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Summer daily activity patterns of mountain rock lizards of the Balkan Peninsula (*Dinarolacerta* spp.)

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Abstract: We studied the daily activity patterns of *Dinarolacerta* rock lizards, endemic to the Dinaric mountains of the Western Balkans, during the summer season. The study was conducted in Montenegro at four sites for *D. mosorensis* and three sites for *D. montenegrina*. The air temperature at which the lizards were observed varied significantly both within and between species and decreased with altitude, while the temperature of the rocky ground was more stable and higher than the air temperature at each study site. Males and females of both species displayed similar activity patterns, while immature individuals tended to be active when most of the adults were basking. In the single low-altitude population of *D. mosorensis* in the river canyon, all adults were observed at midday and a majority of them were active, whereas in all other mountain populations studied, adults were observed both in the morning and at midday and a majority of them were basking. *Dinarolacerta* lizards showed a unimodal pattern of daily activity. Individuals were most frequently observed in the morning and midday and rarely in the afternoon. They mostly stayed in full sun on the slope or on top of rocks, and only a small percentage were inactive (hiding in crevices or in the shade). The exposure of the occupied rock surface was very heterogeneous within the samples for both adults and immature individuals. There were no consistent differences in daily activity patterns between the two *Dinarolacerta* species, and the differences found between some populations both within and between species were more likely to reflect certain microclimatic and microhabitat characteristics at specific sites.

Key words: Thermoregulatory behavior, high altitude, *Dinarolacerta mosorensis*, *Dinarolacerta montenegrina*, Montenegro

1. Introduction

For reptiles as ectotherms, the ambient temperature is crucial for their physiological processes and overall performance (Huey, 1982; Adolph and Porter, 1993). Therefore, maintaining a relatively constant body temperature is important for locomotion, prey capture and digestion, evasion of predators, production of gonads and mating, growth, and ultimately the survival of an individual (Angilletta et al., 2002; Pianka and Vitt, 2003). Most reptiles regulate their body temperature through behavioral adjustments such as the use of thermally suitable microhabitats, variations in activity patterns, and changes in body posture and orientation, while others passively conform their body temperature to that of the environment (Huey, 1982; Castilla et al., 1999; Pianka and Vitt, 2003). In lizards, behavioral thermoregulation can lead to shifts in microhabitat use and cause differences between species (e.g., Adolph, 1990; Labra et al., 2001; Muñoz and Lossos, 2018).

For reptiles in cold environments, the availability of heat is a key limiting factor (e.g., Adolph and Porter, 1993; Pianka and Vitt, 2003). At high altitudes, the large daily thermal fluctuations pose a challenge to the ability of reptiles to maintain their body temperature within a preferred temperature range (Huey, 1982). However, a number of studies have shown that despite the unfavorable thermal conditions in these environments, most lizards exhibit high thermoregulation efficiency based primarily on behavioral adjustments (e.g., Hertz and Huey, 1981; Bauwens et al., 1990; Carothers et al., 1998; Arribas, 2010, 2013; Vidal et al., 2010; Vicenzi et al., 2019). On the other hand, thermoregulation in environments where the ambient temperature has large amplitudes or deviates strongly from the thermal preferences of the lizards is time-consuming and reduces the time that could be used for other activities such as foraging, social interactions, or escape from predators (Huey, 1982; Dunham et al., 1989; Gvoždík, 2002; Vicenzi et al., 2019).

