Peculiarities of Thermal Biology in Two Parthenogenetic Rock Lizard Species, *Darevskia armeniaca* and *Darevskia unisexualis*, and One Bisexual Species, *Darevskia valentini* (Lacertidae, Squamata)

O. D. Nikolaev^{a,} *, D. A. Belova^a, B. A. Novikov^a, I. B. Simis^a, R. K. Petrosyan^b, M. S. Arakelyan^b, V. A. Komarova^c, and E. A. Galoyan^{c, d, **}

^a School Number 179, Moscow, 125009 Russia ^b Yerevan State University, Yerevan, 0025 Republic of Armenia ^c Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, 119071 Russia ^d Zoological Museum, Moscow State University, Moscow, 125009 Russia *e-mail: fencov@yandex.ru **e-mail: saxicola@mail.ru

Received July 3, 2020; revised September 22, 2020; accepted October 3, 2020

Abstract—Some aspects of thermal biology were considered in three species of the lizard genus *Darevskia*: the parthenogenetic *Darevskia armeniaca* and *D. unisexualis*, and their parental bisexual species *Darevskia valentini*. The main objective of the present research was to compare the thermal biology of these species in a mixed population. Material was captured at four localities in Armenia: Kuchak, Dilijan, Mets Sepasar, and Artavaz in summer 2007, 2013, 2016, and 2018, respectively. Their snout-vent length and cloacal body temperature, as well as air and substrate temperatures were measured. The following differences in the thermal biology of the study species were revealed: *D. unisexualis* had a relatively low activity temperature range ($T = 22.0-32.8^{\circ}$ C, vs. 25.6–35.6°C for *D. armeniaca* or 25.3–35.4°C for *D. valentini*). The body temperatures of different species were found to correlate differently with both the air temperature and the substrate temperature under the conditions of their coexistence at Kuchak.

Keywords: sympatry, snout-vent length, cloacal body temperature, air temperature, substrate temperature, correlation, Armenia

DOI: 10.1134/S1062359022080155

INTRODUCTION

Rock lizards belong to the genus Darevskia (Lacertidae), which is divided into seven supraspecific complexes (raddei, rudis, saxicola, caucasica, chlorogaster, defilippii, and steineri (Arribas, 1999; Ahmadzadeh et al., 2013)) and includes 34 species, seven of which reproduce parthenogenetically (Ahmadzadeh et al., 2013). The latter were formed as a result of hybridization of bisexual species (Darevsky, 1967; Darevsky et al., 2000). According to one version, the parthenogenetic species D. armeniaca (Mehely 1909) arose as a result of hybridization of specimens belonging to bisexual species: male D. valentini (Boetlger 1892) (group rudis) and female D. mixta (Mehely 1909) (group raddei) (Fu et al., 2000). According to another version, the origin of this species is associated with the hybridization of the male of the bisexual species D. valentini and the parthenogenetic female D. dahli (Darevsky 1957) (Tarkhnishvili et al., 2017). Another parthenogenetic species, D. unisexualis (Darevsky 1966), arose as a result of hybridization of female *D. raddei nairensis* (Darevsky, 1967) (group *raddei*) and male *D. valentini* (group *rudis*) (Murphy et al., 1996). Despite the considerable time of divergence of the main phylogenetic clades in the genus *Darevskia*, about 18 Ma (Murtskhvaladze et al., 2020), rock lizards are a group of biologically similar species adapted to life in mountains (Darevsky, 1967). The hybrid origin of parthenogenetic species of rock lizards and the presence of genomes of two species within the same organism (Spangenberg et al., 2020), as in other reptile species (Sites et al., 1990), indirectly indicate the combining of the adaptive properties of parents by the daughter species (Anderson and Stebbins, 1954).

The modern ranges of the bisexual parent species *D. valentini* and its daughter parthenogenetic species *D. armeniaca* and *D. unisexualis* overlap significantly (Arakelyan et al., 2011). In central Armenia, they form joint settlements, where both parthenogenetic species can be found simultaneously, and sometimes all three species together (Danielyan et al., 2008; Galoyan, 2010). In this case, they use the same shelters and

basking sites and constantly interact (Galoyan, 2013). It is known that the pattern of daily activity of D. armeniaca and D. unisexualis is different: D. armeniaca leave their overnight shelters later in the morning than D. unisexualis and hide in them later in the evening (Abrahamyan et al., 2014). However, some features of the thermal biology of these three species remain unexplored. In particular, it remains unclear how their temperature depends on the temperature of the air and the substrate: there is no data on the activity temperature range of D. unisexualis; it is unknown if the features of thermal biology are similar for *D. armeniaca*, D. unisexualis, and D. valentini in cohabitation conditions. We set ourselves the goal of determining the thermal biological characteristics of these species under conditions of syntopy and allopatry.

