Keep in touch: The influence of weather conditions on aggregation probability in the rock lizards, *Darevskia armeniaca* and *D. valentini*

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Abstract. Since individual metabolic activity depends on body temperature, maintaining this temperature within the optimal range is important for living organisms. Behavioural adaptations allow body temperature to stay within a narrow range. Huddling helps animals conserve energy more efficiently and improves environmental adaptability under cold conditions. Rock lizards of the *Darevskia* genus also actively engage in huddling on basking sites; thermoregulation, however, has not been previously considered as a possible reason for their grouping. We hypothesise that lizard aggregations might help to maintain body temperature in cold conditions. To test this suggestion, we conducted route surveys in an area with a high population density of two coexisting *Darevskia* species and determined the influence of external conditions on grouping behaviour. We found that the number of lizard groups and the number of individuals per group are significantly larger in cloudy weather and low irradiance than in sunny weather and high irradiance. Correlation analyses did not show a significant effect of air temperature and wind speed on the formation of groups. We suggest that small lizards huddle during poor irradiance to maintain internal body temperature and prolong their activity.

Keywords. Huddling, Irradiance, Lacertidae, Social thermoregulation

Introduction

Social behaviour may be defined as the cooperative group living of several individuals for adaptation to environmental conditions (Fricke, 1973). It may be manifest in affiliative and aggressive interactions (Rubenstein and Abbot, 2017) that often involve physical contact, such as grooming, hugging, and fighting (Tinbergen, 1953). Sociality has arisen many times in different groups of animals (Dunbar and Shultz, 2010) and the reasons for its origin include protection from enemies (Morse, 1977; Lanham, 2001), foraging (Foster, 1985; Dinets, 2017), reproduction (Brown, 1978; Lang, 1984; Socias-Martinez and Kappeler, 2019), and thermoregulation (Moss and While, 2021). The benefits of social thermoregulation have been extensively studied in several endothermic species (Ebensperger, 2001; Gilbert et al., 2010).

Endotherm animals (birds and mammals) can efficiently maintain their body temperature at a high level, because they generate heat through high metabolism rate (Hulbert and Else, 1989; Ruben, 1995). They also use various behavioural adaptations such as posturing, nest-housing, increased locomotor activity (e.g., shivering), and grouping (huddling) under extreme external conditions (Terrien et al., 2011), like bats (Spitzenberger and Weiss, 2021) and penguins (Zitterbart et al., 2011). Dense contact between a large number of individuals allows them to maintain their body temperature and reduce heat loss more efficiently (Gilbert et al., 2010). This occurs because of the change in the body surface-volume ratio (Canals et al., 1989, 1997). Several individuals form a single physical body with high thermal inertia, which reduces the impact of ambient temperature fluctuations on their inner temperature. For the same reason, large reptiles can maintain their body temperature better than small ones (Bogert, 1949; Schmidt-Neilsen, 1964; Stevenson, 1985).

Ectotherms (fishes, amphibians, and reptiles) are not able to generate heat at a constant level from internal resources, except for such special cases as shivering (Harlow and Grigg, 1984) and postprandial thermogenesis (Stuginski et al., 2011). Some of them,

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known as thermoconformers, passively follow ambient temperature, while thermoregulators actively maintain their internal body temperature (Huey and Slatkin, 1976) by behaviour, e.g., exposed or not to an environmental heat source such to the heating effect of solar energy (heliotherms) or warm substrates (thigmotherms) (Pough and Gans, 1982). Reptiles have reached the highest level of thermoregulation among ectotherms, since they use different morphological (Fox, 1948; Schmidt-Neilsen, 1964; Horton, 1972), physiological (Heath, 1966; Gonzalez and Porcell, 1988) and behavioural adaptations (Brattstrom, 1965; Muth, 1977; Tingle, 2020), which include social interactions. One example of a reptile that forms aggregations for better temperature maintenance is the gecko — *Nephrurus millii* (Shah et al., 2003). Similar behaviour has also been observed in the small heliothermic lizards of the genus *Darevskia* (Lacertidae), which are generally known for their diverse sociality (Tsellarius and Tsellarius, 2005; Tsellarius et al., 2016). Numerous field studies have shown that individuals aggregate tightly, clinging to each other during basking (Darevsky, 1967; Galoyan et al., 2019). However, the reason for this behaviour has not been studied before. We hypothesise that aggregations in these lizards are influenced by suboptimal weather conditions, and such behaviour allows maintaining the optimal body temperature of these animals. Thereby, we should expect a higher number of individuals within the groups when irradiance and ambient temperature are low compared to conditions with high irradiance.