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The genus *Dinarolacerta* (Arnold, Arribas & Carranza, 2007) includes two allopatric rock-dwelling, small-bodied lacertids, namely the Mosor rock lizard (*Dinarolacerta mosorensis* Kolombatović, 1886) and the Prokletije rock lizard (*D. montenegrina* Ljubisavljević, Arribas, Džukić & Carranza, 2007a), which are relic and endemic species of the mountains of the Dinaric Arc in the Western Balkans. Their ranges are separated by a gap in central Montenegro, with *D. mosorensis* occurring in the mountains of the western and southwestern part of the country, while *D. montenegrina* is restricted to the Prokletije Mountains in the eastern part of the country. Both species are well adapted to limestone rocky terrains at higher altitudes (1100–1900 m) and only rarely descend to lower elevations in canyons and along the slopes of the mountains of the Adriatic hinterland (*D. mosorensis*) (Ljubisavljević et al., 2016). The Mosor rock lizard is found in relatively shadier and wetter places on rocks near vegetation and leaf litter, while *D. montenegrina* prefers more open, rocky terrain (Ljubisavljević et al., 2017). *Dinarolacerta mosorensis*, which is generally better studied than *D. montenegrina*, has been shown to be well adapted to unfavorable thermal conditions and a short annual activity period in the mountains, having developed a relatively long-lived, late-maturing reproductive strategy (Dunham et al., 1988), reaching sexual maturity after the second year of life and producing one clutch per year with prolonged oviductal egg retention (Ljubisavljević et al., 2007b; Tomašević Kolarov et al., 2010). However, nothing is known about the daily activity patterns of either species, with the exception of some anecdotal observations for *D. mosorensis* (Bosch, 1989; Veith, 1991).

In this study, we analyze the summer daily activity patterns within and between *Dinarolacerta* spp. to determine whether there are different behavioral patterns by which these range-restricted species cope with variations in microhabitat thermal conditions. Due to the unfavorable climatic conditions in mountainous regions, the activity season of these rock lizards is delayed (Ljubisavljević et al., 2007b), so we assumed that the first half of summer is a period when these species are fully active and that possible variations in daily activity patterns would be identified.

2. Materials and methods

2.1. Study site and species

The activity pattern of *D. mosorensis* was studied at four sites in Montenegro (1. Mt. Orjen, 1150 m a.s.l., 42.56°N, 18.64°E; 2. Mt. Lovćen, 1220 m, 42.22°N, 18.50°E; 3. Mt. Prekornica, 1500 m, 42.41°N, 19.16°E; 4. Mrtvica River Canyon, 270 m, 42.74°N, 19.33°E), whereas *D. montenegrina* was studied at three sites (1. Kučka Korita Plateau, 1300 m, 42.48°N, 19.50°E; 2. Mt. Žijovo, 1460 m, 42.34°N, 19.29°E; 3. Mt. Đebeza, 1600 m, 42.61°N, 19.56°E). The lizards were found on limestone rocky outcrops surrounded by natural open mixed forests of subalpine beech (*Fagus sylvatica*) and whitebark pine (*Pinus heldreichii*) (most sites), planted coniferous stands (Mt. Lovćen), or sub-Mediterranean forests of oriental hornbeam (*Carpinus orientalis*) (Mrtvica River Canyon).

2.2. Fieldwork

The study was conducted from mid-June to the end of July in 2014 and 2016, on days with favorable weather conditions (i.e. sunny days without rain and strong wind) during the daily activity period of the lizards. The observations were made within walked transects that were on average 200 m long, at least 15 m apart, and regularly distributed across the study area (Ljubisavljević et al., 2017). For each specimen observed we noted the age class (adult or immature) and sex, time of day (morning: up to 11:00 hours; midday: 11:00 to 16:00; or afternoon: after 16:00), exposure of the occupied rock (north, east, south, west, northeast, northwest, southeast, or southwest), behavior (basking, active (e.g., moving, foraging, or feeding), or inactive (e.g., hiding in a crevice or shade)), position on the rock (base, slope, top, or crevice), and exposure to sunlight (full sun, full shade, sun/shade mosaic). We also recorded the air temperature (T_a) at the spot where each lizard was first seen (10 cm above the ground) with a digital thermometer (±0.1 °C, TFA Dostmann GmbH & Co., Wertheim am Main, Germany) and ground temperature (T_g) with a digital infrared thermometer (±0.1 °C RAXX, AHS GmbH, Austria).

