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Age, growth and survival rate in two populations of *Darevskia derjugini* (Nikolsky, 1898) from different altitudes (Squamata: Sauria: Lacertidae)

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Abstract
We investigated age structure, age at sexual maturity, lifespan, growth and survival rate and adult life expectancy (as demographic life-history traits) as well as body size of two *Darevskia derjugini* (Artvin lizard) populations from different altitudes, using skeletochronology. Our findings indicated that age upon attaining sexual maturity was two or three years in the low-altitude population (Fındıklı) while it was three years in the high-altitude population (Murgul) for both sexes. The maximum longevity was seven years in the high-elevation site while it was six years in the low-elevation site. As reported for many lizards, we found a significant positive relationship between age and body size within each sex of Artvin lizard at both altitudes. High- and low-altitude populations did not differ in age structure, survival rates, adult life expectancy and body size. Rather than the effect of altitude, which is hard to compare without replication of other low and high altitude populations, the fact that these two populations have similar growth rates and the similarity of local conditions (food availability and predator density) may indicate similarity between the two regions.

Keywords
Age; Artvin lizard; body size; elevation; sexual dimorphism; skeletochronology

Introduction

In studies conducted without knowing the age of animals, data accumulation is quite low because many important characteristics of a population's life history can be explained by knowing the age and growth rate of each individual in that population (Roff, 1992; Stearns, 1992). Tinkle (1969) and Tinkle et al. (1970) identified lizards in two groups based on life history traits: (1) species with a small body size

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that have a short life, rapid growth rate, small clutch size, multiple clutches within a season, oviparity, smaller snout-vent length (SVL) at birth, and an association with tropical environments, versus (2) species with a large body size that are long-lived, with a slow growth rate, a single clutch during the reproductive season, hatchlings with small/larger size at birth, oviparity or viviparity and an association with temperate or tropical environments (reviewed in Cruz-Elizalde & Ramírez-Bautista, 2016). Whether organisms are long-lived or short-lived is closely related to factors such as density, fecundity and selection type (Stearns, 1984; Le Galliard et al., 2010). For example, density-independent regulation (*r*-selection), was supposed to lead to short-lived organisms with high fecundity; density-dependent regulation, i.e., *K*-selection, was supposed to lead to long-lived organisms with low fecundity (Tinkle et al., 1970; Stearns, 1984; Dunham et al., 1988; Mesquita et al., 2016).

Life-history traits are often associated with patterns of growth, development, reproductive investment and survival and can be studied at the level of individuals, populations and species (Ramírez-Bautista et al., 2013, 2016a; Liao et al., 2016). In most ectotherms such as lizards with indeterminate growth, life-history characteristics show distinct specific geographical variation consistent with the variation of some features of the environment (Cabezas-Cartes et al., 2015; Ramírez-Bautista et al., 2016b; Comas et al., 2019; Torres Barragán et al., 2020). An environmental factor such as variation in quantity and quality of food and temperature differences among environments (Dunham et al., 1988; Adolph & Porter, 1993; Mesquita & Colli, 2010) can easily create stress and impacts on life history (e. g., growth rate, age at maturity, body size, clutch/litter size, among others) of individuals (Mesquita et al., 2016). Thus, it is quite easy to observe the impact of the environment on physical development at the population level (Mugabo et al., 2010). Altitude, one of these geographic variations, is a commonly used factor to show differences in mean age, growth, longevity, size at sexual maturity and sexual dimorphism between reptile populations (Gutiérrez et al., 2013; Ramírez-Bautista et al., 2015; Bülbül et al., 2016; Altunışık et al., 2017; Kurnaz et al., 2018; Comas et al., 2019; Cruz-Elizalde et al., 2020). Knowing such life history traits of these organisms enables us to learn about their ecology and thus to carry out other studies (Gadsden & Casteñada, 2013).

Skeletochronology studies the bone resting lines (LAG: Line of Arrested Growth), which are lines formed in the bone tissue as a result of the reduction of bone growth (Gibbons & McCarthy, 1983; Castanet & Baez, 1991; Pal et al., 2009). This is a widely preferred method for investigating population age structure of many ectothermic species without sacrificing specimens (Gutiérrez et al., 2013; Altunışık, 2017; Eroğlu et al., 2018; Yıldırım et al., 2019; Beşer et al., 2019).