Species Studied

Rock lizards are common in the Caucasus, the Crimea, and Asia Minor. They tend to dwell in habitats with a large number of rocks or stones, which they use as shelters (Darevsky, 1967; Galoyan, 2010). Some species (*D. brauneri* (Mehely 1909), *D. mixta* (Mehely 1909)) in the forests switch to an arboreal way of life, and some leave the rocks for the steppes and meadows (*D. valentini*, *D. caucasica* (Mehely 1909)). Rock lizards use not only natural habitats, but also anthropogenic ones (stone walls, ruins of buildings, bridges, and dams), and sometimes their numbers in artificial habitats are even higher than in natural ones (Darevsky, 1967; Galoyan, 2010).

D. armeniaca was detected in Armenia, Georgia, northeastern Turkey, and northwestern Azerbaijan. The snout-vent length (SVL) of sexually mature specimens is 51–73 mm. The color of the dorsum ranges from green or olive to brown. From the head to the tail along the middle of the back there is an occipital band, consisting of specimen spots elongated across the body. On the sides of the back there are temporal bands formed by fused dark rings with white centers. In the region of the forelimbs, two spots have blue centers. Below the temporal bands are the lower temporal bands, also consisting of merged dark circles. The belly is pale yellow, sometimes with blue or black spots on the outer plates. The head is covered with small dark spots (Darevsky, 1967).

D. unisexualis occurs in Armenia, and its habitats are separated and located on the borders of the range of *D. r. nairensis*. The snout–vent length of mature specimens is 56-70 mm. The upper part of the body is beige–gray, covered with small dark spots. On the sides of the body, there are rows of larger contiguous spots, all of them, except for one blue one at the level of the forelimbs, are black with white centers (Darevsky, 1967).

D. valentini belongs to the *rudis* species group. This species is found in Turkey, Georgia, and Armenia. The

color of the back of representatives of this species varies from yellow-olive to brown-green. The occipital band consists of large black or brown spots of irregular shape. The temporal bands consist of 1-3 rows of merged dark circles with blue centers (Darevsky, 1967). This species is considered the parent of *D. armeniaca* and *D. unisexualis*.

Sites and Times of Study

This work included data from four study sites. Within them, we selected trial areas where the necessary measurements were performed. The first site was inhabited by D. armeniaca. The study site was located in Dilijan National Park (40°45' N. 44°52' E. Tavush district, in the vicinity of the city of Dilijan, 1400 m a.s.l.). in a beech-hornbeam forest. The trial site was located at the bottom of a valley between two watersheds on the southern macroslope of the Ijevan Range. A stream bed runs along the bottom of the gorge, which partially dries up in summer. The slopes of the valley are steep up to 50°. The main forest-forming species of the forest are *Quergus* spp. and *Carpinus orientalis* with an admixture of Sorbus sp. and Betula sp. The surface is formed by a "large stone slope," on which litter is well retained, the thickness of which reaches 15-20 cm; single plants are found, and in some places the vegetation forms thickets. The study was carried out from June 21 to August 3, 2007.

The second site inhabited by *D. armeniaca*, *D. uni-sexualis*, and *D. valentini* was located in the vicinity of the city of Aparan (Aragatsont oblast), near the village of Kuchak (40°31" N, 44°23" E; 1920 m a.s.l.) on the northern macroslope of Aragats Mountain. The landscape is an alpine forb meadow, on which there are stony hills of moraine origin 20–30 m high, inhabited by lizards. Outcrops of basalt bedrocks located along the road are penetrated by deep cracks in which lizards hibernate. Rosehip bushes (*Rosa* sp.) grow on top of the hills. The research was carried out in June and July 2013.

The third site was located in northwestern Armenia in Shirak province, in the vicinity of the settlement of Mets Sepasar, at an altitude of 2000 m a.s.l. (41.031482 N, 43.829823 E). More lizards were observed in segments with a high number of stones. The herbaceous layer mainly did not exceed a height of 20–30 cm, reaching a maximum of 40–50 cm, and was composed mainly of *Bromus* sp., *Poa* sp., *Veronica* sp., *Trifolium* spp., *Myosotis alpestris, Ornithogalum* sp., *Rumex confertus*, and *Tragopogon pratensis*. The collection of *D. valentini* material occurred from May 13 to June 15, 2016.

The fourth study site was located in the vicinity of the village of Artavaz (Armenia, Kotai oblast, 40°37' N, 44°34' E, height about 2000 m a.s.l.) in a small area of an "Unmanaged mesic grassland" (type E2.7; Fayvush and Aleksanyan, 2016). Here *D. armeniaca* and *D. unisexualis* were revealed; however, only specimens of the first species were included in the samples. Among the plants on the site, various cereals predominated; the family Fabaceae was represented mainly by Trifolium repens, Trifolium campestre, and Trifolium ambiguum. The family Asteraceae was represented by the common dandelion (Taraxacum officinale) and Achillea biebersteinii. Plantago lanceolata was also detected everywhere on the site. The site was limited on three sides by roads, and on the fourth side by the left bank of the Marmarik River. A concrete building with cracks in the north wall was located on the left bank of the Marmarik River. These cracks served as hiding places for the lizards. In addition, from east to west the site had a shallow ravine filled with concrete slabs. Lizards also hid in the cracks between them. Here, the studies were carried out on June 16 and 17, 2018.