We analyzed possible species/population, age (adult, immature), and sexual (male, female) differences in air and ground temperature using analysis of variance (ANOVA) and the Tukey test for pairwise comparisons of means, while differences in frequencies of activity variables (time of day, exposure of the occupied rock, behavior, position on the rock, and exposure to sunlight) were analyzed using the G-test (Sokal and Rohlf, 1995). Data for different sampling years (tested only for the Mt. Đebeza locality, where records were available for both years) and sexes were pooled, as tests confirmed the absence of differences. All subsequent statistical analyses were conducted on two separate datasets, one for adults and one for immature individuals. Due to the limited sample sizes for immature individuals in certain populations (comprising only a few individuals), we decided to retain populations with a sample size greater than 8 for subsequent analyses. Statistical analyses were performed with Statistica 10 (StatSoft Inc., Tulsa, OK, USA). All statistical tests were performed considering $p < 0.05$ as the level for significance.

3. Results

3.1. Temperature

Air temperatures at the spots where adults were sighted showed considerable variation both within and between species, as pairwise comparisons revealed significant differences between most sites (Tukey post hoc test, $p < 0.01$). The highest mean T_a (28.6 °C) was recorded at a low-altitude site of *D. mosorensis* in the canyon of the Mrtvica River, while the lowest T_a was recorded at a high-altitude site of *D. montenegrina* (Mt. Žijovo, 19.7 °C) (Table 1). These two sites differed significantly from each other in T_a (Tukey post hoc test, $p < 0.001$) and from all other sites (Tukey post hoc test, $p < 0.01$). For immature individuals analyzed in a limited number of samples, there was a significant difference in mean T_a between the two sites of *D. mosorensis*, with somewhat higher T_a values recorded in the southern and lower Mt. Lovćen site than in the central and higher Mt. Prekornica site (24.7 °C and 22.5 °C, respectively; Tukey post hoc test, $p = 0.0299$). Temperatures of the rocky ground where the lizards were observed showed a relatively uniform pattern for both adult and immature individuals at all sites (Table 1), with the exception of Mt. Orjen (*D. mosorensis*), where the ground occupied by adult lizards was significantly colder compared to other localities (Tukey post hoc test, $p < 0.05$).

3.2. Activity

Adults showed a statistically significant difference in behavior compared to immature individuals at one out of three localities where sufficient sample sizes of immature lizards were available. Specifically, a greater proportion of immature individuals of *D. montenegrina* from the Kučka Korita Plateau were found to be active while the majority of adults basked ($G = 4.88$, $p = 0.0272$). A similar trend was also observed for *D. mosorensis* (Mt. Lovćen population).

In the overall G-test among the study sites, statistically significant differences were found for adults for all activity variables tested, with the exception of exposure to sunlight, while for immature lizards a significant difference was only found for the exposure of the occupied rock (Table 2). The pairwise G-test (for each pair of the study sites) revealed that the low-altitude population of *D. mosorensis* in the Mrtvica River Canyon differed from the mountain populations studied in terms of activity time during the day ($G = 6.48$–14.49, $p < 0.05$) and type of behavior ($G = 6.39$–11.75, $p < 0.05$). In the Mrtvica River Canyon all adults were observed at midday and a majority of them were active, while in the other studied populations adults were observed both in the morning and at midday and a majority of them were basking at each study site (Figure 1).

At all study sites, adult lizards were rarely observed in the afternoon (Figure 1a), occupying rock surfaces with varying exposure (Figure 1b). Only a small percentage of them were inactive (hiding in a crevice or in the shade; Figure 1c), with most positioned on the slope or on top of rocks in full sun (Figures 1d and 1e). However, the adult *D. mosorensis* on Mt. Lovćen stood out from the other populations studied mainly because they occupied a higher percentage of west- and southwest-facing rocks ($G = 14.84$–27.10, $p < 0.05$). There were also significant differences in the distribution of positions on the rocks between adult *D. mosorensis* from Mt. Lovćen and *D. montenegrina* from Mt. Đebeza ($G = 11.72$, $p = 0.0084$) and the Kučka Korita Plateau ($G = 9.50$, $p = 0.0233$), as

Table 1. Descriptive statistics (mean ± standard deviation) of air (T_a) and ground (T_g) temperature (in °C) at seven study sites in Montenegro where adult and immature specimens of *Dinarolacerta mosorensis* and *D. montenegrina* were recorded.

