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Article in *Canadian Journal of Zoology* · February 2022

DOI: 10.1139/cjz-2021-0197

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Canadian Journal of Zoology

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| | |
|---|--|
| Journal: | <i>Canadian Journal of Zoology</i> |
| Manuscript ID | cjz-2021-0197.R2 |
| Manuscript Type: | Article |
| Date Submitted by the Author: | 10-Jan-2022 |
| Complete List of Authors: | ALTUNIŞIK, Abdullah; Recep Tayyip Erdoğan University, Biology Department YILDIZ, Mehmet Zülfü; Adıyaman University, Department of Biology ÜÇEŞ, Fatma; Adıyaman University, Department of Biology Bozkurt, Mehmet Akif; Özel Sınay Anadolu High School Çamlıyayla Neighborhood SÖMER, Mehtap; Adıyaman University, Department of Biology |
| Is your manuscript invited for consideration in a Special Issue?: | Not applicable (regular submission) |
| Keyword: | Bergmann rule, GROWTH < Discipline, sexual dimorphism, AGE < Discipline, SURVIVAL RATE < Discipline, Mediodactylus heterocercus, Asia Minor thin-toed gecko |
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Altitude impacts body size but not age in a gecko

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Running Title: Altitudinal variation in a gecko

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Abstract

Animals' age and size-related life-history traits are influenced by a variety of factors. In connection with climate, the effect of altitude on demographic parameters may differ among different populations of the same species. In the present study, it was analyzed that how body size and longevity of the Asia Minor thin-toed gecko, *Mediodactylus heterocercus* (Blanford, 1874), vary along with an elevational gradient in Turkey. For this purpose, a total of 138 (52 males, 75 females, and 11 young) *M. heterocercus* specimens from 11 different populations were analyzed. Populations at inter-mediate altitude had shorter lifespans than in both low and high elevations (marginal environments). Furthermore, the adult life expectancy (ESP), which indicates the expected lifespan of individuals having sexual maturity, was higher in high altitude populations (ESP: 6.59 years) than in intermediate populations (ESP: 5.40 years) and low altitude populations (ESP: 6.01 years). The results of the study suggest that Asia Minor thin-toed geckos' body size increases with altitude, but their age does not.

Key words: The Asia Minor thin-toed gecko, *Mediodactylus heterocercus*, Bergmann rule, growth, sexual dimorphism, survival rate

1. Introduction

The habitat is a fundamental determinant of diversification and evolution. Habitats with optimal or close to optimal conditions are defined as core habitats according to the central–marginal hypothesis, which claims that range margins have less genetic diversity and more inter-population genetic divergence (Eckert et al. 2008). According to this theory, the ecosystem becomes less and less desirable for the species as it moves farther away from core habitat areas, implying a lower likelihood of survival and/or breeding success. An environmental factor such as variation in quantity and quality of food and temperature differences among habitats (Adolph and Porter 1993; Dunham et al. 1998) can easily create stress and impact life-history traits (e. g., growth rate, age upon attaining maturity, body size, clutch/litter size among others) of individuals (Mesquita et al. 2016; Ramírez-Bautista et al 2011; Ramírez-Bautista et al. 2016 ; Ramírez-Bautista et al. 2017).

Different habitats (core, marginal habitats, etc.) inhabited by the species can be found along the altitudinal gradient (Comas et al. 2020). In this regard, elevation is a commonly used factor to show differences in lifespan, growth, mean age, size at sexual maturity, and sexual dimorphism among populations (Ramírez-Bautista et al 2011; Gutiérrez et al. 2013; Ramírez-Bautista et al. 2015; Bülbül et al. 2016; Cruz-Elizalde et al. 2017; Kurnaz et al. 2018; Comas et al. 2020; Altunışık and Eksilmez 2021). Bergmann’s Rule describes a pattern where individuals are larger in colder habitats. Bergmann (1847) explained this trend through the heat conservation hypothesis: in colder climates, larger animals increase their ability to conserve heat by means of a lower surface/volume relationship. Bergmann’s rule is an ecogeographical pattern that was described first for endotherms and later tested with ectotherms, with different and sometimes contradictory results (e.g.: Zamora-Camacho et al. 2014; González-Morales et al. 2021). It has been reported in many studies that lifespan increases with altitude (Zhang and Lu 2012; Altunışık and Özdemir 2015; Bülbül et al. 2016). Several concomitant factors are

thought to be responsible for this pattern such as: 1) decreased predator pressure with altitude, 2) shorter activity periods at higher altitudes which decreases metabolic damage and the time spent in the presence of predators and, 3) variations in life-history traits since higher-altitude populations live more slowly and put more effort into self-preservation rather than reproduction (Cabezas-Cartes et al. 2018; Comas et al. 2020).