Methods

Data collection. In the field, data collection took place on an old dark tuff bridge in Lake Arpi National Park, near the village of Mets Sepasar, Shirak province, northwest of Armenia (41.0305°N, 43.8210°E) (Fig. 1A), elevation 1994 m. We studied the population of two syntopically living species of rock lizards: the parthenogenetic Armenian Rock Lizard, *Darevskia armeniaca* (Mehely, 1909), and the bisexual Valentin's Rock Lizard, *Darevskia valentini* (Boettger, 1892). These small diurnal species live sintopically in high-elevation meadows in Armenia, Georgia, and Turkey (Darevsky, 1967). The Armenian Rock Lizard originated from the hybridisation between *D. valentini* and *Darevskia mixta* (Fu et al., 2000); hence, both species are closely related to each other and possess similar morphology, environmental adaptations and thermobiological requirements (Galoyan et al., 2019; Nikolaev et al., 2022).

Data collection was carried out on a 50-m line transect across the bridge (Fig. 1B). We know that neither of the studied species from the study area has significant
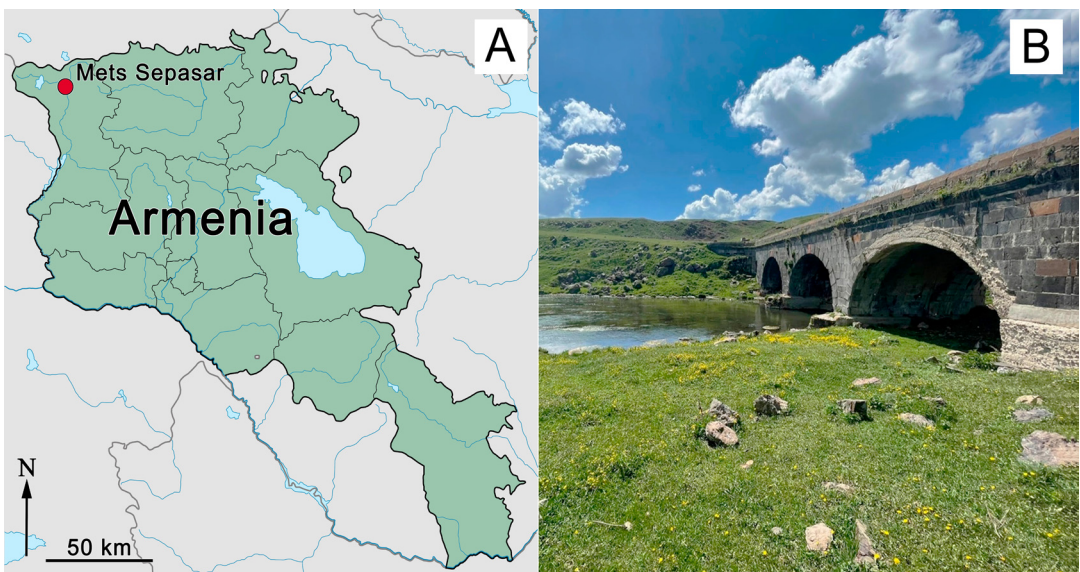

Figure 1. Study area near the village of Mets Sepasar (**A**). General view of the study site on the old bridge (**B**). (Map from Wikimedia Commons author NordNordWest, licensed under CC BY-SA 3.0; colours were changed, labels, scale bar and north arrow were added for the article).

differences in body temperature and diurnal activity (Nikolaev et al., 2022). To locate and determine the lizards, we used Nikon Monarch 8x35 binoculars from a distance of 2–5 metres. Our study was conducted from 31 May 2022 to 14 June 2022 (breeding season) and from 10 to 16 July 2022 (post-breeding season) (Galoyan et al., 2019). One observer slowly and carefully followed the route (along one side of the bridge in the southeast direction, then along other side in the northwest direction), counting the lizards on the walls of the bridge from 10:00 h to 17:00 h, when the lizards were active and remained on the surface of the rocks. We conducted 41 routes during the breeding season and 22 in the post-breeding season. We chose cloudy and sunny days, and avoided periods when the illumination changed rapidly due to fractus clouds. The intervals between route surveys were at least 40 minutes. The duration of each route was about 10 minutes.