		Adults			Immatures		
Species	Study site	N	T_g	T_a	N	T_g	T_a
D. mosorensis	1. Mt. Orjen	20	24.0 ± 4.6	22.4 ± 2.9			
	2. Mt. Lovćen	30	27.6 ± 3.4	25.3 ± 3.0	8	29.3 ± 2.2	24.7 ± 1.4
	3. Mt. Prekornica	20	27.4 ± 3.0	22.2 ± 1.9	11	26.9 ± 2.8	22.5 ± 1.1
	4. Mrtvica canyon	14	28.9 ± 3.9	28.6 ± 0.8			
D. montenegrina	5. Kučka Korita	21	30.2 ± 4.6	25.0 ± 3.1	9	28.0 ± 2.9	23.5 ± 1.5
	6. Mt. Žijovo	29	27.7 ± 3.0	19.7 ± 1.4			
	7. Mt. Đebeza	31	29.3 ± 2.9	23.7 ± 1.4			

Table 2. Summary of the results of G tests for activity variables in adult (seven study sites) and immature (three study sites) *Dinarolacerta* lizards. Significant differences ($p < 0.05$) are presented in boldface.

	Adults			Immatures		
	G	df	p	G	df	p
Time of the day	21.37	15	**0.0453**	0.21	2	0.8990
Exposure of the rock	71.61	42	**0.0030**	23.60	2	**0.023**0
Behavior	23.19	12	**0.0261**	2.08	2	0.3532
Position on the rock	32.64	18	**0.0184**	9.58	6	0.1433
Exposure to sunlight	13.78	12	0.3153	1.40	2	0.4971