Demography is a tool that makes important contributions to many biological, ecological, and evolutionary phenomena (Roff 1992; Sinsch 2015). Many demographic parameters such as lifespan, fertility, and age structure are directly affected by ecological conditions and habitat quality (Iraeta et al. 2006; Leskovar et al. 2006; Cvetković et al. 2009; Comas et al. 2020; Mani et al. 2021). Longevity has a significant effect on different ecological and evolutionary effects as it is affected by and affects other life-history characteristics (Metcalf and Pavard 2007; Comas et al. 2020; Altunışık and Eksilmez 2021). Based on life-history traits, lizards are divided into two groups (Tinkle 1969): (i) species with a small body size 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, and (ii) species with a large body size that have a long life, slow growth rate, a single clutch during the reproductive season, and hatchlings with small/larger size at birth, oviparity or viviparity and an association with temperate or tropical environments (Ramírez-Bautista and Vitt 1997; Cruz-Elizalde and Ramírez-Bautista, 2016).

The Asia Minor thin-toed gecko, *Mediodactylus heterocercus* (Blanford, 1874), is a relatively long-lived gecko whose genus (family Gekkonidae) comprises 18 species (Reptile Database, Uetz et al., 2020). Although it shows diurnal characteristics, it is especially active at night. *Mediodactylus heterocercus* is distributed in Iran, southeastern Turkey, southern Iraq, and Syria and is listed as Least Concern by the IUCN since 2009 (Tok et al. 2009) (Figure 1). Since our knowledge on the demographic life history characteristics of the genus *Mediodactylus*

is very limited and there are no life history characteristics studies on the other species of the genus other than *Mediodactylus kotschyi* (Çiçek et al., 2015), we examined *M. heterocercus* (the Asia Minor thin-toed gecko) in terms of the demographic life-history parameters. In addition, we tested the hypothesis that lifespan and body size could be dependent on altitude. In this context, we analyzed how the age structure and some life-history traits (e.g. growth rate, longevity, body size, and sexual dimorphism) of the Asia Minor thin-toed gecko vary with the altitude gradient.

2. Material and Methods

2.1. Study area and sampling

A total of 138 (52 males, 75 females, and 11 juveniles) specimens were provided from the museum of the Department of Biology Zoology Section at Adıyaman University, Turkey (Table 1). The sex of the individuals were determined by using secondary sexual characters (Çiçek et al. 2015).

The specimens were collected from 11 different localities according to the museum records between the years 2006 and 2015. The authors received special permission for the field studies from the Republic of Turkey, Ministry of Forestry and Water Affairs, Directorate of Nature Conservation and National Parks (permit number: 11.02.2014-33465). Since these examples were museum material (preserved in ethanol), there was no need for ethics committee permission. The specimen collection localities are shown on the map (Figure 1).

The snout-vent length (SVL) of the individuals was measured by a digital caliper (Mitutoyo Corp., Kawasaki, Japan). Then, the fourth toe, including the first and second phalanges of the left hind limb, were clipped and preserved in 70% ethanol solution for the subsequent histological analysis which were performed according to Smirina (1994).

Like all species of the group Gekkonidae, the Asia Minor thin-toed gecko is nocturnal

in southeastern Turkey and often prey around the lights on the walls of buildings at night. A female lays 1-2 eggs among stones, sometimes in groups with other females. They are active during the period from the end of April to the end of September (Baran et al. 2021). It was presumed that the habitat condition for this gecko is optimal at moderate altitudes (700–1100 m) in Turkey (Table 1) and deteriorates outside this range (Baran et al. 2021).

2.2. Age Determination

Skeletochronology is based on the counting of traces called resting lines (LAG: Line of Arrested Growth), formed on bone tissues in consequence of the metabolic reduction of bone growth along with estivation or hibernation periods in Squamata (Gibbons and McCarty 1983; Castanet and Baez 1991), is a widely preferred method for investigating population age structure of many ectothermic species without sacrificing the specimens (Çiçek et al. 2015; Comas et al. 2016; Altunışık 2018; Beşer et al. 2020; Xiong et al. 2020).

