some lizards (*D. rudis* and *D. bithynica*) from lowland populations were older than those from highland ones (Gül et al., 2014, 2015).

# Sexual size dimorphism (SSD)

Sexual size dimorphism in body size is commonly seen among lizard species (Herrel et al., 2010). According to Andersson (1994) and Fairbairn et al. (2007), females have a larger body size and SSD appears female-biased. On the other hand, there are also studies including male-biased SSD (Kaliontzopoulou et al., 2007; Bülbül et al., 2016a; Eroğlu et al., 2017a, b). In the present study, P. muralis showed malebiased SSD in both lowland and highland populations, in accordance with the resuls of Castanet and Roche (1981). In addition, Eroğlu et al. (2017a, b) reported a malebiased SSD in Turkish populations of *P. tauricus* and *P. siculus*. These findings may be due to the fact that males are advantaged by larger size and consume energy for male combat. Bigger male body size occurs in those species where males engage in fights and copulation enforces male-male combats for female partner choice (Olsson et al., 2002; Cox et al., 2003; Kaliontzopoulou et al., 2007). Moreover, Gül et al. (2014) reported higher levels of SSD in results from colder environmental temperatures at the higher elevation sites of the highland population in their study. Although the highland areas had a colder climate than the lowland ones, the individuals from the lowland population exhibited a higher level of male-biased SSD than those from the highland one in the present study. On the other hand, SSD is shaped by disparities in growth rates in many adult lizards (John-Alder & Cox, 2007; Kolarov et al., 2010; Bülbül et al., 2016a). We found that the growth rates were not different between the sexes in both populations.

# Growth rates of the populations

Growth rate is an important component of the life-history strategy of any organism (Shine & Charnov, 1992; Lemos-Espinal & Ballinger, 1995). In addition, many factors such as temperature (Christian, 1986; Dunham et al., 1989), altitude (Fox, 1983), food availability (Ballinger, 1977; Dunham, 1978), presence of predators (Williams, 1966), water supplies (Jenssen & Andrews, 1984), inter- or intraspecific competition (Pianka, 1970; Tokarz, 1985), age at sexual maturity (Gadgil & Bossert, 1970; Andrews, 1976), active period (Grant & Dunham, 1989) and energy requirement (Williams, 1966) affect growth rates of lizards among different populations. Although food availability, presence of predators and intraspecific competition are lower in the highland population (personal observation), both populations mentioned here had similar growth rates. After reaching sexual maturity, longer activity periods of the individuals in a population allow them to grow faster and have smaller size (Adolph & Porter, 1993). Moreover, the faster growing population reaches sexual maturation earlier (Cabezas-Cartes et al., 2015).

# Conclusion

Climatic data indicate that individuals from the lowland population have a longer activity period, compared to those from the highlands. Although the activity period was longer in the lowland, age at maturity was similar in both populations. Similar growth rates of both *P. muralis* populations appear to be a result of similar age at maturity and mean rainfall in the activity periods. In conclusion, even though the age at maturity and growth rate were similar, the mean age, longevity and mean SVL were different in the *P. muralis* populations studied.

#### Acknowledgements

This study was financially supported by the Karadeniz Technical University Scientific Research Unit (FDK-2015-5215). The study was carried out with permission from the Ministry of Forest and Water Affairs (number of permission to capture: 72784983-488.04-96747) and the Karadeniz Technical University Animal Care and Ethics Committee. The authors wish to thank the 11th Trabzon Meteorology Regional Directorate for providing climate data for the years 2015-2016. Spelling errors in the English have been reviewed and corrected by Paul Renna from California, USA and Atalay Sökmen, who is a Professor at Konya Food and Agriculture University.

