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Altitude impacts body size but not age in a gecko

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1   **Altitude impacts body size but not age in a gecko**

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13   **Running Title:** Altitudinal variation in a gecko

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23 **Abstract**

24 Animals' age and size-related life-history traits are influenced by a variety of factors. In

25 connection with climate, the effect of altitude on demographic parameters may differ among

26 different populations of the same species. In the present study, it was analyzed that how body

27 size and longevity of the Asia Minor thin-toed gecko, *Mediodactylus heterocercus* (Blanford,

28 1874)*,* vary along with an elevational gradient in Turkey. For this purpose, a total of 138 (52

29 males, 75 females, and 11 young) *M. heterocercus* specimens from 11 different populations

30 were analyzed. Populations at inter-mediate altitude had shorter lifespans than in both low and

31 high elevations (marginal environments). Furthermore, the adult life expectancy (ESP), which

32 indicates the expected lifespan of individuals having sexual maturity, was higher in high altitude

33 populations (ESP: 6.59 years) than in intermediate populations (ESP: 5.40 years) and low

34 altitude populations (ESP: 6.01 years). The results of the study suggest that Asia Minor thin-

35 toed geckos' body size increases with altitude, but their age does not.

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38 **Key words:** The Asia Minor thin-toed gecko, *Mediodactylus heterocercus,* Bergmann rule,

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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; Gónzalez-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

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75   thought to be responsible for this pattern such as: 1) decreased predator pressure with altitude,

76   2) shorter activity periods at higher altitudes which decreases metabolic damage and the time

77   spent in the presence of predators and, 3) variations in life-history traits since higher-altitude

78   populations live more slowly and put more effort into self-preservation rather than reproduction

79   (Cabezas-Cartes et al. 2018; Comas et al. 2020).

80   Demography is a tool that makes important contributions to many biological, ecological,

81   and evolutionary phenomena (Roff 1992; Sinsch 2015). Many demographic parameters such as

82   lifespan, fertility, and age structure are directly affected by ecological conditions and habitat

83   quality (Iraeta et al. 2006; Leskovar et al. 2006; Cvetković et al. 2009; Comas et al. 2020; Mani

84   et al. 2021). Longevity has a significant effect on different ecological and evolutionary effects

85   as it is affected by and affects other life-history characteristics (Metcalf and Pavard 2007;

86   Comas et al. 2020; Altunışık and Eksilmez 2021). Based on life-history traits, lizards are

87   divided into two groups (Tinkle 1969): (i) species with a small body size that have a short life,

88   rapid growth rate, small clutch size, multiple clutches within a season, oviparity, smaller snout-

89   vent length (SVL) at birth, and an association with tropical environments, and (ii) species with

90   a large body size that have a long life, slow growth rate, a single clutch during the reproductive

91   season, and hatchlings with small/larger size at birth, oviparity or viviparity and an association

92   with temperate or tropical environments (Ramírez-Bautista and Vitt 1997; Cruz-Elizalde and

93   Ramírez-Bautista, 2016).

94   The Asia Minor thin-toed gecko, *Mediodactylus heterocercus* (Blanford, 1874), is a

95   relatively long-lived gecko whose genus (family Gekkonidae) comprises 18 species (Reptile

96   Database, Uetz et al., 2020). Although it shows diurnal characteristics, it is especially active at

97   night. *Mediodactylus heterocercus* is distributed in Iran, southeastern Turkey, southern Iraq,

98   and Syria and is listed as Least Concern by the IUCN since 2009 (Tok et al. 2009) (Figure 1).

99   Since our knowledge on the demographic life history characteristics of the genus *Mediodactylus*

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100 is very limited and there are no life history characteristics studies on the other species of the

101 genus other than *Mediodactylus kotschyi* (Çiçek et al., 2015), we examined *M. heterocercus*

102 (the Asia Minor thin-toed gecko) in terms of the demographic life-history parameters. In

103 addition, we tested the hypothesis that lifespan and body size could be dependent on altitude.

104 In this context, we analyzed how the age structure and some life-history traits (e.g. growth rate,

105 longevity, body size, and sexual dimorphism) of the Asia Minor thin-toed gecko vary with the

106 altitude gradient.