The skeletochronological analysis (Smirina 1994; Comas et al. 2016) was carried out using Altunışık and Eksilmez's modified methods (2018). The preserved second phalanx was bathed in distilled water for one day before being decalcified in a 5% HNO₃ (Nitric acid) solution for about two hours. A freezing microtome (Shandon Cryostat) was used to take cross-sections of 16-17 µm thickness which were then immersed in Erlich's hematoxylin stain for 15 minutes. Then, cross-sections with a narrow medullary cavity were chosen and mounted in a solution of water-based mounting media. The Olympus BX51 light microscope was used to inspect all preparations at 10x and 20x magnifications and a camera (Pixera) connected to that microscope was used to take images of the selected sections (Figure 2). The authors examined all photos and counted and verified the number of LAGs independently (Altunışık and Eksilmez 2018).

2.3. Statistical analyses

Shapiro-Wilks and Levene tests were used to test for normality and homogeneity of

variances for all variables, respectively. Because the data has a normal distribution ($p > 0.05$), parametric tests (e.g. Student t-test) were used for statistical significance. Pearson's correlation coefficient was used to test the affinity between the life history parameters.

The Chi-square test was used to estimate whether there were any variations in age structure among locations or sexes. A t-test was used to compare morphological characteristics between males and females within a locality. An ANOVA was used to see how the mean age of the geckos differed with altitude and sex, using altitude (11 levels, referring to the 11 locations sampled), sex (2 levels), and interaction as factors. In addition, these 11 populations were divided into 3 clusters (low, intermediate, and high) to represent marginal and optimal habitats. Accordingly, those with an altitude of 500-700 m were determined as low, those between 700-1100 m as intermediate, and those with an altitude of 1100-1600 m and above as high (Table 1).

All statistical analyses were performed by using SPSS 21 (IBM SPSS Statistics for Windows).

The sexual size dimorphism was estimated by using Lovich and Gibbons (1992) sexual dimorphism index (SDI).

$$SDI = \left(\frac{\text{size of larger sex}}{\text{size of smaller sex}} \right) - 1$$
, (size, $SDI < 0$ when males are larger than females; $SDI > 0$ when females are larger than males; arbitrarily expressed as positive if females are larger and negative if males are larger.

Age upon attaining sexual maturity was assumed that the lowest age determined among the breeding specimens (Altunışık et al. 2016) and the survival rates were calculated with Robson and Chapman (1961)'s formula.

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

For all the species studied, a constant survival rate is assumed using this formula and age classes where $T=N_1+2N_2+3N_3+\dots$, $R=\sum N_i$, and N_i =the number of specimens in the age group i . The S_r in the formula corresponds to the limited annual survival rate.

The adult life expectancy (ESP) that indicates the expected longevity of animals attaining sexual maturity was estimated by using Seber's (1973) formula:

$$ESP = 0.5 + \frac{1}{1 - S_r}$$

S_r is the survival rate.

While estimating growth patterns, the growth model of von Bertalanffy was used as in previous studies (Roitberg and Smirina 2006; Guarino et al. 2010). A generalized formula of Von Bertalanffy growth is:

$$SVL_t = SVL_{\max} (1 - e^{-k(t-t_0)})$$

Where SVL_t is a size at age t , SVL_{\max} is a parameter that expresses the asymptotic maximum SVL, the curve's shape is defined by the growth coefficient k and thus, the level at which the SVL_{\max} is attained, e is the Euler's number (2.718...), and t_0 is hatching age that corresponds to the beginning of the growth interval. Since the information on the size at hatching is not available for the populations of this gecko under study, we accepted size at hatching ($SVL_{t_0} = 18$ mm) of *M. kotschyi danilewskii* as indicated by Szczerbak and Gloubey (1996). The growth rates were computed by using the equation $r = k (SVL_{\max} - SVL_t)$ and estimated parameters SVL_{\max} and k by means of the MS Excel program. We used the Chi-square test to compare intrapopulation and interpopulation differences in growth rate.