MATERIALS AND METHODS

Collection of Field Material

Field studies were carried out during the period of activity of lizards in the first half of the day. Lizards were caught by noosing. Immediately after capture, the snout-vent length (SVL) was measured with a ruler with an accuracy of 1 mm and the cloacal body temperature was measured with a thermocouple (AZ8803) with an accuracy of 0.1°C. During the measurements, we held the lizards in our hands; therefore, we tried to measure the temperature within 10 s so that the body temperature of the lizards did not have time to change due to contact with the hands and the stress of the animal. After the necessary manipulations with the lizard, a thermocouple was used to measure the temperature of the substrate on which the lizard was caught and the air temperature near the surface of the substrate at a height of 2-3 cm.

The study did not include data on immature specimens, the snout-vent length of which was less than 50 mm (Darevsky, 1967). The rate of heating and cooling in small lizards is higher than this in large lizards of the same species (Carothers et al., 1997), which is why their inclusion in the sample could distort the results. In this study, we used data of 22 *D. armeniaca* specimens from the neighborhood of Artavaz, 26 *D. armeniaca* specimens and 21 *D. unisexualis* specimens from Kuchak, 18 *D. armeniaca* specimens from Dilijan, eight males and 21 females of *D. valentini* from Mets Sepasar and 19 males and four females of *D. valentini* from Kuchak.

The body temperature range of a reptile at which it can exhibit activities such as movement, feeding, hunting, etc., although it may remain motionless or to regulate body temperature, is the activity temperature range (Bauwens et al., 1996; Espinoza and Tracy, 1997). In order to achieve and maintain this temperature, reptiles use physiological (darkening or lightening of covers, increasing or decreasing heart rate) and behavioral (transition from illuminated areas to shade and vice versa, movement between substrates with different temperatures) reactions (Espinoza and Tracy, 1997). In Artavaz, we caught only lizards that lay near shelter, more or less motionless on a sunlit surface (i.e., probably engaged in heating, or basking). In other study sites, only lizards showing forms of routine activities such as moving, feeding, etc., were caught (Cherlin, 2015).

Material Treatment

For each species of lizard, we found the mean activity temperature (Huey, 1982; Espinoza and Tracy, 1997), which made it possible to compare the obtained data with the available data on other species of rock lizards (Tsellarius and Tsellarius, 2001). We also calculated the median (Me) for each sample of cloacal body temperatures of lizards. In addition, for the description of the body temperature of the lizards studied, the dependence of the cloacal body temperature on the temperature of the substrate and the ambient air temperature were plotted and regression equations for these dependences were obtained (in all equations x is air or the substrate temperature, and y is the cloacal body temperature).

We divided the sample of *D. armeniaca* from Artavaz into two groups: those that reached and those that did not reach the activity temperature. For this, the cloacal body temperatures of lizards from Artavaz with the cloacal body temperatures of lizards from the combined sample from Kuchak and Dilijan were compared, since significant differences between the body temperatures of lizards from these places were not revealed (Mann–Whitney test, N = 26, 18, respectively, p = 0.684).

We considered that these samples reflect the range of activity temperatures of Armenian lizards, since in these research sites body temperature was measured only in active specimens, based on their behavior. In the combined sample of Armenian lizards from Kuchak and Dilijan, we found the mean body temperature and values limiting the 95% confidence interval (they were calculated as $M \pm 2SD$, where M is the mean, SD is the standard deviation; M = 30.7, SD = 1.84, M + 2SD = 34.41, M - 2SD = 27.05). We considered it possible to use such a formula, since the distribution of the mean cloacal body temperature in the combined sample from Kuchak and Dilijan did not differ significantly from normal (Shapiro-Wilk test, p = 0.192, N = 44, Fig. 1). Values below the lower limit of the calculated confidence interval were then removed from the sample of body temperatures of lizards from Artavaz.

We also carried out all calculations for the sample from Artavaz, from which we did not remove data on lizards with a temperature below the calculated confidence interval. The samples from which the values of

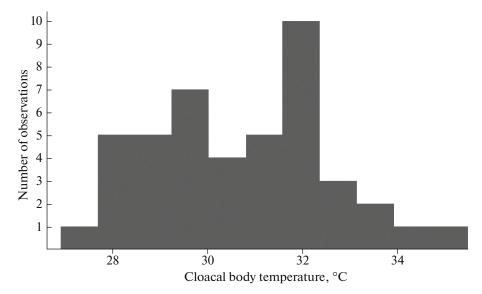


Fig. 1. Distribution of the body temperature of D. armeniaca from Kuchak and Dilijan.

lizard body temperatures below the calculated confidence interval were removed or not removed were called "truncated" and "untruncated" samples, respectively.