We measured the main environmental parameters before each route. For air temperature and wind speed measurements, we used a portable weather station, Kestrel 5500 (precision of 0.1 °C and 0.1 m/s, respectively). To measure the intensity of the visible light (VL) of the irradiance we used a lux meter UNI-T UT383, which measures a range of illuminance from 0–199,900 lx (precision of 100 lx, and a limit of permissible basic relative measurement errors of 5%). To measure the infrared irradiance (IR), we used a nonselective radiometer ARGUS-03, which measures values in the spectral range of 1100–10,000 nm and the range of irradiance from 1.0–2000 W•m^{-2} (precision of 1 W•m^{-2} and a limit of permissible basic relative measurement errors of 5%).

Whilst counting we noted the contact (when two or more individuals have been in physical contact with each other) among the lizards. Then, we considered two types of contact: undense, when individuals touched each other with only a small part of their body such as limbs, tails, or heads (Fig. 2A); and dense, when individuals lay on each other or closely snuggle next to each other (Fig. 2B).

Statistical analysis. The obtained data sets were preliminarily tested for normality using the Shapiro–Wilk test and we used non-parametric tests only according to the results of this test. First of all, we compared the number of individuals per route between breeding and post-breeding seasons to evaluate if we could combine the data into the same data set. For this, we calculated the medians of the total number of observed individuals in all route surveys and applied the Mann–Whitney U test. Though the number of individuals per route varied

within each season, we observed a significant decrease in the number of encountered individuals after the breeding season finished (Mann–Whitney U test $p < 0.01$, $n = 63$). The median number of individuals was 67 ($n = 41$; min = 19 ind.; max = 263 ind.) during the breeding season and only seven ($n = 22$; min = 2 ind.; max = 34 ind.) after it. In this regard, it was necessary to consider these seasons as two separate samples. Hence, our calculations and plots were made using data from the breeding season.

We introduced two coefficients during the observations: C_d (Dense contact coefficient) – the number of individuals encountered in dense contact divided by the total number of individuals encountered in the route survey; C_u (Undense contact coefficient) – the number of individuals encountered in undense contact divided by the total number of individuals encountered in the route survey, and $C_{d+u} = C_d + C_u$. To compare the C_{d+u} coefficient in the breeding and post-breeding seasons, we conducted a robustified non-parametric analysis of covariance (rANCOVA) (Forstner, 2016). We used the total number of individuals for the route surveys as a covariate factor to exclude its influence on the coefficient. The results of the analysis also showed that the samples were significantly different and therefore, they could not be combined ($p = 0.01$, $n = 63$).

To determine the effect of infrared irradiance (IR) and the intensity of visible light (VL) on C_d, we made correlation plots (only using breeding season data) between this coefficient and the intensity of IR or VL. Then we drew a least squares regression line with a 0.95 confidence interval and made a bubble plot to illustrate the differences in the number of individuals per dense contact with IR and VL.

We used Spearman's rank correlation method (Rs) to find the relation of the parameters and weighted Rs to estimate the relation between C_d and C_u and the environmental parameters. For weighting we used the total numbers of individuals for the route surveys.

We used statistical methods according to the biometric manual of Sokal and Rohlf (2012). All the mean values are presented with the standard error (*SE*). The adopted significance level was at *p*-value < 0.05. For data analyses, we used the R environment and the *wCorr* package (Emad and Bailey, 2017). We made plots using the *ggplot2* package (Wickham, 2016).

Results

Weather conditions. The lowest air temperature during the survey was 15.0 °C and the highest was 29.0

Figure 2. Types of contact: (**A**) undense male *D. valentini* and *D. armeniaca* and (**B**) dense contact among lizards (male *D. valentini* underneath, female *D. valentini* above and three females *D. armeniaca* between them). Photos by Eugene Iryshkov.