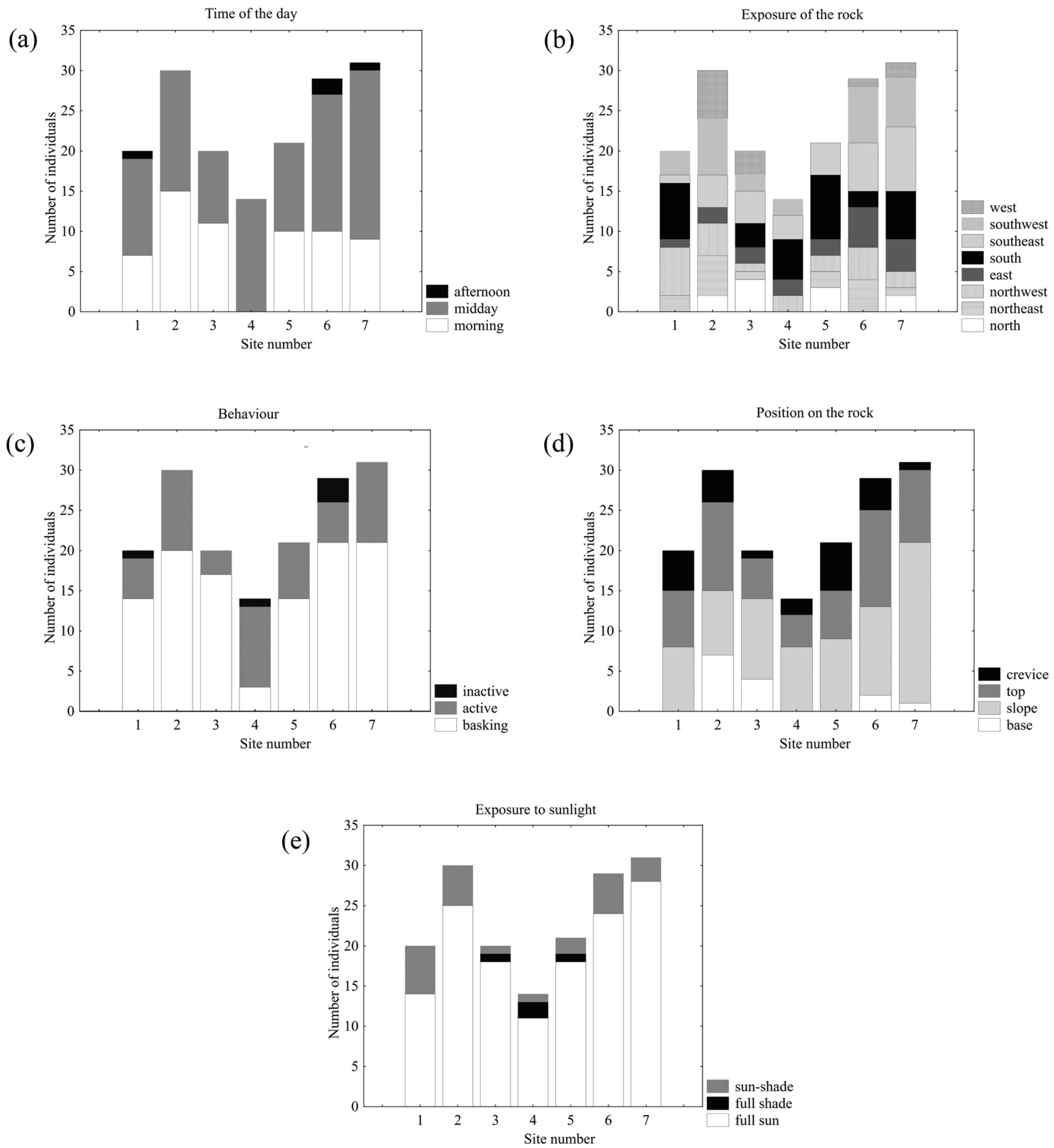

Figure 1. Observed frequencies of activity trait states in adult *Dinarolacerta* spp. at study sites. The numbers of the study sites correspond to those in Table 1.

individuals from the Lovćen population were mainly found on top of rocks, while at the other two sites, lizards were mostly observed on the slopes of the rocks.

Apart from behavior, immature individuals showed activity patterns similar to those of adults (Figure 2). They were not seen in the afternoon (Figure 2a) and, while occupying rocks with varying exposure (Figure 2b), they were mainly active (Figure 2c) on the slopes or on top of the rocks in full sun (Figures 2d and 2e). Immature individuals of *D. mosorensis* from Mt. Lovćen were also found mainly on rocks with the same orientation as the adults, which significantly distinguished them from immature individuals of *D. montenegrina* from the Kučka Korita Plateau, which mainly occupied north-facing rocks ($G = 13.92$, $p = 0.0306$).

4. Discussion

Our study showed that there were no consistent differences in daily activity patterns in the summer season between two *Dinarolacerta* species. The differences in some activity traits found both within species and between some populations of the two species are more likely to reflect microclimatic and microhabitat differences between specific sites. It has already been shown that between-site variation in