## References

- Adolph, S.C. & Porter, W.P. (1993) Temperature, activity, and lizard life histories. *Am. Nat.*, 142, 273-295.
- Allan, G.M., Prelypchan, C.J. & Gregory, P.T. (2006) Population profile of an introduced species, the common wall lizard (*Podarcis muralis*), on Vancouver Island, Canada. *Can. J. Zool.*, 84, 51-57.
- Andersson, M. (1994) Sexual Selection. Princeton University Press, Princeton, NJ, USA.
- Andrews, R.M. (1976) Growth rate in island and mainland anole lizards. Copeia, 1976, 477-482.
- Ballinger, R.E. (1977) Reproductive strategies: food availability as a source of proximal variation in a lizard. *Ecology*, 58, 628-635.
- Barbault, R. & Mou, Y.-P. (1988) Population dynamics of the common wall lizard, *Podarcis muralis*, in southwestern France. *Herpetologica*, 44, 38-47.
- Böhme, W., Pérez-Mellado, V., Cheylan, M., Nettmann, H.K., Krecsák, L., Sterijovski, B., Schmidt, B., Lymberakis, P., Podloucky, R., Sindaco, R. & Avci, A. (2009) *Podarcis muralis. The IUCN Red List of Threatened Species 2009.* http://dx.doi.org/10.2305/IUCN.UK.2009.RLTS. T61550A12514105.en. Accessed on 17 February 2017.
- Boretto, J.M., Cabezas-Cartes, F. & Ibargüengoytía, N.R. (2015) Energy allocation to growth and reproduction in a viviparous lizard endemic to the highlands of the Andes, Argentina. *J. Zool.*, 297, 77-86.
- Bülbül, U., Kurnaz, M., Eroğlu, A.İ., Koç, H. & Kutrup, B. (2016a) Age and growth of the red-bellied lizard, *Darevskia parvula*. Anim. Biol., 66, 81-95.
- Bülbül, U., Kurnaz, M., Eroğlu, A.İ., Koç, H. & Kutrup, B. (2016b) Body size and age structure of the endangered Clark's lizard (*Darevskia clarkorum*) populations from two different altitudes in Turkey. *Amphibia-Reptilia*, 37, 450-456.
- Cabezas-Cartes, F., Boretto, J.M. & Ibargüengoytía, N.R. (2015) Age, growth and life-history parameters of an endemic vulnerable lizard from Patagonia, Argentina. *Herpetol. J.*, 25, 215-224.
- Caley, M.J. & Schwarzkopf, L. (2004) Complex growth rate evolution in a latitudinally widespread species. *Evolution*, 58, 862-869.
- Castanet, J. (1994) Age estimation and longevity in reptiles. Gerontology, 40, 174-192.
- Castanet, J. & Roche, E. (1981) Détermination de l'âge chez le lézard des murailles, *Lacerta muralis* (Laurenti, 1768) au moyen de la squelettochronologie. *Rev. Suisse Zool.*, 88, 215-226.
- Castanet, J. & Smirina, E.M. (1990) Introduction to the skeletochronological method in amphibians and reptiles. Ann. Sci. Nat. Zool., 11, 191-196.
- Christian, K.A. (1986) Physiological consequences of nightime temperature for a tropical herbivorous lizard (*Cyciura nubila*). *Can. J. Zool.*, 64, 836-840.