107 **2. Material and Methods**

108 *2.1. Study area and sampling*

109 A total of 138 (52 males, 75 females, and 11 juveniles) specimens were provided from

110 the museum of the Department of Biology Zoology Section at Adıyaman University, Turkey

111 (Table 1). The sex of the individuals were determined by using secondary sexual characters

112 (Çiçek et al. 2015).

113 The specimens were collected from 11 different localities according to the museum

114 records between the years 2006 and 2015. The authors received special permission for the field

115 studies from the Republic of Turkey, Ministry of Forestry and Water Affairs, Directorate of

116 Nature Conservation and National Parks (permit number: 11.02.2014-33465). Since these

117 examples were museum material (preserved in ethanol), there was no need for ethics committee

118 permission. The specimen collection localities are shown on the map (Figure 1).

119 The snout-vent length (SVL) of the individuals was measured by a digital caliper

120 (Mitutoyo Corp., Kawasaki, Japan). Then, the fourth toe, including the first and second

121 phalanges of the left hind limb, were clipped and preserved in 70% ethanol solution for the

122 subsequent histological analysis which were performed according to Smirina (1994).

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

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124   in southeastern Turkey and often prey around the lights on the walls of buildings at night. A

125   female lays 1-2 eggs among stones, sometimes in groups with other females. They are active

126   during the period from the end of April to the end of September (Baran et al. 2021). It was

127   presumed that the habitat condition for this gecko is optimal at moderate altitudes (700–1100

128   m) in Turkey (Table 1) and deteriorates outside this range (Baran et al. 2021).

129   2.2. *Age Determination*

130   Skeletochronology is based on the counting of traces called resting lines (LAG: Line of

131   Arrested Growth), formed on bone tissues in consequence of the metabolic reduction of bone

132   growth along with estivation or hibernation periods in Squamata (Gibbons and McCarty 1983;

133   Castanet and Baez 1991), is a widely preferred method for investigating population age

134   structure of many ectothermic species without sacrificing the specimens (Çiçek et al. 2015;

135   Comas et al. 2016; Altunışık 2018; Beşer et al. 2020; Xiong et al. 2020).

136   The skeletochronological analysis (Smirina 1994; Comas et al. 2016) was carried out

137   using Altunışık and Eksilmez's modified methods (2018). The preserved second phalanx was

138   bathed in distilled water for one day before being decalcified in a 5% HNO_3 (Nitric acid)

139   solution for about two hours. A freezing microtome (Shandon Cryostat) was used to take cross-

140   sections of 16-17 μm thickness which were then immersed in Erlich's hematoxylin stain for 15

141   minutes. Then, cross-sections with a narrow medullary cavity were chosen and mounted in a

142   solution of water-based mounting media. The Olympus BX51 light microscope was used to

143   inspect all preparations at 10x and 20x magnifications and a camera (Pixera) connected to that

144   microscope was used to take images of the selected sections (Figure 2). The authors examined

145   all photos and counted and verified the number of LAGs independently (Altunışık and Eksilmez

146   2018)

147   *2.3. Statistical analyses*

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

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149   variances for all variables, respectively. Because the data has a normal distribution (p> 0.05),

150   parametric tests (e.g. Student t-test) were used for statistical significance. Pearson's correlation

151   coefficient was used to test the affinity between the life history parameters.

152   The Chi-square test was used to estimate whether there were any variations in age

153   structure among locations or sexes. A t-test was used to compare morphological characteristics

154   between males and females within a locality. An ANOVA was used to see how the mean age

155   of the geckos differed with altitude and sex, using altitude (11 levels, referring to the 11

156   locations sampled), sex (2 levels), and interaction as factors. In addition, these 11 populations

157   were divided into 3 clusters (low, intermediate, and high) to represent marginal and optimal

158   habitats. Accordingly, those with an altitude of 500-700 m were determined as low, those

159   between 700-1100 m as intermediate, and those with an altitude of 1100-1600 m and above as

160   high (Table 1).

161   All statistical analyses were performed by using SPSS 21 (IBM SPSS Statistics for

162   Windows).

163   The sexual size dimorphism was estimated by using Lovich and Gibbons (1992) sexual

164   dimorphism index (SDI).

165        $SDI = (\frac{size\ of\ larger\ sex}{size\ of\ smaller\ sex})- 1$, (size, SDI < 0 when males are larger than females; SDI > 0

166   when females are larger than males; arbitrarily expressed as positive if females are larger and

167   negative if males are larger.