For the analysis of data on the temperature values, nonparametric methods were used (Mann-Whitney test, Kruskal-Wallis test, Spearman correlation coefficient). For a comparison of the coefficients of the regression equations of the body temperature of lizards and the ambient temperature, we used the Chow test with the χ^2 distribution. Before the Chow test, the studied samples were checked for equality of the residual variances using the F-test. In cases with significant differences in the residual variances found according to this test, we did not perform the Chow test. For all analyses, the alternative hypothesis was accepted at p <0.05. The data was processed using the R language strucchange (Zeileis et al., 2002) and dunn.test (Dino, 2017) packages. The plots were made using the ggplot2 package (Wickham, 2016).

RESULTS

Air Temperature

Significant differences between air temperatures in Mets Sepasar and Dilijan and Mets Sepasar and Kuchak were revealed, while significant differences between other study sites were not detected (Kruskal– Wallis test, Dunn test, Holm method) (Table 1).

Effects of Body Size and Gender on Temperature

A significant correlation between the snout-vent length of lizards and their cloacal temperature was not revealed for *D. armeniaca* from Dilijan, Kuchak, or Artavaz with and without taking into account lizards with a body temperature below the range of body temperatures of active lizards (Rs = 0.29, 0.1, 0.09, 0.007,p = 0.249, 0.644, 0.703, 0.977; N = 18, 26, 21, 22,respectively) and *D. unisexualis* from Kuchak (Rs =0.03, p = 0.915, N = 20). Significant differences between the activity temperatures of *D. valentini* males and females were also not found (Mann–Whitney test, p = 0.634, N = 27, N = 25, respectively); therefore, in further analyses, we used data on males and females as a single sample.

Activity Temperature

Significant differences between activity temperatures of *D. armeniaca* from Kuchak, Artavaz, and Dilijan using "truncated" and "untruncated" samples from Artavaz (Kruskal–Wallis test, p = 0.192, 0.221; N = 26, 21, 22, 18, respectively) and *D. valentini* from Kuchak and Mets Sepasar (Mann–Whitney test, p =

Table 1. p-Values obtained by a pairwise comparison of air temperatures in different places of the study using the Dunn test

Location of the study	Artavaz ($N = 22$)	Dilijan ($N = 18$)	Kuchak ($N = 70$)
Dilijan	0.166	_	_
Kuchak	0.212	0.177	_
Mets Sepasar ($N = 26$)	0.254	0.006	0.006

N is the sample size.

			М		Med		Max		Min			S	D
Species	Sex	Locality	separately	general sample	Ν	separately	general sample						
D. armeniaca	Females	Artavaz	31.8	31.1	31.7	30.95	35.6	35.6	27.3	27.2	21 (22)	2.35 (2.66)	2.08 (2.17)
		TZ 1 1	20.0		21		25		27.0		. ,	. ,	(2.17)
		Kuchak	30.9		31		35		27.8		26	1.94	
		Dilijan	30.6		30.85		33.4		27.2		18	1.72	
D. unisexualis	Females	Kuchak	27.8	—	29	—	32.8	—	22	_	21	3.07	_
D. valentini	Females	Mets Sepasar	31.4	31.5	31.3	31.6	35.4	35.4	26.7	25.3	21	2.52	2.17
		Kuchak	32.8		32.65		34.6		31.2		4	1.52	
	Males	Mets Sepasar	31.2		31.15		34.2		28.3		8	2.19	
		Kuchak	31.4		31.8		33.8		25.3		19	1.91	

Table 2. Indicators of the cloacal body temperature of the lizards studied

Figures in parentheses are the data obtained on the "untruncated" sample from Artavaz.

0.549, N = 23, 29, respectively) were not revealed; therefore, the *D. armeniaca* and *D. valentini* samples from different locations were combined for the calculation of the activity temperatures (Table 2).

The lower limit of the activity temperature range of Armenian lizards according to the combined "truncated" sampling from Artavaz, Kuchak, and Dilijan was 27.2°C, according to the "untruncated" sample it was 25.6°C, and the upper limit was 35.6°C. The average body temperature taking into account the data of the "truncated" sample was 31.1 (± 2.08)°C, and the median was 31°C; taking into account the data of the "untruncated" sample, the mean value was 31 (± 2.17)°C and the median was 30.95°C.

The body temperature range of *D. unisexualis* was within 22–32.8°C. At the same time, the mean value was 27.8 (\pm 3.25)°C, and the median was 29°C and significantly differed from the median body temperature of Armenian lizards using data from both "truncated" and "untruncated" samples from Artavaz (Dunn test, Holm method, *p* < 0.001).

The comparison of the activity temperatures of parthenogenetic species with the activity temperatures of the bisexual parental species *D. valentini* showed that it is similar to *D. armeniaca* in the analysis of the "truncated" and "untruncated" samples from Artavaz and significantly different from *D. unisexualis* (Dunn test, Holm method, p = 0.127, p = 0.102, p < 0.001, respectively) and the average is $31.5 (\pm 2.17)^{\circ}$ C (25.3– 35.4° C, $Me = 31.6^{\circ}$ C, N = 52) (Fig. 2, Table 2).