3. Results

Our results showed that there are no remarkable differences among altitudes in terms of mean age ($F_2 = 1.230$, $df = 2$, $p = 0.29$). When all of the populations analyzed were evaluated

together, it was revealed that the maximum lifespan of the species was 10 years. The age ranged from two to ten years in low and high altitudes (mean: 5.44 ± 1.55 and 5.94 ± 2.09 years, respectively), while it ranged from two to nine years in intermediate altitudes (mean: 5.24 ± 2.07) (Table 2). The Asia Minor thin-toed geckoes' age structure did not vary between sexes ($\chi^2_6 = 4.234$, $P = 0.64$) or sites ($\chi^2_6 = 5.614$, $P = 0.69$) (Figure 3).

A significant difference was found among low, intermediate, and high-altitude populations with respect to SVL (ANOVA: $F_2 = 3.358$, $df = 2$, $p < 0.05$) with high altitudes being larger than low and intermediate ones that complies with Bergmann's rule. Although no significant difference was detected between males and females in low and intermediate sites (low altitudes: $t = 0.771$, $df = 71$, $p = 0.443$; intermediate altitudes: $t = 0.765$, $df = 19$, $p = 0.454$), females of the high-altitude populations were significantly larger than males ($t = -2.371$, $df = 31$, $p < 0.05$) (Table 2). Sexual dimorphism index (SDI) was computed as 0.017; 0.034 and 0.11 for low, intermediate, and high-altitude populations, respectively. Collectively, SDI was 0.014 indicating a male bias.

The 5th age group that has 5 LAGs is the most common age group in low, intermediate, and high altitudes with 28.76% ($n = 21$), 28.57% ($n = 6$), and 24.4% ($n = 8$), respectively (Figure 3). The age upon attaining sexual maturity was determined as 2 years in low and intermediate populations for both sexes while it was estimated as 2 years for males and 3 years for females of the high-altitude populations.

The body size markedly increased with altitude (Pearson correlation, $r = 0.209$, $P < 0.05$) and age ($r = 0.559$, $P < 0.001$) but no significant relationship between age and altitude (Pearson correlation, $r = 0.104$, $p = 0.24$) was observed (Figure 4).

The adult life expectancy, which indicates the expected lifespan of individuals having sexual maturity, was higher in high altitude populations (ESP: 6.59 years) than intermediate

(ESP: 5.40 years) and low altitude (ESP: 6.01 years) populations. A similar result was observed in survival rates as S_r was higher (0.84) in high altitudes than intermediate (0.79) and low (0.82) altitudes.

The growth parameters predicted by means of the von Bertalanffy equation indicated a fit that reflects the real relationship between age and SVL (Figure 5). Growth rates did not differ among all populations (ANOVA: $F_2=6.708$, $df=2$, $p=0.19$). The computed asymptotic SVL (SVL_{asym} , low: 44.74 mm; intermediate: 44.43 mm; high: 49.98 mm) was lower than the maximum SVL (SVL_{max} , low: 48.83 mm; intermediate: 46.00 mm; high: 54.33 mm) in all populations. Growth coefficient of low ($k=0.49$) and high ($k=0.37$) altitude populations was lower than intermediate-altitude populations ($k=0.62$). Since the age distribution of the populations is quite diverse, some of the populations will be "r" selection and the others "k". Therefore, there may be a difference in growth rates.

4. Discussion

Geckos' life-history features differ considerably between sexes and populations as well as between various ecological environments within the same species. In this study, it was estimated that males and females of *M. heterocercus* live up to 10 years. Considering that there are more females than males, it is more likely to find a maximum lifespan in females because of larger sample size (Figure 5). On the other hand, females of the congener, *Mediodactylus kotschy* (Kotschy's gecko) have a lifespan of eight years while males live seven (Çiçek et al. 2015). Female adult Kotschy's geckos in captivity live for six years but adults live for four years in wild Israel populations (Werner, 1993). Furthermore, the animal's maximum lifespan was recorded to be seven years when it reached maturity in its first year in Jerusalem (Israel). According to those results, it is understood that the lifespan of the studied populations is

relatively higher than the populations of the congener *M. kotschyi*. Additionally, longevity was reported to be 17 years in *Homonota darwini* (Piantoni et al. 2006) and 20 years in *Gekko gekko* (Werner et al. 1993) and *Phelsuma grandis* (Stark et al. 2020). *Woodworthia maculatus*, lived up to 37 years, has a maximum lifespan in 55 geckonid taxa (Werner et al., 1993).