The Artvin lizard, *Darevskia derjugini* (Nikolsky, 1898) is a member of the Lacertidae family which is composed by six subspecies (Ryabinina et al., 2002; Tuniyev & Ostrovskikh, 2006). The distribution of these taxa is limited to the Black Sea coastal regions of Georgia, Russia, Azerbaijan and Turkey (provinces of Artvin, Rize, Trabzon, Giresun) (IUCN, 2020; supplementary fig. S1). *Darevskia derjugini*

Table 1.
Descriptive statistics of growth rate (mm per year), growth coefficient (k), ESP and SR in the studied populations of *Darevskia derjugini* from Fındıklı and Murgul (Turkey). Abbreviations: n, number of specimens; SE, standard error of the mean; SVL_{max}, maximum snout-vent length; ESP, adult life expectancy; SR, survival rate; SDI, sexual dimorphism index.

Population	Altitude (m)	Sex	n	Growth rate ± SE	k	SVL_{max}	ESP	SR	SDI
Fındıklı	203	Males	17	2.87 ± 0.66	0.18	62.39	4.62	0.75	0.065
		Females	19	2.72 ± 0.57	0.22	62.05	4.00	0.71	
Murgul	1156	Males	13	3.69 ± 0.65	0.17	69.79	4.50	0.75	0.079
		Females	17	2.02 ± 0.77	0.26	58.71	4.19	0.72	

occurs at an elevation of 1700 m above sea level and is considered as Near Threatened by the IUCN since 2009 (IUCN, 2020). Being a relatively short-lived species, *D. derjugini* is a saxicolous and oviparous lizard. Oviposition occurs from the first decade of June till the third decade of August and clutches contain from two to eight eggs with sizes of 9.3-14.8 × 5.7-7.1 mm and weights of 0.23-0.28 g (Kidov et al., 2014).

Little is known about demography and life history on the Artvin lizard (Orlova & Smirina, 1981, 1983; Kurnaz et al., 2018). In order to understand the effects of environmental parameters like altitude, we elucidate some demographic life-history traits such as age structure based on body size, mean age, age upon attaining sexual maturity, lifespan, growth, and survival rate of two populations of *D. derjugini* from different elevations by using the skeletochronological method. Moreover, we discuss the similarities and dissimilarities between our species and closely related ones that have been previously studied.

Material and methods

Study area and sampling

Artvin lizards were sampled from two populations living at different altitudes, one in Fındıklı (41°27′92″N, 41°24′24″E; 203 m a.s.l., province of Rize, northeastern Turkey), and the other in Murgul (41°26′34″N, 41°59′12″E, 1156 m a.s.l., province of Artvin, northeastern Turkey) during the breeding season (between May and August) of 2018. All specimens used in this study were treated humanely and ethically following permission to perform the study by Recep Tayyip Erdoğan University's local ethics committee (decision number: RTEÜ.2016/49).

A total of 66 (30 males, 36 females) adult individuals from two different populations of the *D. derjugini* species were used (table 1). Thirty-six (17 males, 19 females) of these samples were obtained from Fındıklı and 30 (13 males, 17 females) from the Murgul population. The presence/absence of a hemipenis retracted in the hemipenial sack at the base of the tail and direct examination of secondary sexual characters such as dark blue stains on the margins of the ventral plates and a

black color of the lateral bands and the wider tail base present in males in particular were used to assess individuals' sex (Kurnaz et al., 2018). The specimens were caught while basking on the stone heaps or hiding in the grass. Both districts show a typical Black Sea climate; while in Fındıklı half of the year is rainy and the humidity is quite high, Murgul has a more rugged land structure. Murgul is also located slightly further inland and therefore the humidity is slightly lower, and it receives less rainfall than the Fındıklı district. Both habitats of this lizard are forested areas of mountainous regions, so lizards can be seen in meadows and grassy grounds, sometimes on stones or walls. In the habitat of Fındıklı, *D. derjugini* lives in sympatry with *D. parvula*.

The Artvin lizards were collected by hand and their SVL was measured to the nearest 0.01 mm using a digital compass vernier caliper (Bülbül et al., 2016; Altunışık & Eksilmez, 2018). Then the longest toe (fourth), including the first and second phalanges, of the right hind limb was taken in all specimens. These bones were fixed in 10% formalin and preserved in 70% ethanol solution for subsequent histological analysis. After sampling, all individuals were released into their original habitats (Guarino et al., 2010; Altunışık, 2018; Yıldırım et al., 2019).