BIOLOGY BULLETIN Vol. 49 No. 8 2022

Relationship of the Cloacal Temperature of Lizards, Air and Substrate Temperatures

We found a positive relationship between the air temperature in the surface layer and the cloacal body temperature of D. armeniaca in Artavaz in the "truncated" Rs = 0.477, N = 21, p = 0.029, y = 0.3382x +24.3588) and "untruncated" (Rs = 0.51, N = 22, p =0.016, y = 0.3854x + 23.0622) samples in Dilijan (Rs = 0.477, N = 18; p = 0.045; y = 0.2734x + 25.0264) and Kuchak (Rs = 0.151, p = 0.459, N = 26, y = 0.3404x +24.2269). However, differences in the coefficients of the regression equations between Kuchak and Dilijan (Chow test, N = 26, 18, p = 0.668, Figs. 3b, 3c), Dilijan and Artavaz (Chow test, N = 18, 21, p = 0.539, Figs. 3a, 3b), and Artavaz and Kuchak using "truncated" (Chow test, N = 21, 26, p = 0.991, Figs. 3a, 3b) and "untruncated" (Chow test, N = 22, 26, p = 0.922) samples were not revealed. The substrate temperature and cloacal body temperature of D. armeniaca from Artavaz in "truncated" (Rs = 0.61, p = 0.003, N = 21, y = 0.31x + 23.09) and "untruncated" (Rs = 0.568, p = 0.006; N = 22; y = 0.355x + 21.631) samples and the sample from Kuchak (Rs = 0.746, p < 0.001, N = 26, y = 0.2851x + 21.8152) were significantly related (Figs. 3e, 3g). Furthermore, the coefficients of the regression equations for the cloacal body temperature and substrate temperature and the cloacal body temperature and air temperature for *D. armeniaca* from the "truncated" (Chow test, = 21, p = 0.026; Figs. 3a, 3e) and "untruncated" (Chow test, N = 22, p = 0.026) samples from Artavaz differed significantly (Figs. 3c, 3g).

The air temperature in the surface layer and the cloacal temperature of *D. unisexualis* from Kuchak turned out to be related (Rs = 0.62, p = 0.004, N = 20,

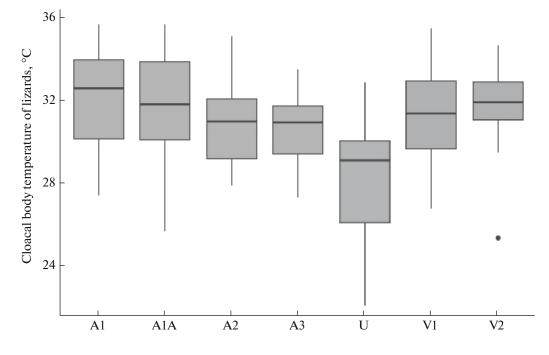


Fig. 2. Activity temperatures of *D. armeniaca* from Artavaz (A1), Kuchak (A2), and Dilijan (A3); *D. unisexualis* from Kuchak (U); and *D. valentini* from Mets Sepasar (V1) and Kuchak (V2). The black line is the median. The borders of the box are the upper and lower quartiles. The ends of the whiskers are the lowest and highest values within 1.5 interquartile ranges, and the dot is the outlier.

y = 0.8085x + 12.7479). A relationship between the temperature of the substrate and the cloacal body temperature of *D. unisexualis* from Kuchak (Rs = 0.254, p = 0.28, N = 20, y = 0.1833x + 22.3913) was not detected. The coefficients of the regression equations for the cloacal body temperature and the substrate temperature and the cloacal body temperature and the air temperature for *D. unisexualis* from Kuchak (Chow test, N = 20, p = 0.005, Figs. 3d, 3f) differed significantly.

The correlation between the cloacal body temperature of *D. valentini* and the temperature of the substrate was not statistically significant in the samples from Kuchak and Mets Sepasar (Rs = 0.32, 0.25, p =0.134, 0.233, N = 23, 24, y = 0.1598x + 27.2479; y =0.097x + 28.645, respectively), but we found a relationship between the cloacal body temperature and the air temperature in the groups from Kuchak (Rs = 0.42, p = 0.046, N = 23, y = 0.1884x + 26.6143) and Mets Sepasar (Rs = -0.53, p = 0.005, N = 26, y = -0.3367x +40.0517), and in the latter case the relationship was inverse. The coefficients of the regression equations for the cloacal body temperature and air temperature did not differ significantly in D. valentini samples from Kuchak and Mets Sepasar (p = 0.404, N = 23, 26), the coefficients of the regression equations for the body temperature and substrate temperature in these samples also did not differ (Chow test, p = 0.993, N = 23, 24, Figs. 3h, 3j).