Our findings indicate that the age structure of Asia Minor thin-toed gecko populations in southeast Turkey varies with elevation in a curvilinear manner: populations at high and low elevations (supposed to be marginal habitats) have older individuals than populations at intermediate altitudes. Some ectothermic animals follow the Bergmann's rule, being larger in colder habitats (Zamora-Camacho et al. 2014) or the inverse (Ashton and Feldman 2003; Blanckenhorn and Demont 2004). However, its applicability to lizards and geckos is still debatable (Ashton and Feldman 2003; Granatosky and Rysko 2014). The findings of this study support that the Asia Minor thin-toed gecko follows the Bergmann rule since its body size increases with altitude. These trends are usually explained as an evolutionary response to reduce heat loss in cooler climates (Bergmann 1847; Olalla-Tárraga and Rodríguez 2007; Zamora-Camacho et al. 2014).

Differentiated evolutionary responses to ecological conditions in females and males are among the possible causes of distinct sexual size dimorphism (SSD) trends between and within species (Cox et al. 2007; Roitberg 2007). For instance, sexual dimorphism was observed in two populations in favor of males and one population in favor of females along 3 elevation gradients. When body size was evaluated collectively, SSD indicated a weak male bias. Various selection pressures may have resulted in the development of different patterns of sexual dimorphism among populations of the same species, resulting in morphological differences between populations. In *M.heterocercus*, male biased sexual size dimorphism might be a result of sexual selection, with larger males having an advantage over smaller ones in attracting mates. This phenomenon also might be maintained by differences in energy allocation between sexes,

resulting in distinct development trajectories (Ramírez-Bautista and Vitt 1997). In addition, the inconsistency in growth rates caused by food abundance and predation pressure are among the factors that can explain the sexual dimorphism in this study as in other studies (Adolph and Porter 1993; Ramírez-Bautista and Vitt 1997; Tomašević Kolarov et al. 2010; Ramírez-Bautista et al. 2021). In accordance with this assumption, the growth rate of high-altitude populations (colder habitats) was faster than low and medium altitude populations. A substantial difference in population growth rates may also have influenced the sexual maturity age. Individuals from the highland population generally continue to develop and attain sexual maturity later as compared to lowland ones. In this study, it was found that Asia Minor thin-toed gecko matures at a higher age (three vs. two years) in highland than in low and medium populations. As a result of the lizards' delayed sexual maturity, they are able to sustain longer periods of rapid growth and therefore, achieve larger body sizes. Similar to our findings on intermediate and low altitude populations, age at sexual maturity was reported as two years for the congener *M. kotschy* (Çiçek et al. 2015).

Several studies with ectotherms have shown that as body size increases so does age (Halliday and Verrell 1988; Sinsch et al. 2007; Kalayci et al. 2015). In addition, there was a high correlation between the age and body size of *M. kotschy* (Çiçek et al. 2015). This trend is consistent with our results that show a positive relationship between age and body size in both males and females.

In conclusion, the body size of the Asia Minor thin-toed geckos increases with altitude, but their age does not. In addition, individuals living in marginal habitats (low and high-altitude populations) have higher mean age as compared to core habitats (mid-altitude populations).

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Acknowledgment

This study was conducted within the framework of different projects; ADYUBAP FEFYL 2017-001, HÜBAK 1111, HÜBAK 13092, and the National Biodiversity Inventory and Monitoring Project coordinated by the Republic of Turkey Ministry of Agriculture and Forestry General Directorate of Nature Conservation and National Parks. The authors wish to thank the directorate and the staff of the Ministry of Agriculture and Forestry Şanlıurfa Department.

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- 516

Table 1. Sampling localities for the Asia Minor thin-toed gecko, *Mediodactylus heterocercus* in this study

| Altitude gradient | Sex | n | Localities |
|----------------------------------|------------|----|--|
| Low (500-700 a.s.l) | Males: | 31 | Şanlıurfa province |
| | Females: | 42 | Batman province |
| | Juveniles: | 8 | Hasankeyf (Batman) |
| | Total: | 81 | Adıyaman province Kahta, (Adıyaman) |
| Intermediate (700-1100 a.s.l) | Males: | 9 | Viranşehir (Şanlıurfa) |
| | Females: | 12 | Hilvan(Şanlıurfa) |
| | Juveniles: | 2 | Bingöl province |
| | Total: | 23 | Tut, (Adıyaman) |
| High (1100-1600 a.s.l) | Males: | 12 | Elazığ province |
| | Females: | 21 | İnlice, (Adıyaman) |
| | Juveniles: | 1 | |
| | Total: | 34 | |