Age determination

We determined age of all 66 adult specimens by skeletochronology. The skeletochronological analysis (Smirina, 1994), which is based on counting the dark-stained rings, i.e., lines of arrested growth (LAG) that occur as a consequence of reduced bone growth in the winter season, was adapted from its standard procedure as previously used by Altunışık & Eksilmez (2018). Thus, each phalange, which had been preserved in 70% ethanol solution, was bathed in distilled water for 24 h and decalcified in 5% HNO_3 (nitric acid) solution for about 1-2 hours depending on the bone size. Phalangeal cross-sections of 16 μm thickness were taken using a freezing microtome (Shandon Cryostat, Burladingen, Germany) and these sections were immersed in Erlich's hematoxylin stain for 15 minutes (Altunışık, 2017). Then, with a small medullary cavity were selected and placed in water-based mounting medium solution. All cross-sections were examined under an Olympus BX51 light microscope (Olympus, Tokyo, Japan) at 10× and 20× magnifications and photos of the selected sections were obtained with a camera (Pixera, Tokyo, Japan) connected to the mentioned microscope (Altunışık & Eksilmez, 2018). Both authors examined all photos and counted and verified the number of LAGs independently (Eroğlu et al., 2018).

Statistical analyses

We used parametric tests (e.g., Student's t-test) when the data met the assumptions (for normality: Shapiro-Wilks test; for homogeneity of variance: Levene test). We used Pearson's correlation coefficient to test the relationship between the life history

parameters and performed statistical analysis using SPSS 22 (IBM Corp., Armonk, NY, USA) at a significance level of $\alpha < 0.05$.

We evaluated the sexual dimorphism index (SDI) with respect to Lovich & Gibbons's (1992) formula:

$$\text{SDI} = \left(\frac{\text{size of larger sex}}{\text{size of smaller sex}} \right) \pm 1$$

(SDI < 0 when males are larger than females; SDI > 0 when females are larger than males).

We assumed that age upon attaining sexual maturity is the lowest age determined among the breeding specimens. We calculated the survival rates with respect to a formula generated by Robson & Chapman (1961):

$$\text{SR} = \frac{T}{(R + T - 1)}$$

According to this formula, a constant survival rate is assumed for all the sampling individuals and age classes where $T = N_1 + 2N_2 + 3N_3 + \ldots$, $R = \Sigma N_i$, and N_i is the number of individuals in age group i. SR refers to the finite annual survival rate.

The adult life expectancy (ESP) that indicates the expected longevity of individuals that are sexually mature was calculated based on Seber's (1973) formula:

$$\text{ESP} = 0.5 + \frac{1}{1 - \text{SR}}$$

where SR is the survival rate.

While estimating growth patterns, we used the Von Bertalanffy growth model which was previously used in various studies on lizard species (Roitberg & Smirina, 2006a; Guarino et al., 2010; Bülbül et al., 2016). A generalized formula of Von Bertalanffy growth is:

$$\text{SVL}_t = \text{SVL}_{\max}\left(1 - e^{-k(t-t0)}\right)$$

where SVL_t is size at age t, $\text{SVL}_{\max}$ is a parameter that expresses the asymptotic maximum SVL, the growth coefficient k defines the form of the curve and, thus, the rate at which the SVLmax is reached, e is a constant, and t_0 is the age at hatching, which corresponds to the beginning of the growth interval. Since the information on the body length at hatching is not available for the populations of Artvin lizard (a short-life species) under study, we accepted size at hatching ($\text{SVL}_{t0} = 22.9$ mm) as indicated by In Den Bosch & Bout (1998). We computed the growth rates by using the equation $r = k\ (\text{SVL}_{\max} - \text{SVL}_t)$ and estimated parameters $\text{SVL}_{\max}$ and k by means of an MS Excel program.