The coefficients of the regression equations for the air temperature (Chow test, N = 23, 20, p = 0.003;

Figs. 3d, 3k) and the cloacal temperature for *D. val*entini and D. unisexualis from Kuchak differed significantly. The coefficients of the regression equations for the cloacal body temperature of D. armeniaca and D. unisexualis and the substrate temperatures (Chow test, N = 26, 20, p < 0.001, Figs. 3f, 3g) and air temperature (Chow test, N = 26, 20, p < 0.001, Figs. 3c, 3d) in Kuchak also differed significantly. The coefficients of the regression equations for air temperature and the cloacal body temperature for D. valentini and D. armeniaca from Kuchak did not differ significantly (Chow test, N = 23, 26, p = 0.669, Figs. 3c, 3k), while the coefficients of the regression equations for the substrate temperature and cloacal temperature bodies differed significantly (Chow test, N = 23, 26, p < 0.001, Figs. 3g, 3j).

DISCUSSION

It is known from the literature that the body temperature of the active forest lizards *D. brauneri* (Mehely 1909) on average is $32.0 (\pm 2.2)$ °C (Tsellarius, Tsellarius, 2001), and it is similar to the temperatures obtained in our study for species living in high mountain meadows. Data on the preferred body temperature of *D. armeniaca* obtained by us are quite close to the literature data on this species (approximately 30°C according to literature data) (Darevsky, 1967) and some other species, although they differ from them by about 1°C. In the literature there are no data on the activity temperatures of *D. unisexualis*, and according

BIOLOGY BULLETIN Vol. 49 No. 8 2022

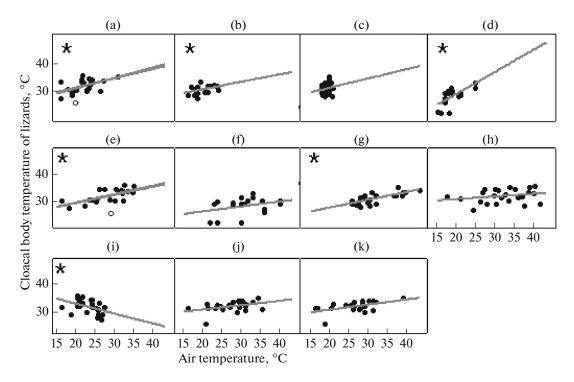


Fig. 3. Relationship of the cloacal temperature of *D. armeniaca* with the air temperature in Artavaz (a), Dilijan (b), and Kuchak (c); the relationship of the cloacal body temperature of *D. unisexualis* with the air temperature (d) and substrate temperature (f); the relationship of the cloacal body temperature of *D. armeniaca* with the substrate temperature in Artavaz (e) and Kuchak (g). Relationship of the cloacal body temperature of *D. armeniaca* with the substrate temperature in Artavaz (e) and Kuchak (g). Relationship of the cloacal body temperature of *D. valentini* with the substrate temperature in Mets Sepasar (h) and Kuchak (j) and the air temperature in Mets Sepasar (i) and Kuchak (k). * Statistically significant relationships, the white dot means data on this specimen were removed from the "truncated" sample.

to our data, the mean values (and median) are $27.8-29.0^{\circ}$ C, which is several degrees lower than that of the other studied representatives of the genus *Darevskia*. Based on some features obtained us for the studied species (the activity temperature range is in the region of 30° C, and for *D. unisexualis* it is even lower, after heating in the morning, there is a long basking, which is noticeable in *D. armeniaca* sample from Artavaz, and optimal body temperatures can be recorded during basking), all of them can be attributed to potentially nocturnal reptiles (Cherlin, 2010).

It has been shown previously that *D. unisexualis* lizards start to leave night shelters earlier in the morning and return into them earlier in the evening than *D. armeniaca* lizards that live syntopicaly (Abrahamyan et al., 2014). The relatively early exit of *D. unisexualis* from shelters can be attributed to the fact that their activity temperatures are lower than those of *D. armeniaca*, which means for the start of routine activities they need a lower body temperature and, probably, a lower environmental temperature.

It can be assumed that the low activity temperature range of *D. unisexualis* in comparison with *D. armeniaca* is associated with the origin of this species from the alpine subspecies of *D. raddei*, *D. raddei* nairensis (Vergun et al., 2020), living at altitudes of 2000–

BIOLOGY BULLETIN Vol. 49 No. 8 2022

3000 m a.s.l. (Arakelyan et al., 2011), while the species that are considered maternal for *D. armeniaca*, *D. mixta* and *D. dahli* (Fu et al., 2000; Vergun et al., 2014), occur in warmer climates and at lower altitudes: 1250–1500 (Petrosyan et al., 2019) and 700–1500 m a.s.l., respectively.

There are reasons to believe that the ecological niches of D. valentini and D. armeniaca are close, since they have similar requirements for temperature, humidity, and other environmental parameters (Petrosvan et al., 2019). The detected similarity in the activity temperatures of these species also indicate their ecological proximity (Fig. 2), which was also confirmed in an experiment in a thermogradient apparatus (Galoyan et al., 2019). Thus, the experimental data and observations show differences in the thermal biology of D. unisexualis, D. armeniaca, and D. valentini, which is interesting from a biological point of view and allows us to hypothesize about the biological differences between these species. In Kuchak the substrate temperature had a different effect on the cloacal temperature of D. valentini and D. armeniaca lizards, which may indicate a different use of substrate heat for heating by these species. Also, the temperature of both of these species depends on ambient temperatures differently than the temperature

of *D. unisexualis*, which may indicate a different use of resources for heating by different species of rock lizards under cohabitation conditions. It is possible that these differences allow coexisting species to reduce interspecies competition in mixed populations with high population densities.