°C; the intensity of the visible spectrum ranged from 10,000 lux to 163,000 lux, and the infrared irradiance ranged from 122 W•m^{-2} to 913 W•m^{-2}. The highest wind speed was 6 m/s. Infrared irradiation (IR) and visible light (VL) significantly correlated with each other (Rs = 0.81, n = 70, p < 0.01); air temperature positively correlated with IR (Rs = 0.44, n = 62, p < 0.01). Wind speed significantly correlated with air temperature (Rs = -0.42, n = 36, p < 0.01).

The influence of external conditions on C_d and C_u. The dense contact coefficient C_d reduced with increasing intensity of infrared irradiance (Fig. 3A) and the visible sun spectrum (Fig. 3B). The weighted Spearman correlation coefficient between the intensity of IR and C_d was -0.49 (p < 0.01, n = 41) and between the intensity of VL and C_d was -0.60 (p < 0.01, n = 41). We did not find a significant correlation of C_d with air temperature (p = 0.06, n = 36) and wind speed (p = 0.39, n = 36).
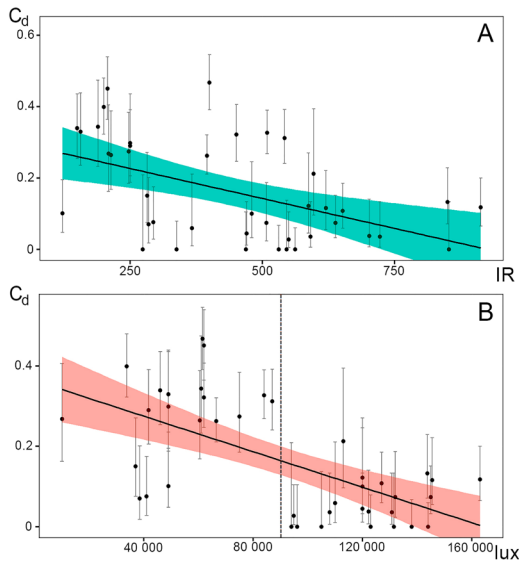
Figure 3. Scatter plot showing the correlation of the dense contact coefficient (C_d) with (**A**) the intensity of infrared irradiance (IR, W•m^{-2}) and (**B**) the intensity of the visible light of the sun (VL, lux). The solid black line represents the least squares regression line, the shaded area represents the confidence interval of 0.95, the whiskers of the points demonstrate the exact binomial confidence interval of 0.95, and the vertical dashed line represents the border at 90,000 lux.

The undense contact coefficient C_u had no significant correlation with IR ($p = 0.81$, $n = 41$), VL ($p = 0.11$, $n = 41$), air temperature ($p = 0.99$, $n = 36$), and wind speed ($p = 0.54$, $n = 36$).

The influence of external conditions on the size of the groups. As the intensity of IR and VL increases, the average size of the groups with dense contacts decreases. Groups of six or more individuals formed only when the irradiance was lower than 90,000 lux. The largest number of comparatively small groups (2–4 individuals) was also detected at low rates of VL (Fig. 4B).

Discussion

Rock lizards are heliotherms and are thus dependent on solar irradiance. The rate of heating of lizards and hence the duration of basking depends on the intensity of solar irradiance. At higher altitudes, the irradiation is stronger and lizards increase their body temperature faster during basking; thereby, this process takes less time than in lower altitudes (Patterson, 1991).

Mets Sepasar is a region with strong irradiation due to the high elevation. According to Global Solar Atlas (globalsolaratlas.info), the irradiation at the lower elevation of the same latitude 41° is less strong. For example, in the city of Tashir, Lori province, Armenia (41.0492°N, 44.3495°E), which has an elevation of 1462 m, regular irradiation is 1242 kWh•m^{-2}; in Mets Sepasar, where the elevation is 1994 m, the irradiation is 1666 kWh•m^{-2}. Therefore, prolonged basking may threaten to reach a critical maximum for lizards (Brattstrom, 1965). This explains the decrease in the encountered number of individuals during sunny days. Similar results were obtained by Tosini et al. (1995): when irradiance was above 700 W•m^{-2}, the lizards *Podarcis muralis* and *Zootoca vivipara* ceased basking due to excessively high heating rate. Hailey (1982) also showed a relationship between infrared irradiance and heating rate in *Z. vivipara*. According to our observations at low irradiance (but not when it rains) the number of observed individuals increased because their heating rate was low and lizards spent most of the day basking.