168   Age upon attaining sexual maturity was assumed that the lowest age determined among

169   the breeding specimens (Altunışık et al. 2016) and the survival rates were calculated with

170   Robson and Chapman (1961)'s formula.

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

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172   For all the species studied, a constant survival rate is assumed using this formula and

173   age classes where T=N1+2N2+3N3+…, R=Σ Ni, and Ni =the number of specimens in the age

174   group i. The Sr in the formula corresponds to the limited annual survival rate.

175   The adult life expectancy (ESP) that indicates the expected longevity of animals

176   attaining sexual maturity was estimated by using Seber's (1973) formula:

177     $ESP = 0.5 + \frac{1}{1 - Sr}$

178   Sr is the survival rate.

179   While estimating growth patterns, the growth model of von Bertalanffy was used as in

180   previous studies (Roitberg and Smirina 2006; Guarino et al. 2010). A generalized formula of

181   Von Bertalanffy growth is:

182     $SVLt = SVLmax (1 - e^{-k(t-t0)})$

183   Where SVLt is a size at age t, SVLmax is a parameter that expresses the asymptotic

184   maximum SVL, the curve's shape is defined by the growth coefficient k and thus, the level at

185   which the SVLmax is attained, e is the Euler's number (2.718...), and t_0 is hatching age that

186   corresponds to the beginning of the growth interval. Since the information on the size at

187   hatching is not available for the populations of this gecko under study, we accepted size at

188   hatching (SVLt$_0$ = 18 mm) of *M. kotschyi danilewskii* as indicated by Szczerbak and Gloubev

189   (1996). The growth rates were computed by using the equation r = k (SVLmax- SVLt) and

190   estimated parameters SVLmax and k by means of the MS Excel program. We used the Chi-

191   square test to compare intrapopulation and interpopulation differences in growth rate.

3. Results

193   Our results showed that there are no remarkable differences among altitudes in terms of

194   mean age (F_2= 1.230, df= 2, p=0.29). When all of the populations analyzed were evaluated

195   together, it was revealed that the maximum lifespan of the species was 10 years. The age ranged

196   from two to ten years in low and high altitudes (mean: 5.44 ± 1.55 and 5.94 ± 2.09 years,

197   respectively), while it ranged from two to nine years in intermediate altitudes (mean: $5.24 \pm$

198   2.07) (Table 2). The Asia Minor thin-toed geckoes' age structure did not vary between sexes (χ

199   $^2_6= 4.234$, P= 0.64) or sites ($\chi^2_6= 5.614$, P= 0.69) (Figure 3).

200   A significant difference was found among low, intermediate, and high-altitude

201   populations with respect to SVL (ANOVA: $F_2=3.358$, df= 2, p<0.05) with high altitudes being

202   larger than low and intermediate ones that complies with Bergmann's rule. Although no

203   significant difference was detected between males and females in low and intermediate sites

204   (low altitudes: t = 0.771, df = 71, p = 0.443; intermediate altitudes: t = 0.765, df = 19, p =

205   0.454), females of the high-altitude populations were significantly larger than males (t =-2.371,

206   df = 31, p <0.05) (Table 2). Sexual dimorphism index (SDI) was computed as 0.017; 0.034 and

207   0.11 for low, intermediate, and high-altitude populations, respectively. Collectively, SDI was

208   0.014 indicating a male bias.

209   The 5th age group that has 5 LAGs is the most common age group in low, intermediate,

210   and high altitudes with 28.76% (n=21), 28.57% (n= 6), and 24.4% (n=8), respectively (Figure

211   3). The age upon attaining sexual maturity was determined as 2 years in low and intermediate

212   populations for both sexes while it was estimated as 2 years for males and 3 years for females

213   of the high-altitude populations.

214   The body size markedly increased with altitude (Pearson correlation, r = 0.209, P <0.05)

215   and age (r = 0.559, P <0.001) but no significant relationship between age and altitude (Pearson

216   correlation, r = 0.104, p= 0.24) was observed (Figure 4).

217   The adult life expectancy, which indicates the expected lifespan of individuals having

218   sexual maturity, was higher in high altitude populations (ESP: 6.59 years) than intermediate

219 (ESP: 5.40 years) and low altitude (ESP: 6.01 years) populations. A similar result was observed

220 in survival rates as Sr was higher (0.84) in high altitudes than intermediate (0.79) and low (0.82)

221 altitudes.