Table 2. Descriptive statistics of growth rate (mm per year), growth coefficient (k), ESP and Sr in the studied populations of *Mediodactylus heterocercus* adults from low, intermediate, and high altitude populations. N - number of specimens, M: Male, F: Female, ESP-adult life expectancy, Sr- survival rate, SDI- sexual dimorphism index

| Population (altitude) | N | Sex | Mean age (years) | Mean SVL (mm) | Growth rate (mm, years) | k | SVLmax (mm) | ESP (years) | Sr | SDI |
|--|----|-----|---------------------|------------------|----------------------------|------|----------------|----------------|------|------|
| Low (500-700 m a.s.l.) | 31 | M | 5.61 | 42.57 | 1.55 | 0.49 | 44.74 | 6.01 | 0.82 | 0.02 |
| | 42 | F | 5.31 | 41.83 | | | | | | |
| Intermediate (700-1100 m a.s.l.) | 9 | M | 4.67 | 43.00 | 1.20 | 0.62 | 44.43 | 5.40 | 0.79 | 0.03 |
| | 12 | F | 5.67 | 41.58 | | | | | | |
| High (1100-1600 m a.s.l.) | 12 | M | 5.92 | 41.58 | 2.51 | 0.37 | 49.98 | 6.59 | 0.84 | 0.11 |
| | 21 | F | 5.95 | 46.28 | | | | | | |

Draft

589 **Figure Legends**

590 **Figure 1.** Distribution map of the Asia Minor thin-toed gecko, *Mediodactylus heterocercus* and
591 locations: 1: Tut (Adıyaman province); 2: Adıyaman province; 3: İnlıce, Sincik (Adıyaman p.);
592 4: Kahta (Adıyaman p.), 5: Elazığ province; 6: Bingöl province; 7: Batman province; 8:
593 Hasankeyf (Batman province); 9: Viranşehir (Şanlıurfa p.); 10: Hilvan (Şanlıurfa); 11:
594 Şanlıurfa province. This map was generated in ArcMap 10.3
595 (<http://www.esri.com/software/arcgis/arcgis-for-desktop>). World Geodetic System of 1984
596 (WGS84) datum was used as the coordinate system.

597 **Figure 2.** Cross-section (16 µm thick) at the diaphysis level of the phalange bone of a
598 *Mediodactylus heterocercus* specimen at the age of 10. Abbreviations: m.c.; marrow cavity, r.l.,
599 resorption line, e.b: endosteal bone.

600

601 **Figure 3.** Age distribution graphic of *Mediodactylus heterocercus*

602 **Figure 4.** Relationship between life history traits (mean age (A) and mean body size (B)) and
603 altitude of *Mediodactylus heterocercus*

604 **Figure 5.** Relationship between age and body size (SVL). (A) low-altitude populations (B)
605 intermediate-altitude populations (C) high-altitude populations of *Mediodactylus*
606 *heterocercus*