- Conover, D.O., Duffy, T.A. & Hice, L.A. (2009) The covariance between genetic and environmental influences across ecological gradients: reassessing the evolutionary significance of countergradient and cogradient variation. *Ann. NY Acad. Sci.*, 1168, 100-129.
- Cox, R.M., Skelly, S.L. & John-Alder, H.B. (2003) A comparative test of adaptive hypotheses for sexual size dimorphism in lizards. *Evolution*, 57, 1653-1669.
- Dunham, A.E. (1978) Food availability as a proximate factor influencing individual growth rates in the iguanid lizard Sceloporus merriami. Ecology, 59, 770-778.
- Dunham, A.E., Grant, B.W. & Overall, K.L. (1989) Interfaces between biophysical and physiological ecology and the population ecology of terrestrial vertebrate ectotherms. *Phys. Zool.*, 62, 335-355.
- Eroğlu, A.İ., Bülbül, U. & Kurnaz, M. (2017a) Age structure and growth in a Turkish population of the Crimean wall lizard, *Podarcis tauricus* (Pallas, 1814) (Squamata: Sauria: Lacertidae). *Herpetozoa*, 29, 125-133.
- Eroğlu, A.İ., Bülbül, U. & Kurnaz, M. (2017b) Age structure and growth in a Turkish population of the Italian wall lizard *Podarcis siculus* (Rafinesque-Schmaltz, 1810) (Reptilia: Lacertidae). Acta Zool. Bulg., 69, 209-214.
- Fairbairn, D.J., Blanckenhorn, W.U. & Szekely, T. (2007) Sex, Size and Gender Roles: Evolutionary Studies of Sexual Dimorphism. Oxford University Press, Oxford, UK.
- Fox, S.F. (1983) Fitness, home-range quality, and aggression in Uta stansburiana. In: R.B. Huey, E.R. Pianka & T.W. Schoener (Eds) Lizard Ecology: Studies of a Model Organism, pp. 149-168. Harvard University Press, Cambridge, MA, USA.
- Gadgil, M. & Bossert, W.H. (1970) Life historical consequences of natural selection. Am. Nat., 104, 1-24.
- Grant, B.W. & Dunham, A.E. (1988) Thermal imposed time constraints on the activity of the desert lizard *Sceloporus merriami*. *Ecology*, 69, 167-176.
- Guarino, F.M., Gia, I.D. & Sindaco, R. (2010) Age and growth of the sand lizards (*Lacerta agilis*) from a high alpine population of north-western Italy. *Acta Herpetol.*, 5, 23-29.
- Gül, S., Özdemir, N., Kumlutas, Y. & Ilgaz, Ç. (2014) Age structure and body size in three populations of *Darevskia rudis* (Bedriaga, 1886) from different altitudes (Squamata: Sauria: Lacertidae). *Herpetozoa*, 26, 151-158.
- Gül, S., Özdemir, N., Avcı, A., Kumlutas, Y. & Ilgaz, Ç. (2015) Altitudinal effects on the life history of the Anatolian lizard (*Apathya cappadocica*, Werner 1902) from southeastern Anatolia, Turkey. *Turk. J. Zool.*, 39, 507-512.
- Halliday, T.R. & Verrell, P.A. (1988) Body size and age in amphibians and reptiles. *J. Herpetol.*, 22, 253-265.
- Herrel, A., Moore, J.A., Bredeweg, E.M. & Nelson, N.J. (2010) Sexual dimorphism, body size, bite force and male mating success in tuatara. *Biol. J. Linn. Soc.*, 100, 287-292.
- In den Bosch, H.A.J. & Bout, R.G. (1998) Relationships between maternal size, egg size, clutch size, and hatchling size in European lacertid lizards. *J. Herpetol.*, 32, 410-417.
- James, C.D. (1991) Growth rates and ages at maturity of sympatric scincid lizards (*Ctenotus*) in central Australia. J. Herpetol., 25, 284-295.
- Jenssen, T.A. & Andrews, R.M. (1984) Seasonal growth rates in the Jamaican lizard, Anolis opalinus. J. Herpetol., 18, 338-341.
- John-Alder, H.B. & Cox, R.M. (2007) The development of sexual size dimorphism in sceloporus lizards: testosterone as a bipotential growth regulator. In: D.J. Fairbairn, W.U. Blanckenhorn & T. Székely (Eds) Sex, Size and Gender Roles: Evolutionary Studies of Sexual Size Dimorphism, pp. 195-204. Oxford University Press, London, UK.