222   The growth parameters predicted by means of the von Bertalanffy equation indicated a

223 fit that reflects the real relationship between age and SVL (Figure 5). Growth rates did not differ

224 among all populations (ANOVA: $F_2=6.708$, df= 2, p=0.19). The computed asymptotic SVL

225 (SVLasym, low: 44.74 mm; intermediate: 44.43 mm; high: 49.98 mm) was lower than the

226 maximum SVL (SVLmax, low: 48.83 mm; intermediate: 46.00 mm; high: 54.33 mm) in all

227 populations. Growth coefficient of low (k= 0.49) and high (k=0.37) altitude populations was

228 lower than intermediate-altitude populations (k= 0.62). Since the age distribution of the

229 populations is quite diverse, some of the populations will be "r" selection and the others "k".

230 Therefore, there may be a difference in growth rates.

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232 **4. Discussion**

233   Geckos' life-history features differ considerably between sexes and populations as well

234 as between various ecological environments within the same species. In this study, it was

235 estimated that males and females of *M. heterocercus* live up to 10 years. Considering that there

236 are more females than males, it is more likely to find a maximum lifespan in females because

237 of larger sample size (Figure 5). On the other hand, females of the congener, *Mediodactylus*

238 *kotschyi* (Kotschy's gecko) have a lifespan of eight years while males live seven (Çiçek et al.

239 2015). Female adult Kotschy's geckos in captivity live for six years but adults live for four years

240 in wild Israel populations (Werner, 1993). Furthermore, the animal's maximum lifespan was

241 recorded to be seven years when it reached maturity in its first year in Jerusalem (Israel).

242 According to those results, it is understood that the lifespan of the studied populations is

243 relatively higher than the populations of the congener *M. kotschyi*. Additionally, longevity was

244 reported to be 17 years in *Homonota darwini* (Piantoni et al. 2006) and 20 years in *Gekko gecko*

245 (Werner et al. 1993) and *Phelsuma grandis* (Stark et al. 2020). *Woodworthia maculatus*, lived

246 up to 37 years, has a maximum lifespan in 55 geckonid taxa (Werner et al., 1993).

247   Our findings indicate that the age structure of Asia Minor thin-toed gecko populations in

248 southeast Turkey varies with elevation in a curvilinear manner: populations at high and low

249 elevations (supposed to be marginal habitats) have older individuals than populations at

250 intermediate altitudes. Some ectothermic animals follow the Bergmann's rule, being larger in

251 colder habitats (Zamora-Camacho et al. 2014) or the inverse (Ashton and Feldman 2003;

252 Blanckenhorn and Demont 2004). However, its applicability to lizards and geckos is still

253 debatable (Ashton and Feldman 2003; Granatosky and Rysko 2014). The findings of this study

254 support that the Asia Minor thin-toed gecko follows the Bergmann rule since its body size

255 increases with altitude. These trends are usually explained as an evolutionary response to reduce

256 heat loss in cooler climates (Bergmann 1847; Olalla-Tárraga and Rodríguez 2007; Zamora-

257 Camacho et al. 2014).

258   Differentiated evolutionary responses to ecological conditions in females and males are

259 among the possible causes of distinct sexual size dimorphism (SSD) trends between and within

260 species (Cox et al. 2007; Roitberg 2007). For instance, sexual dimorphism was observed in two

261 populations in favor of males and one population in favor of females along 3 elevation

262 gradients. When body size was evaluated collectively, SSD indicated a weak male bias. Various

263 selection pressures may have resulted in the development of different patterns of sexual

264 dimorphism among populations of the same species, resulting in morphological differences

265 between populations. In *M.heterocercus*, male biased sexual size dimorphism might be a result

266 of sexual selection, with larger males having an advantage over smaller ones in attracting mates.