According to Gilbert et al. (2010), the more individuals huddle and the denser they aggregate, the lower the
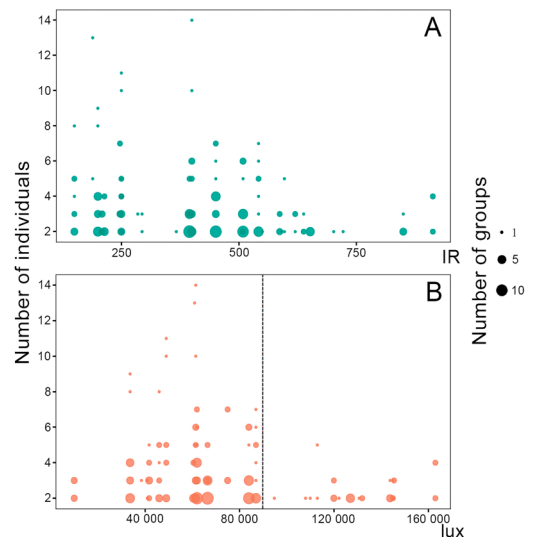

Figure 4. Bubble plot representing the dependence of the number of individuals in dense contact groups on: (**A**) the intensity of infrared irradiance (IR, W•m^{-2}) and (**B**) the intensity of the visible light of the sun (VL, lux). The size of the points depends on the number of groups encountered, with a constitution of a certain number of individuals during one route survey. The vertical dashed line represents the border at 90,000 lux

energy losses observed, while the effect of ambient temperature on the energy benefits of huddling is not so clear. For laboratory mice (*Mus musculus*), the effect of reducing food intake was influenced by both the size of the groups and the ambient temperature to which these groups were exposed (Prychodko, 1958); however, that was not the case for the different species of rodents (Gebczynski, 1969; Gebczynska, 1970; Fedyk, 1971; Tertil, 1972; Martin et al., 1980). For ectotherms, the issue of energy conservation during huddling has not been previously considered, but we can assume that external conditions might influence energy conservation in huddling animals. It is plausible that lizards do indeed tend to form dense contacts at lower irradiance (Fig. 3). There are some differences in the frequency of contacts according to IR and VL intensity: a smoother decrease in the C_d with an increase of IR is observed, while two distinguished clouds are formed on the distribution graph of C_d depending on VL (Fig. 3B): the first at lower lux values and the second with values higher than 90,000 lux. This may be a boundary between the conditions for high motivation to form aggregations and the conditions for its decrease. This hypothesis is also confirmed by the correlation data on the number of individuals within the groups and the number of groups with VL (Fig. 4B). There was also a steep decrease in the number of groups encountered and their size after the border of about 90,000 lux. Tosini et al. (1995) concluded that changes in illuminance (VL here) did not affect set point temperatures, basking duration, and foraging. However, regarding huddling, we observed that the correlation between C_d and VL is even stronger than between C_d and IR. This may indicate that not only information from dorsal skin receptors, but also the visual system can have an important influence on the formation of thermoregulatory behaviour.

The lack of a significant correlation between C_u and other parameters suggests that such contact does not provide any significant thermoregulatory benefits for lizards and may occur randomly due to high population density and limited space for basking. Besides, it can be assumed that such contact may also occur for other reasons, such as courtship in the breeding season (Tsellarius et al., 2016). Strong bonds between males and females of rock lizards were previously described and the main social behaviour between individuals within the couple is joint basking, when both individuals initiate physical contact and spend much time with each other (Tsellarius and Tsellarius, 2005). Joint basking with physical contact or huddling behaviour, which has been observed among parthenogenetic rock lizards

(Galoyan, 2010, 2013), is not socially crucial for them during reproduction due to their unisexual reproduction mode. However, our results demonstrate that huddling behaviour might be one of the most important triggers for the evolutional establishment of social behaviour in lizards.

Finally, experiments should be carried out in laboratory conditions to test the presence of a thermoregulatory benefit of grouping and compare the rates of temperature change both in single lizards and lizards in groups of different sizes. In addition, it is necessary to prove the existence of a real motivation for huddling to exclude the possibility of random formation of groups due to high population density.

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