Results

Results of SVL and age in the two populations of *Darevskia derjugini* are summarized in supplementary table S1. In fig. 1, a cross-section of the second phalangeal

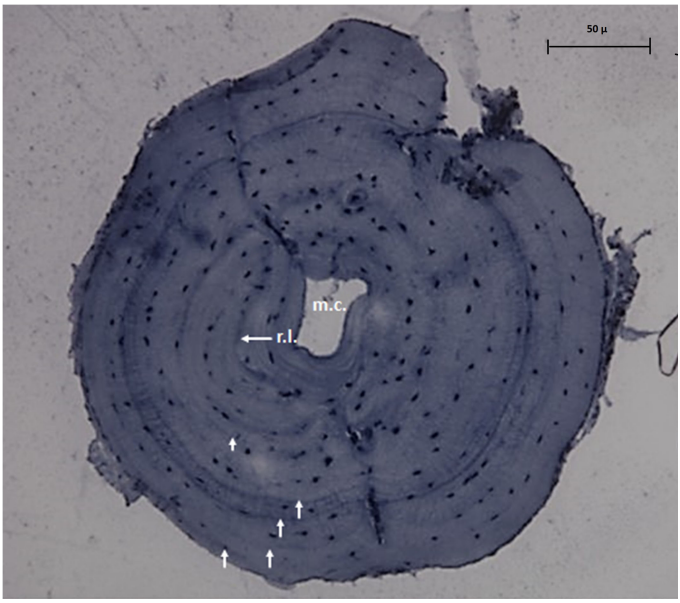


Figure 1. Cross-section (20 μm thick) at the diaphysis level of the second phalangeal bone of the toe of a female *Darevskia derjugini* individual from the Fındıklı population. Abbreviations: m.c., medullary cavity; r.l., resorption line.

bone of a female *D. derjugini* individual from the Fındıklı population is shown; a periostal growth zone and thin hematoxylinophilic lines of arrested growth, which serve as an equivalent for the winter season, were present in all cross-sections. These LAGs were relatively easy to compute in the periosteal zone. The oldest females and males were seven and six years old, respectively, in the high-altitude and six years old in the low-altitude populations (fig. 2). When the data are evaluated collectively, sexual dimorphism was observed between males and females of the Artvin lizard in terms of SVL (independent-sample t-test, $t = -4.491$ df $= 64$; $P < 0.001$). The sexual dimorphism index (SDI) was determined as 0.072, indicating a female bias.

In the Fındıklı population, the age ranged from two to six years in both males (mean: 3.94 ± 1.19) and females (mean: 4.36 ± 0.95) (supplementary table S1). There is no statistical difference between female and male individuals with respect to mean age in this low-altitude site (t-test, $t = -1189$, df $= 34$, $P > 0.05$). As can be seen in fig. 2A and supplementary table S2, the fourth age group is the most common age group in the population with 33.33% ($n = 12$). The age upon attaining sexual maturity was determined to be 2-3 years for both sexes. The adult life expectancy, the expected longevity of individuals having reached sexual maturity, was calculated as 4.62 years for males and 4.00 years for females. The survival rate was calculated as 0.75 and 0.71 for males and females, respectively.