267 This phenomenon also might be maintained by differences in energy allocation between sexes,

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268   resulting in distinct development trajectories (Ramirez-Bautista and Vitt 1997). In addition, the

269   inconsistency in growth rates caused by food abundance and predation pressure are among the

270   factors that can explain the sexual dimorphism in this study as in other studies (Adolph and

271   Porter 1993; Ramírez-Bautista and Vitt 1997; Tomašević Kolarov et al. 2010; Ramírez-Bautista

272   et al. 2021). In accordance with this assumption, the growth rate of high-altitude populations

273   (colder habitats) was faster than low and medium altitude populations. A substantial difference

274   in population growth rates may also have influenced the sexual maturity age. Individuals from

275   the highland population generally continue to develop and attain sexual maturity later as

276   compared to lowland ones. In this study, it was found that Asia Minor thin-toed gecko matures

277   at a higher age (three vs. two years) in highland than in low and medium populations. As a

278   result of the lizards' delayed sexual maturity, they are able to sustain longer periods of rapid

279   growth and therefore, achieve larger body sizes. Similar to our findings on intermediate and

280   low altitude populations, age at sexual maturity was reported as two years for the congener *M.*

281   *kotschyi* (Çiçek et al. 2015).

282   Several studies with ectotherms have shown that as body size increases so does age

283   (Halliday and Verrell 1988; Sinsch et al. 2007; Kalayci et al. 2015). In addition, there was a

284   high correlation between the age and body size of *M. kotschyi* (Çiçek et al. 2015). This trend is

285   consistent with our results that show a positive relationship between age and body size in both

286   males and females.

287   In conclusion, the body size of the Asia Minor thin-toed geckos increases with altitude,

288   but their age does not. In addition, individuals living in marginal habitats (low and high-altitude

289   populations) have higher mean age as compared to core habitats (mid-altitude populations).

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516

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

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567 **Table 2.** Descriptive statistics of growth rate (mm per year), growth coefficient (k), ESP and Sr
568 in the studied populations of *Mediodactylus heterocercus* adults from low, intermediate, and
569 high altitude populations. N - number of specimens, M: Male, F: Female, ESP-adult life
570 expectancy, Sr- survival rate, SDI- sexual dimorphism index
571

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

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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: İnlice, 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.; marrov 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*

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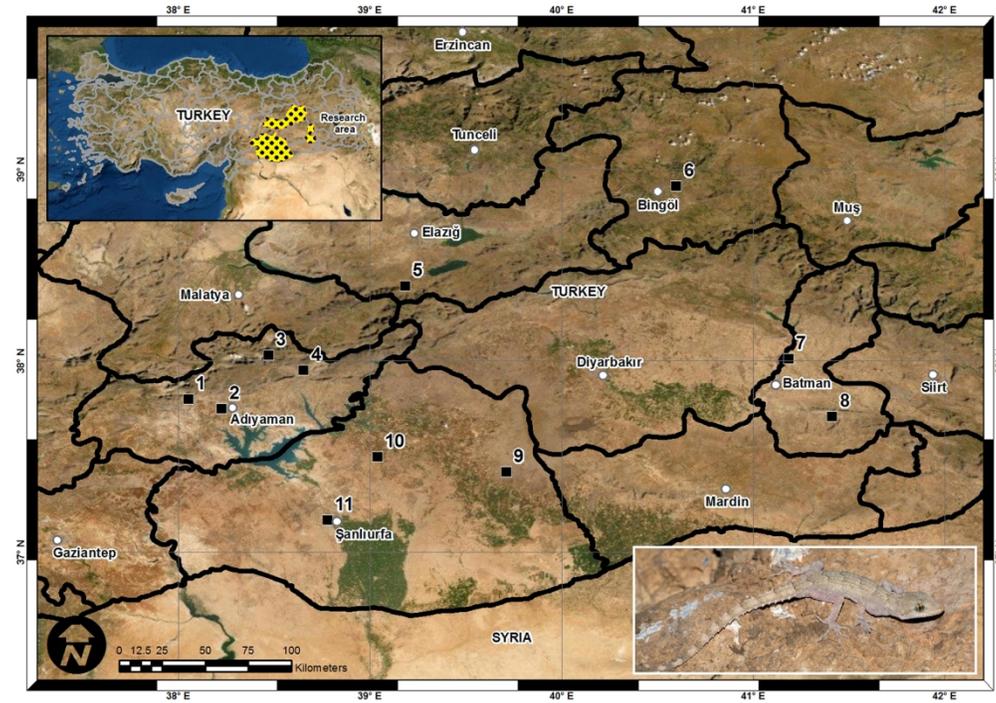
Figure 1