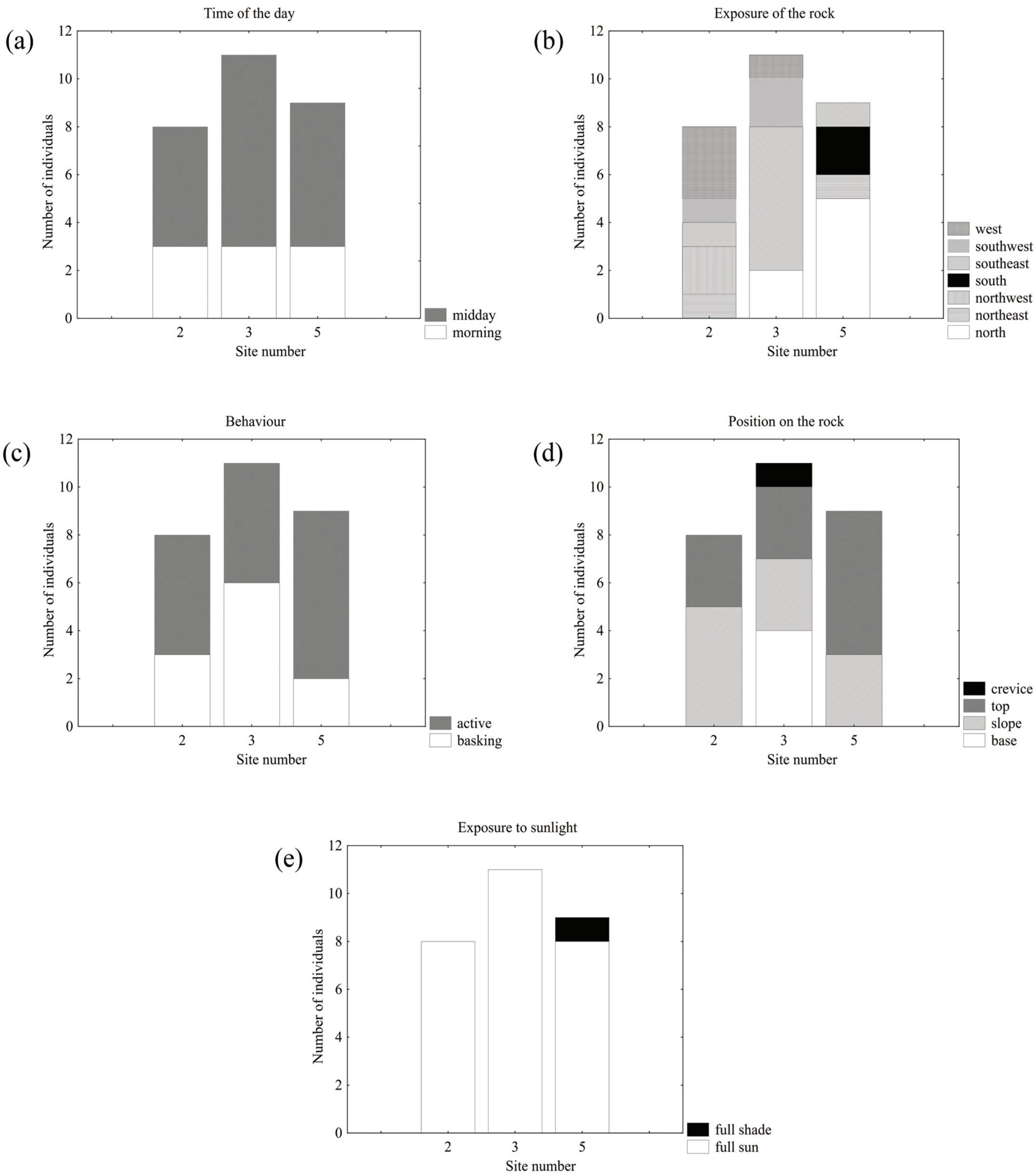

Figure 2. Observed frequencies of activity trait states in immature *Dinarolacerta* spp. at study sites. The numbers of the study sites correspond to those in Table 1.

microhabitat characteristics appears to be greater within *D. mosorensis* than between the two *Dinarolacerta* species (Ljubisavljević et al., 2017). Similar activity patterns in closely related allopatric mountain lizards correspond to their similar ecological traits, which are largely imposed by thermal constraints in mountain environments (Arribas, 2010). Divergence in thermal microhabitat is generally expected to minimize interspecific interactions in closely related sympatric species (Rand, 1964).

Dinarolacerta lizards showed a unimodal pattern of daily activity with individuals observed in the morning and midday and very little or no activity in the afternoon. A similar pattern was found in some other lizards at high altitudes, being attributed to the high temperatures of the rocks (Arribas, 2009; Vicenzi et al., 2019), the orography that shaded the lizards' habitats (Arribas, 2009), and the lower activity of prey insects in the afternoon (Arribas, 2009).