The revealed statistically significant negative correlation coefficient between the air temperature in Mets Sepasar and the cloacal temperature of *D. valentini* may be due to the small sample size, since it is difficult to find an explanation for this phenomenon. The statistically significant correlation coefficient between the air temperature in Kuchak and the cloacal temperature of *D. valentini* shows a rather weak relationship. Thus, we did not reveal biologically significant relationships between the cloacal body temperatures of representatives of this species and the environmental temperatures.

ACKNOWLEDGMENTS

The authors are grateful to E.I. Kudryavtseva and E.G. Petrash for help in collecting material and writing the article; S.N. Lysenkov for help with statistical data processing; and K.A. Tyurin, E.L. Stelmakhova, and Yu.A. Trifonova for help with plant identification. The authors express their special gratitude to the anonymous reviewer for the significant improvement of the proposed manuscript.

FUNDING

This study was carried out within the framework of topic AAAA-A16-116021660077-3 and was supported by the Russian Science Foundation (project no. 22-14-00227).

COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interest. The authors declare that they have no conflicts of interest.

Statement on the welfare of animals. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

REFERENCES

Abrahamyan, M.R., Petrosyan, R.K., Galoyan, E.A., Danielyan, F.D., and Arakelyan, M.S., Seasonal and daily activities of two syntopic parthenogenetic lizards of genus *Darevskia, Chem. Biol.*, 2014, no. 2, pp. 39–42.

Ahmadzadeh, F., Flecks, M., Carretero, M.A., Mozaffari, O., Bohme, W., et al., Cryptic speciation patterns in Iranian rock lizards uncovered by integrative taxonomy, *PLoS One*, 2013, vol. 8, no. 12, pp. 1–17.

Anderson, E. and Stebbins, G., Hybridization as an evolutionary stimulus, *Evolution*, 1954, vol. 8, no. 4, pp. 378–388.

Arakelyan, M.S., Danielyan, F., Corti, C., Sindaco, R., and Leviton, A., *Herpetofauna of Armenia and Nagorno-Karabakh*, Salt Lake City: Society for the Study of Amphibians and Reptiles, 2011. Arribas, O.J., Phylogeny and relationships of the mountain lizards of Europe and Near East (*Archaeolacerta* Mertens, 1921, sensu lato) and their relationships among the Eurasian lacertid radiation, *Russ. J. Herpetol.*, 1999, vol. 6, no. 1, pp. 1–22.

Bauwens, D., Hertz, P.E., and Castilla, A.M., Thermoregulation in a lacertid lizard: the relative contributions of distinct behavioral mechanisms, *Ecology*, 1996, vol. 77, no. 6, pp. 1818–1830.

Carothers, J.H., Fox, S.F., Marquet, P.A., and Jaksis, F.M., Thermal characteristics of ten andean lizards of the genus *Liolaemus* in central Chile, *Rev. Chil. Hist. Nat.*, 1997, vol. 70, pp. 297–309.

Cherlin, V.A., *Termobiologiya reptilii. Obshchie svedeniya i metody issledovanii (rukovodstvo)* (Thermobiology of Reptiles. General Information and Research Methods (Manual)), St. Petersburg: Russ.-Balt. Inf. Tsentr BLITs, 2010.

Cherlin, V.A., Thermal adaptations of reptiles and mechanisms of their formation, *Prints. Ekol.*, 2015, no. 1, pp. 17–76.

Danielyan, F., Arakelyan, M., and Stepanyan, I., Hybrids of *Darevskia valentini, D. armeniaca* and *D. unisexualis* from a sympatric population in Armenia, *Amphibia-Reptilia*, 2008, vol. 29, pp. 487–504.

Darevsky, I.S., Skal'nye yashcheritsy Kavkaza: Sistematika, ekologiya, filogeniya polimorfnoi gruppy kavkazskikh skal'nykh yashcherits podroda Archaeolaserta (Rock Lizards of the Caucasus: Systematics, Ecology, Phylogeny of the Polymorphic Group of Caucasian Rock Lizards of the Subgenus Archaeolacerta), St. Petersburg: Nauka, 1967.

Darevsky, I.S., Grechko, V.V., and Kupriyanova, L.A., Lizards breeding without males, *Priroda* (Moscow, Russ. Fed.), 2000, no. 9, pp. 131–133.

Dinno, A., Dunn's test of multiple comparisons using rank sums, 2017. https://cran.r-project.org/web/packages/dunn.test/. Accessed October 27, 2017.

Espinoza, R.E. and Tracy, R.C., *The Biology, Husbandry and Health Care of Reptiles*, vol. 1: *Biology of Reptiles*, Biological Resources Research Center and Department of Biology, 1997.