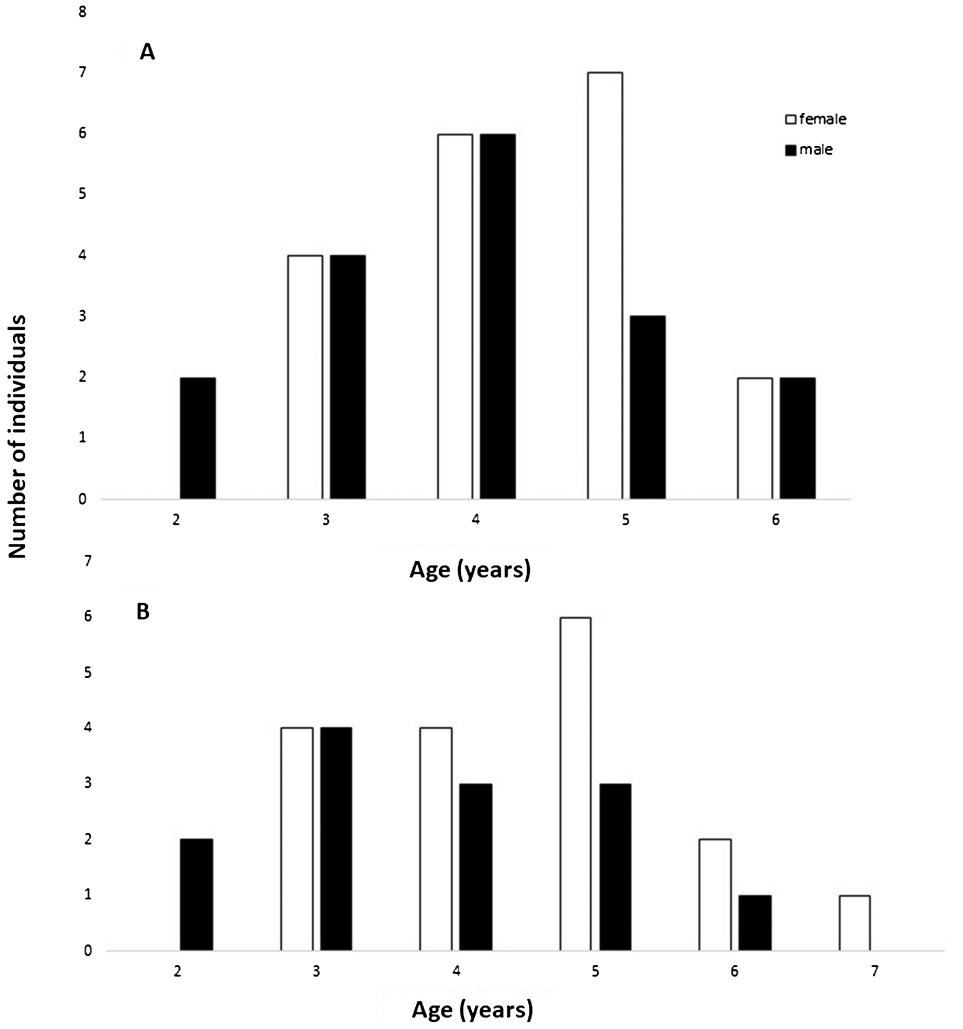


Figure 2. Age distribution of *Darevskia derjugini*'s two populations, Fındıklı (A) and Murgul (B).

Results of the Independent t-test ($t = -3056$, df $= 34$, $P < 0.01$) showed that females of the Fındıklı population (mean SVL $= 49.95$ mm) were larger than males (mean SVL $= 46.87$ mm). Intersexual disparity in body size was female-biased (SDI: 0.065). There was a significant correlation between SVL and age in males ($r = 0.721$, $p < 0.01$) and females ($r = 0.730$, $P < 0.001$). As expected, the computed asymptotic SVL (SVL_{asym}, males: 62.39 mm; females: 62.05 mm) was higher than the maximum SVL recorded in this population for both males and females. The growth parameters predicted by means of the Von Bertalanffy equation indicate a fit that reflects the real relationship between age and SVL (fig. 3A). Growth rates of the males and females were similar in the Fındıklı population ($t = 0.359$, df $=$ 7, $P > 0.05$; table 1).

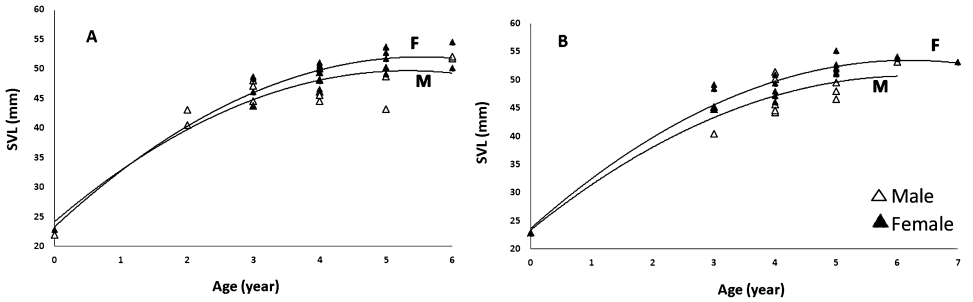


Figure 3. Relationship between age and body size (snout-vent length, SVL of the lowland population Fındıklı (A), and the highland population Murgul (B).

In the Murgul population, the age ranged from three to six years (mean: 4.08 ± 0.95) in males and three to seven years (mean: 4.59 ± 1.12) in females (supplementary table S1). No statistical disparity was detected between males and females with respect to mean age in this high-altitude population (t-test, $t = -1318$, df = 28, $P > 0.05$). The fifth age group is the most common age group in this population with 30% ($n = 9$), as can be seen in fig. 2B and supplementary table S2. The age of reaching sexual maturity was determined to be three years for both male and female individuals. The adult life expectancy, the expected longevity of individuals having reached sexual maturity, was calculated as 4.50 years for males and 4.19 years for females. The survival rate was calculated as 0.75 and 0.72 for males and females, respectively.