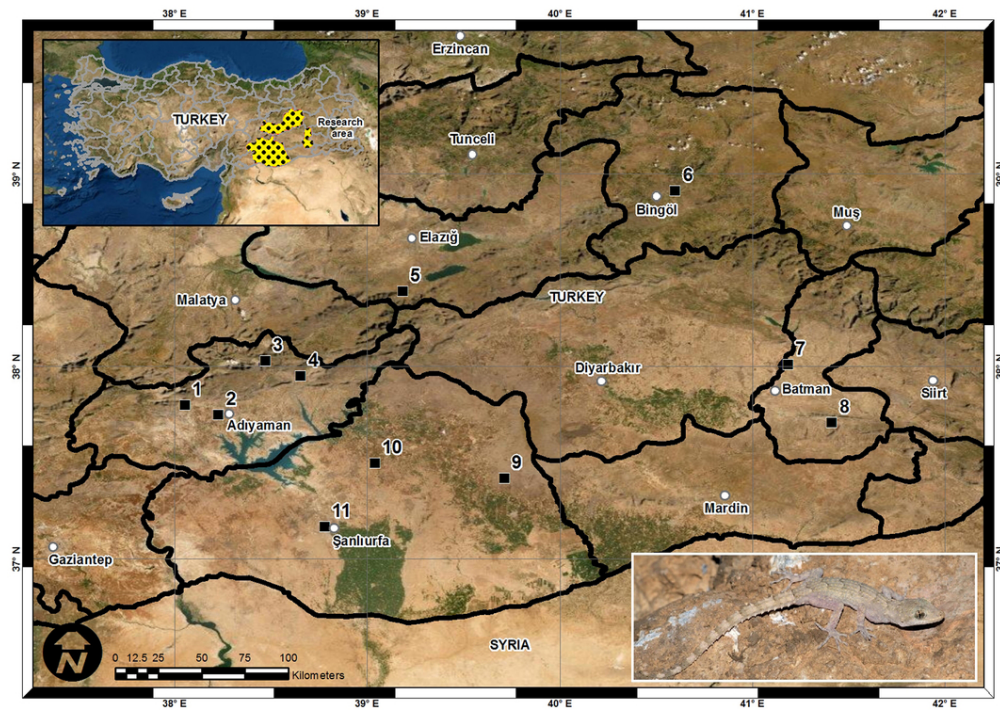


Figure 1

179x126mm (150 x 150 DPI)

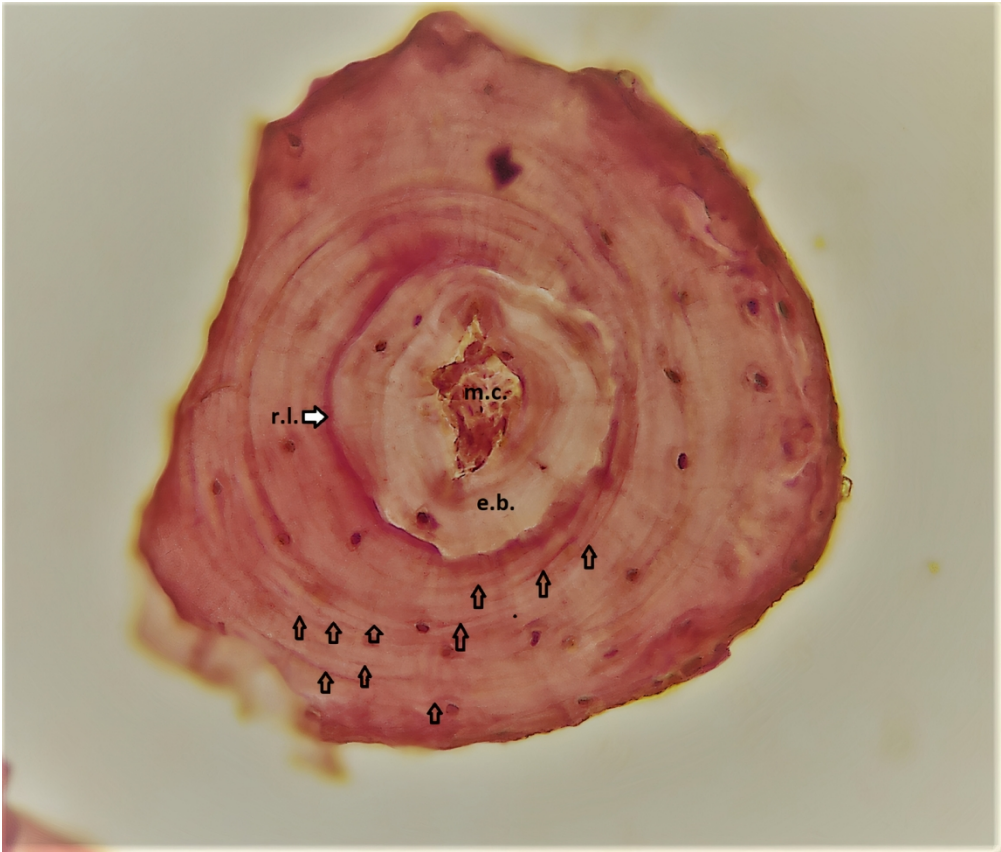


Figure 2

272x231mm (150 x 150 DPI)

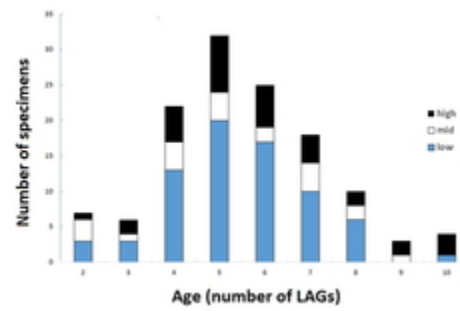


Figure 3

38x26mm (150 x 150 DPI)