- Kaliontzopoulou, A., Carretero, M.A. & Llorente, G.A. (2007) Multivariate and geometric morphometrics in the analysis of sexual dimorphism variation in *Podarcis* lizards. J. Morph., 268, 152-165.
- Kleinenberg, S.E. & Smirina, E.M. (1969) On the method of determination of age in amphibians. Zool. Zh., 48, 1090-1094 [in Russian].
- Kolarov, T.N., Vljevic, L.K., Polovic, L.D.G. & Kalezic, M.L. (2010) The body size, age structure and growth pattern of the endemic Balkan mosor rock lizard (*Dinolacerta mosorensis* Kolombatovich, 1886). Acta Zool. Hung., 56, 55-71.
- Lemos-Espinal, J.A. & Ballinger, R.E. (1995) Ecology of growth of the high altitude lizard Sceloporus grammicus on the eastern slope of Iztaccihuatl Volcano, Puebla, Mexico. Trans. Nebraska Acad. Sci., 22, 77-85.
- Lovich, J.E. & Gibbons, J.W. (1992) A review of techniques for quantifying sexual size dimorphism. Growth Dev. Aging, 56, 269-281.
- Lu, H.L., Xu, C.X., Jin, Y.T., Hero, J.M. & Du, W.G. (2017) Proximate causes of altitudinal differences in body size in an agamid lizard. *Ecol. Evol.*, 8, 645-654.
- Newman, S.J. & Dunk, I.J. (2002) Growth, age validation, mortality, and other population characteristics of the red emperor snapper *Lutjanus sebae* (Cuvier, 1828), off the Kimberley Coast of north-western Australia. *Estuar. Coast. Shelf Sci.*, 55, 67-80.
- Olsson, M., Shine, R., Wapstra, E., Ujvari, B. & Madsen, T. (2002) Sexual dimorphism in lizard body shape: the roles of sexual selection and fecundity selection. *Evolution*, 56, 1538-1542.
- Pianka, E.R. (1970) On r- and K-selection. Am. Nat., 102, 592-597.
- Rahman, M.D.H. & Tachihara, K. (2005) Age and growth of *Sillago aeolus* in Okinawa Island, Japan. J. Oceanogr., 61, 569-573.
- Roitberg, E.S. & Smirina, E.M. (2006a) Adult body length and sexual size dimorphism in *Lacerta agilis boemica* (Reptilia, Lacertidae): between-year and interlocality variation. In: C. Corti, P. Lo Cascio & M. Biaggini (Eds) *Mainland and Insular Lacertid Lizards: a Mediterranean Perspective*, pp. 175-187. Firenze University Press, Florence, Italy.
- Roitberg, E.S. & Smirina, E.M. (2006b) Age, body size and growth of *Lacerta agilis boemica* and *L. agilis strigata*: a comparative study of two closely related lizard species based on skeletochronology. *Herpetol. J.*, 16, 133-148.
- Ryser, J. (1988) Determination of growth and maturation in the common frog, *Rana temporaria*, by skeletochronology. J. Zool. Lond., 216, 673-685.
- Shine, R. & Charnov, E.L. (1992) Patterns of survival, growth, and maturation in snakes and lizards. Am. Nat., 139, 1257-1269.
- Sillero, N., Campos, J., Bonardi, A., Corti, C., Creemers, R., Crochet, P.-A., Isailovic, J.C., Denoël, M., Ficetola, G.F., Gonçalves, J., Kuzmin, S., Lymberakis, P., de Pous, P., Rodríguez, A., Sindaco, R., Speybroeck, J., Toxopeus, B., Vieites, D.R. & Vences, M. (2014) Updated distribution and biogeography of amphibians and reptiles of Europe. *Amphibia-Reptilia*, 35, 1-31.
- Sinsch, U. (2015) Skeletochronological assessment of demographic life-history traits in amphibians. *Herpetol. J.*, 25, 5-13.
- Sinsch, U., Pelster, B. & Ludwig, G. (2015) Large-scale variation of size- and age-related life-history traits in the common frog: a sensitive test case for macroecological rules. *J. Zool.*, 297, 32-43.
- Strijbosch, H., Bonnemayer, J.J.A.M. & Dietvorst, P.J.M. (1980) The northernmost population of Podarcis muralis (Lacertilia, Lacertidae). Amphibia-Reptilia, 1, 161-172.
- Tao, Y., Mingru, C., Jianguo, D., Zhenbin, L. & Shengyun, Y. (2012) Age and growth changes and population dynamics of the black pomfret (*Parastromateus niger*) and the frigate tuna (*Auxis thazard thazard*), in the Taiwan strait. *Lat. Am. J. Aquat. Res.*, 40, 649-656.

- Tinkle, D.W., Wilbur, A.M. & Tilley, S.J. (1970) Evolutionary strategies in lizard reproduction. *Evolution*, 24, 55-74.
- Tokarz, R.R. (1985) Body size as a factor determining dominance in stage agonistic encounters between male brown anoles (*Anolis sagrei*). *Anim. Behav.*, 33, 746-753.
- Vogrin, N. (1999) Preliminary note on the morphometric differences between two populations of *Podarcis muralis muralis* (Laurenti, 1768) and *Podarcis muralis maculiventris* (Werner, 1891) in Slovenia. *Nat. Croat.*, 8, 325-329.
- Vollono, C. & Guarino, F.M. (2002) Analisi scheletrocronologica in alcune specie di Anfibi e rettili del Parco Regionale del Matese. In: G. Odierna & F.M. Guarino (Eds) *I Vertebrati Ectotermi del Parco Regionale del Matese*, pp. 163-171. Centro Stampa dell'Universita degli Studi di Napoli Federico II, Naples, Italy.
- Wapstra, E., Swan, R. & O'Reilly, J.M. (2001) Geographic variation in age and size at maturity in a small Australian viviparous skink. *Copeia*, 2001, 646-655.
- Williams, G.C. (1966) Adaptation and Natural Selection. Princeton University Press, Princeton, NJ, USA.