Female individuals were significantly larger than male individuals (Student's t-test, SVL: $t = -3.191$, df = 28, $P < 0.01$), and SDI was computed as 0.079 (table 1). The correlation between age and SVL was statistically significant in both males ($r = 0.707$, $P < 0.01$) and females ($r = 0.785$, $P < 0.001$). As in the lowland population, the computed asymptotic SVL (SVL_{asym}, males: 69.79 mm; females: 58.71 mm) was higher than the maximum SVL recorded in the highland population for both sexes. The growth parameters predicted by means of the Von Bertalanffy equation indicated a fit that reflects the real relationship between body size and age (fig. 3B). Males of the Murgul population (highland) had significantly higher growth rates than those of females ($t = 3.459$, df = 7, $p < 0.05$). Associated descriptive statistics are given in the table (table 1).

When comparing both populations, neither male (M) nor female (F) high-altitude individuals nor both (M + F) individuals together were significantly different from their counterparts from the low altitude with regard to mean age (M: $t = 0.335$, df = 28, $P > 0.05$; F: $t = 0.635$, df = 34, $P > 0.05$; M + F: $t = 0.753$, df = 64, $P > 0.05$) and SVL (M: $t = -0.047$, df = 28, $P > 0.05$; F: $t = 0.632$, df = 34, $P > 0.05$; M + F: $t = 0.501$, df = 64, $P > 0.05$). In addition, no significant difference was determined between the two populations with respect to age structure ($\chi^2_4 = 6.641$, $p = 0.156$). However, the growth coefficient of females was higher in the highland site as compared to the lowland site (k, Murgul population: 0.26;

Fındıklı population: 0.22) but the growth coefficient of males was lower (k, Murgul population: 0.17; Fındıklı population: 0.18). Growth rates of both sexes did not differ between the two populations (Males: t-test; $t = -1.845$, df = 7, $P > 0.05$; Females: t-test; $t = 1.517$, df = 7, $P > 0.05$). However, SDI of the lowland population was found to be lower than that of the highland population (Murgul: 0.079; Fındıklı: 0.065).

Discussion

Although there have been some studies on the age structure of *D. derjugini* from different environments, none of them have explored the adult life expectancy and survival rate of Artvin lizard living in Turkey and as far as we are aware, this is the first survey to document them. In the present study, we revealed the demographic structure of two *D. derjugini* populations living at different altitudes by the skeletochronology method and obtained information about variation in some life-history characteristics (e.g., growth rates, adult life expectancy, survival rates, body size differences). The variation in life-history evolution is influenced by two main components, the environment (e.g., resources such as food and space; temperature) and genetics (evolutionary history) (Ballinger, 1979; Dunham & Miles, 1985; Roff, 1992; Stearns, 1992; Ramírez-Bautista et al., 2015, 2016b; Torres Barragán et al., 2020).

Generally, individuals from higher-elevation sites or cold climates live longer (Guarino et al., 2010; Bülbül et al., 2016; Eroğlu et al., 2018) than those from lower sites or warmer climates. We may have found a similar trend, although it was not shown to be statistically significant at it is hard to properly compare without information about more low and high altitude populations. Also, in a previous study, researchers did not report any differences between high and low populations in terms of longevity, mean age, age at sexual maturity and growth rates (Kurnaz et al., 2018). Orlova & Smirina (1981) found the maximum lifespan to be 5-6 years for female specimens and four years for male specimens of *D. derjugini*. In our study, we found relatively higher lifespan values: six years for the low-altitude population (both sexes) and 6-7 years (for males and females, respectively) for the high-altitude population. Another previous study (Kurnaz et al., 2018) reported higher longevity values than our values: maximum age was eight years in females and seven years in males of the high-elevation site while it was seven years in both sexes at the low-elevation site. Differences in terms of longevity among different populations are probably related to local conditions (e.g., food availability, temperature) (Adolph & Porter, 1993). In addition, the fact that there was a lower annual growth rate in the populations we studied as compared to a previous study (Kurnaz et al., 2018) may have caused the relatively shorter lifespan.