179x126mm (300 x 300 DPI)
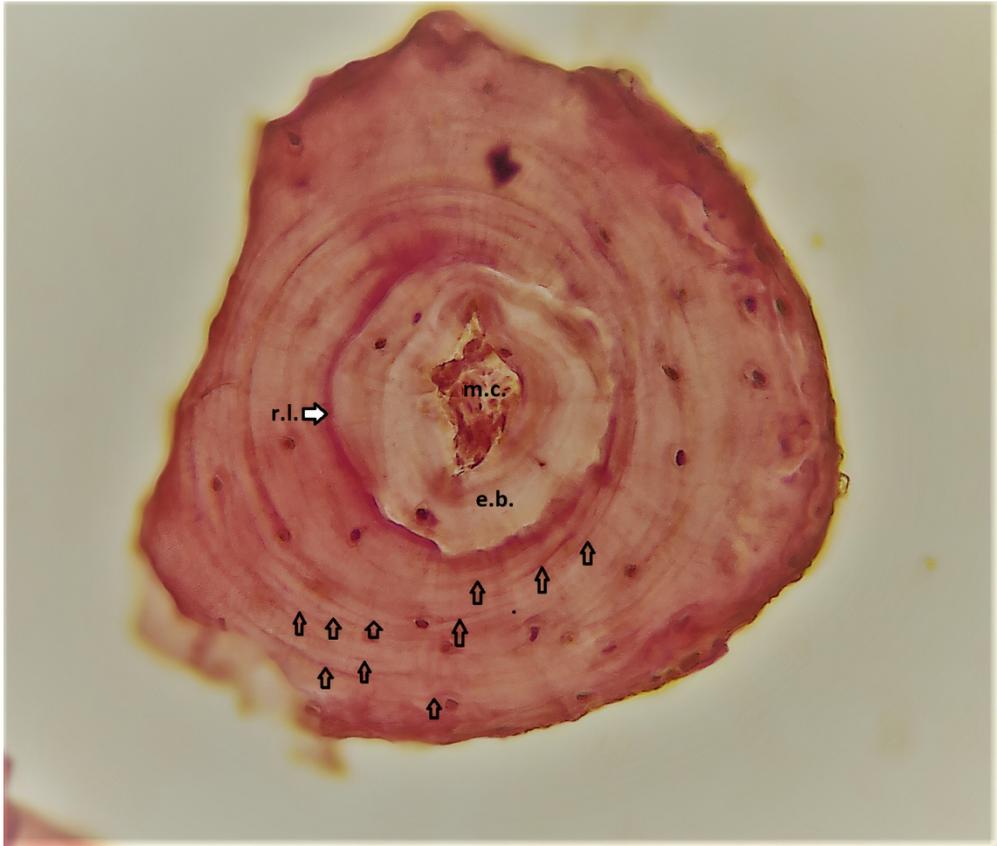
Figure 2

272x231mm (300 x 300 DPI)
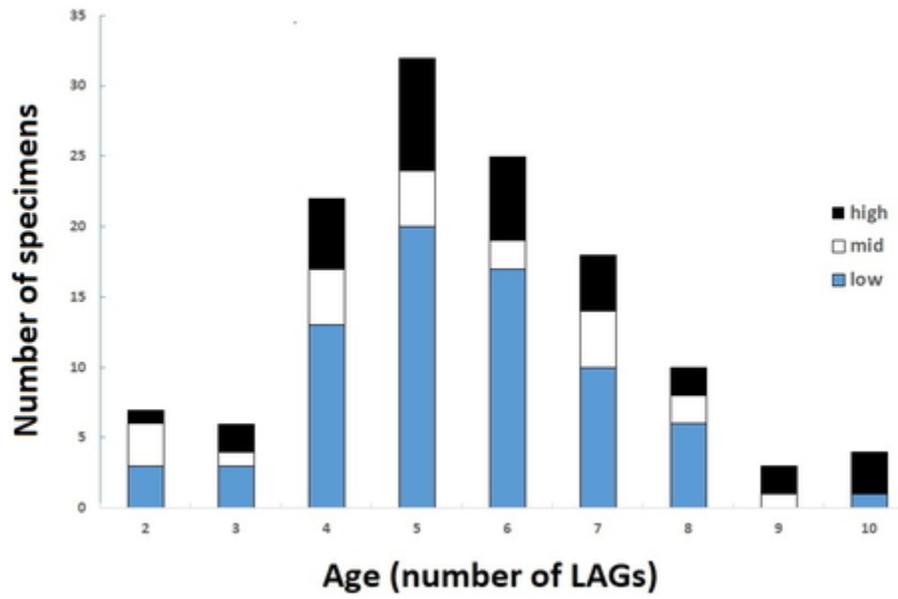
Figure 3