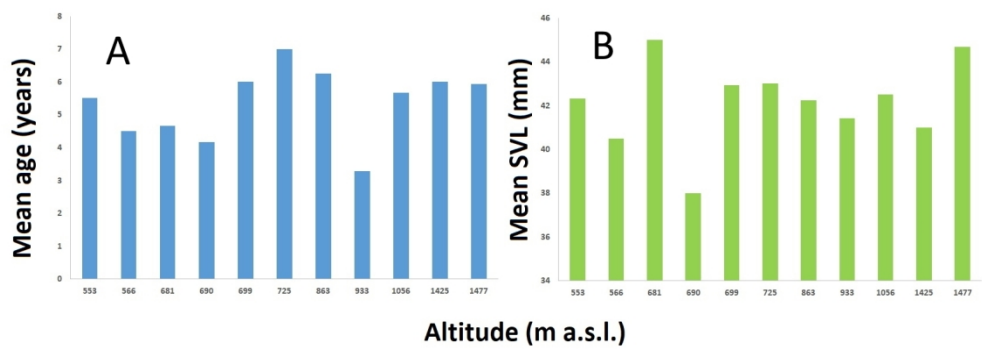


Figure 4

72x26mm (600 x 600 DPI)

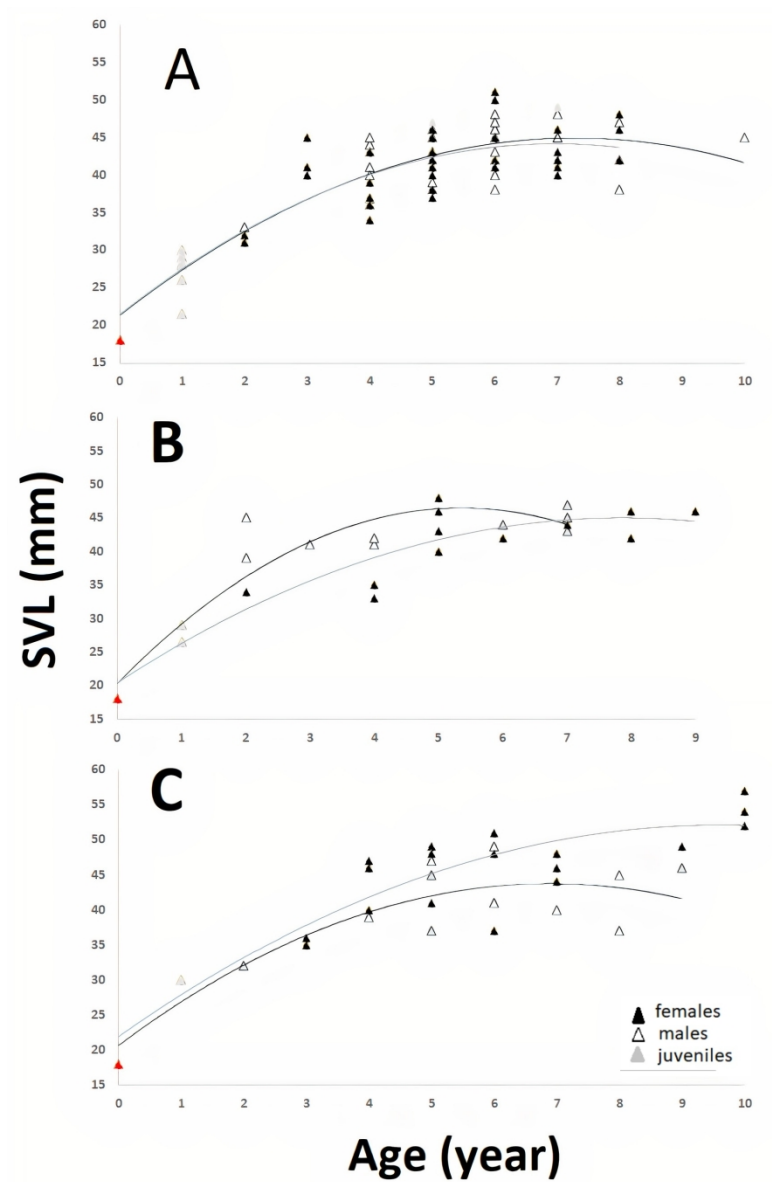


Figure 5

147x226mm (300 x 300 DPI)