We have evidence for both larger and smaller body size, depending on the species and populations analysed (Roitberg & Smirina, 2006a; Kurnaz et al., 2018; Beşer et al., 2020). It is known that proximal variations arising from food availability occur

in the life history characteristics of certain species (Ballinger, 1977, 1979). In our study, when comparing the body size between the high-altitude and low-altitude sites, the mean SVL of the Murgul population (high altitude) was not significantly greater than that of the Fındıklı population (low altitude). The fact that we did not observe any difference in terms of food availability (i.e., quality and quantity of food; Iraeta et al., 2006; Mugabo et al., 2010) and predator density between the two habitats makes it easier for us to explain the similarity between some life history traits of these two populations.

In addition, size-dependent sexual dimorphism is common among lizards and males are larger than females in the majority of species (Fitch, 1981). Contrary to this phenomenon, this study and also previous studies (Orlova & Bischoff, 1984; Kurnaz et al., 2018) support that females of the Artvin lizard are larger than males. However, in the congeneric *D. parvula* (Bülbül et al., 2016) and *D. dryada* (Altunışık & Eksilmez, 2018) sexual size dimorphism was observed to be male-biased. The potential causes of distinct SSD patterns between and within species are diverse (Roitberg, 2007; Cox et al., 2007) and include differentiated evolutionary responses to ecological conditions in males and females. Besides, sexual size dimorphism (SSD) is formed by discrepancy in growth rates which depend upon food abundancy and temperature conditions (Adolph & Porter, 1993) in several lizard species (John-Alder & Cox, 2007; Tomašević Kolarov et al., 2010). In summary, populations inhabiting colder habitats were expected to grow faster (Caley & Schwarzkopf, 2004; Conover et al., 2009) and lizards were observed to grow faster at high elevations due to an environment boosting growth by increased precipitation levels (Iraeta et al., 2006). Accordingly, in our study the growth rates were different between males and females in the highland population, but not in the lowland population. The pattern of female-biased sexual dimorphism is usually explained by the female fecundity hypothesis (e.g., clutch size and egg size; Anderson, 1994; Vitt & Caldwell, 2009). Since our data about initial characteristics of populations such as sexual selection pressure, clutch/litter size, and egg size are fairly limited they are not sufficient to understand the main reason for this particular female-biased SSD. Apart from different possible causes, this could be a result of diverse growth rate of males and females, as mentioned above.

Lizards that live in colder climates can delay age when sexual maturity is attained, and possibly before reaching maturity invest energy in their growth and care to maximize future breeding (Roitberg & Smirina, 2006b). In the present study, the high-elevation site (Murgul) was subjected to cooler temperature conditions (18.9°C vs. 19.8°C during the activity periods) than the low-elevation site (Fındıklı). Correspondingly, longevity (7 vs 6 years) and age at maturity (3 vs. 2-3 years) were found to be slightly higher in the Murgul population. Individuals from the highland population continue to grow and reach sexual maturity at a later age. This delayed sexual maturity, in turn, enables the lizards to maintain longer periods of high growth rate and therefore to reach larger body sizes. Similar to our findings, Kurnaz et al. (2018) reported age at sexual maturity as three years in 80% and

two years in 20% of the highland population of Artvin lizard. In addition to this, in the studies of Kurnaz et al. (2018; in a lowland population) and Orlova & Smirina (1983), age of reaching sexual maturity was reported as one or two years. Several studies with ectotherms show that age increases with increased body size (Halliday & Verrell, 1988; Piantoni et al., 2006; Kurnaz et al., 2018; Beşer et al., 2020). This tendency is also in line with our findings and a positive relationship was found between age and SVL for both sexes.

In conclusion, we generated data on longevity, age structure, age of sexual maturity, growth rate, body size, adult life expectancy and survival rate of two *D. derjugini* populations from different altitudes, using skeletochronology. High- and low-altitude populations showed no differences in age structure, survival rates, ESP or body size. Rather than the impact of altitude, the fact that these two populations have similar growth rates and the similarity of local conditions (food availability and predator density; Halit Eksilmez, pers. com.) may explain the similarity between the two regions. The information given about some life history characteristics (e.g., age structure, survival and growth rate) of a near-threatened species in this study may contribute to effective conservation management in the future.

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Supplementary material

Supplementary material is available online at:
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