38x26mm (300 x 300 DPI)
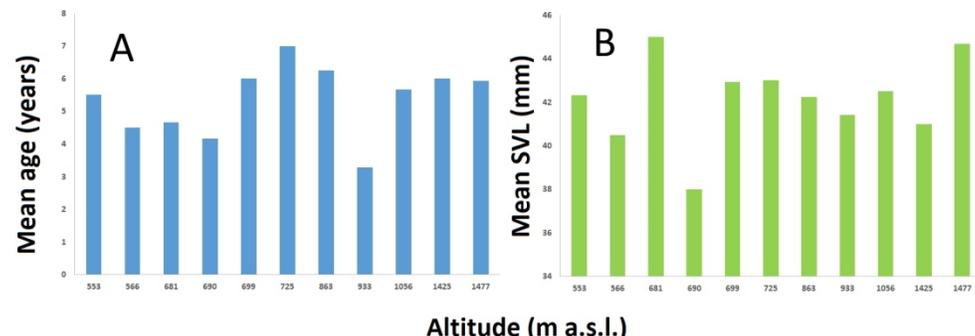
Figure 4

72x26mm (600 x 600 DPI)
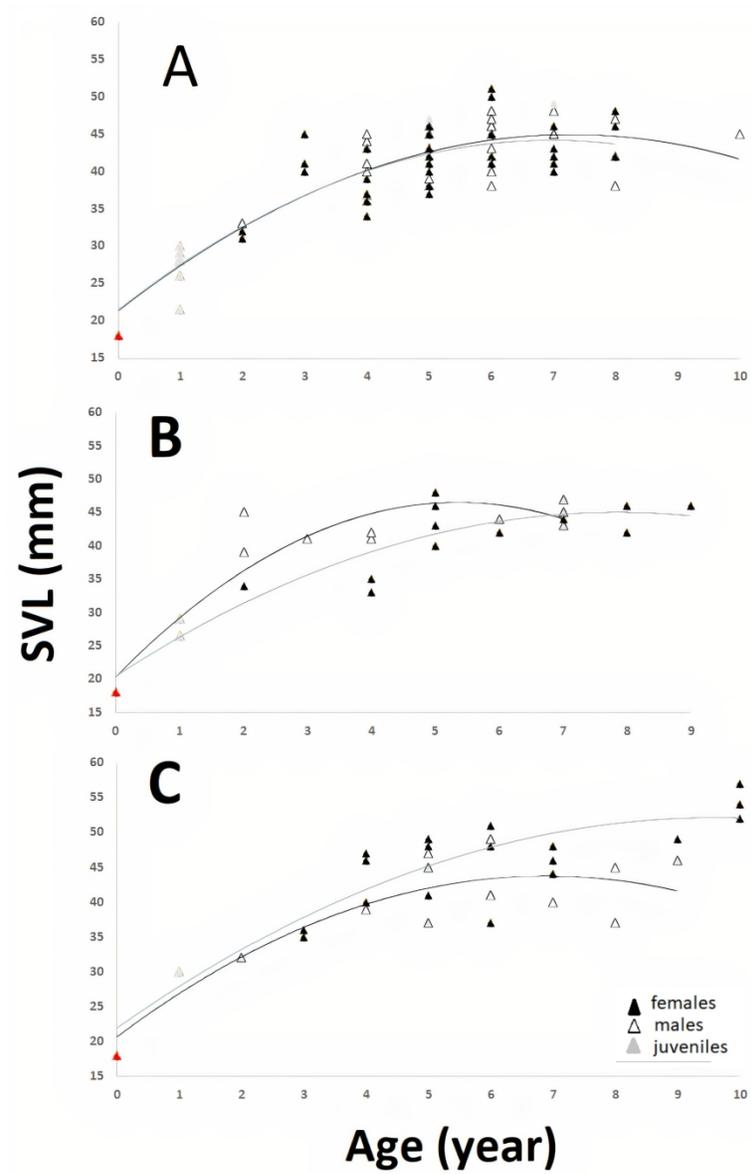
Figure 5

147x226mm (300 x 300 DPI)