Faivush, G.M. and Aleksanyan, A.S., *Mestoobitaniya Armenii* (Habitats of Armenia), Yerevan: Nats. Akad. Nauk Resp. Armenia, Inst. Bot., 2016.

Fu, J., McCulloch, R.D., Murphy, R.W., and Darevsky, I.S., Clonal variation in the caucasian rock lizard *Lacerta armeniaca* and its origin, *Amphibia-Reptilia*, 2000, vol. 21, pp. 83–89.

Galoyan, E.A., Distribution of parthenogenetic rock lizards *Darevskia armeniaca* and *Darevskia unisexualis* in northern Armenia and comparison with bisexual species, *Zool. Zh.*, 2010, vol. 89, no. 4, pp. 470–474.

Galoyan, E.A., Interspecific and intraspecific intersex relationships in rock lizards of the genus Darevskia, in *Stat'i po materialam dokladov Pervoi mezhdunarodnoi molodezhnoi konferentsii gerpetologov Rossii i sopredel'nykh stran* (Articles Based on the Materials of the Reports of the First International Youth Conference of Herpetologists of Russia and Neighboring Countries), St. Petersburg: Zool. Inst. Ross. Akad. Nauk, 2013, pp. 61–66.

Galoyan, E., Bolshakova, A., Abrahamyan, M., Petrosyan, R., Komarova, V., et al., Natural history of Valentin's rock lizard (*Darevskia valentini*) in Armenia, *Zool. Res.*, 2019, vol. 40, no. 4, pp. 277–292.

BIOLOGY BULLETIN Vol. 49 No. 8 2022

Huey, R.B., *Temperature, Physiology, and the Ecology of Reptiles*, New York: Academic Press, 1982, vol. 12, pp. 25–91.

Murphy, R.W., Darevsky, I.S., MacCulloch, R.D., Fu, J., and Kupriyanova, L.A., Evolution of the bisexual species of Caucasian rock lizards: a phylogenetic evaluation of allozyme data, *Russ. J. Biol.*, 1996, vol. 3, no. 1, pp. 18–31.

Murtskhvaladze, M., Tarkhnishvili, D., Anderson, C., and Kotorashvili, A., Phylogeny of Caucasian rock lizards (darevskia) and other true lizards based on mitogenome analysis: optimisation of the algorithms and gene selection, *PLoS One*, 2020, no. 15, article ID e0233680.

https://doi.org/10.1371/journal.pone.0233680

Petrosyan, V., Osipov, F., Bobrov, V., Dergunova, N., Nazarenko, E., et al., Analysis of geographical distribution of the parthenogenetic rock lizard *Darevskia armeniaca* and its parental species (*D. mixta*, *D. valentini*) based on ecological modelling, *Salamandra*, 2019, vol. 55, no. 3, pp. 173–190.

Sites, J.W., Peccinini-Seale, D.M., Moritz, C., Wright, J.W., and Brown, W.M., The evolutionary history of parthenogenetic *Cnemidophorus lemniscatus* (Sauria, Teiidae). I. Evidence for a hybrid origin, *Evolution*, 1990, vol. 44, no. 4, pp. 906–921.

Spangenberg, V., Arakelyan, M., Cioffi, M.D.B., Liehr, T., et al., Cytogenetic mechanisms of unisexuality in rock lizards, *Sci. Rep.*, 2020, vol. 10, no. 8697. Tarkhnishvili, D., Murtskhvaladze, D., and Anderson, C.L., Coincidence of genotypes at two loci in two parthenogenetic rock lizards: how backcrosses might trigger adaptive speciation, *Biol. J. Linn. Soc.*, 2017, vol. 121, pp. 365–378.

Tsellarius, A.Yu. and Tsellarius, E.Yu., Dynamics of the spatial structure of the population of *Lacerta saxicola* in broad-leaved forests of the Navagir Ridge, *Zool. Zh.*, 2001, vol. 80, no. 7, pp. 1-8.

Vergun, A.A., Girnyk, A.E., Korchagin, V.I., Semyenova, S.K., Arakelyan, M.S., et al., Origin, clonal diversity, and evolution of the parthenogenetic lizard *Darevskia unisexualis*, *BMC Genom.*, 2020, vol. 21, no. 351.

Vergun, A.A., Martirosyan, I.A., Semyenova, S.K., Omelchenko, A.V., Petrosyan, V.G., et al., Clonal diversity and clone formation in the parthenogenetic Caucasian rock lizard *Darevskia dahli*, *PLoS One*, 2014, vol. 9, no. 3.

Wickham, H., ggplot2: Elegant Graphics for Data Analysis, New York: Springer-Verlag, 2016. ISBN 978-3-319-24277-4.

Zeileis, A., Leisch, F., Hornik, K., and Kleiber, C., strucchange: an R package for testing for structural change in linear regression models, *J Stat. Software*, 2002, vol. 7, no. 2, pp. 1–38.

Translated by V. Mittova