At higher elevations, where T_a is lower, most adult *Dinarolacerta* lizards were observed basking in full sun during the morning and midday hours, indicating that they bask frequently or for long periods of time and spend less time on other activities. Lizards in habitats with low thermal quality generally devote a considerable amount of time to basking (Bauwens et al., 1990; Gvoždík, 2002; Aguado and Braña, 2014). Although we did not detect differences in activity patterns between the sexes, it should be noted that the timeframe of fieldwork coincided with the period of gravidity in *D. mosorensis* (Ljubisavljević et al., 2007b), a period in which the females of some species may increase basking time (Shine, 1980; Schwarzkopf and Shine, 1991). In other seasons, differences in thermoregulatory behavior between males and females may occur (Vidal et al., 2010; Vicenzi et al., 2019). Some studies suggest that there is a trade-off between basking and antipredator behavior due to rapid temperature loss in cold rock crevices (Martín and López, 1999; Polo et al., 2005), while others describe the long duration of basking itself as an antipredatory tactic, as motionless individuals are less conspicuous to predators than when they frequently switch from basking to active behavior (Carrascal et al., 1992).

The activity of *D. mosorensis* at a single site at low altitude (Mrtvica River Canyon) was restricted to midday hours. This was attributed to the steep and high canyon walls, which allowed the sun to reach the lizards' habitat at the bottom of the canyon only at midday. Although T_a was quite high in the Mrtvica River Canyon, *D. mosorensis* could avoid overheating by dwelling in a humid microhabitat on the moist canyon floor (Kirchhof et al., 2010). The majority of individuals were found to be active and only a small percentage was basking or inactive, suggesting that these lizards basked for a shorter period of time. Populations of a lacertid lizard living at different altitudes may have the same preferred temperature range (Díaz et al., 2006), and through different thermoregulatory behaviors could use dissimilar environmental thermal conditions to reach similar body temperatures (Zamora-Camacho et al., 2013). This could also be the case with *Dinarolacerta* spp. or at least with *D. mosorensis*.

Although we did not measure the body temperature of the specimens (T_b) and could not explore its relationship with T_a and T_g, the use of thermoregulatory strategies such as changes in activity patterns and basking positions suggests that *Dinarolacerta* spp. are active thermoregulators, like many other lizards of medium and high altitudes (e.g., Bauwens et al., 1990; Arribas, 2009; Vicenzi et al., 2019).

Our observations suggest that heliothermy plays a prominent role in the thermoregulatory behavior of *Dinarolacerta* spp. but additional heat gain could be achieved by conduction from warm limestone rocks (thigmothermy) (Bauwens et al., 1990; Carrascal et al., 1992; Arribas, 2009). While the mean T_a at which lizards were observed decreased with altitude, T_g was more stable and higher than T_a at each study site. This is not unusual in karst areas, where rocks heat up easily (e.g., Arribas, 2009). The lower T_g at the study site on Mt. Orjen could be the result of the specific perhumid conditions on this mountain in the Adriatic hinterland, which is characterized by the highest precipitation regime in Europe (Ducić et al., 2012).

Although analyses of activity patterns of immature individuals could only be performed on a limited number of samples, they showed the tendency of different behavioral patterns between immature and adult *Dinarolacerta* lizards in the way that immature lizards were more active at the time when the majority of observed adults were basking. Immature individuals with lower body mass and higher surface-to-volume ratios warm up and cool down faster than adults (Carothers et al., 1998). Consequently, they bask more frequently and for shorter periods of time, making them more likely to be observed as active (Carrascal et al., 1992).

Apparently, *D. mosorensis* can adjust its thermoregulatory behavior depending on the thermal conditions of low- or high-elevation habitats. Mountain lizards with behavioral adjustments could potentially buffer the increase in environmental temperatures due to global warming (Aguado and Braña, 2014; Vicenzi et al., 2019), but only in the short term until it becomes too costly (Ortega et al., 2016). There are many other components that modulate the interaction of the main factors and form the lizards' microenvironment (Arribas, 2009). As *D. mosorensis* occurs only sporadically at altitudes below 1000 m (Ljubisavljević et al., 2016), low-altitude habitats probably need to provide some other particular microclimatic and microhabitat components to be suitable for the survival of this endemic species (e.g., high humidity in Mrtvica River Canyon). On the other hand, according to the available data, *D. montenegrina* is isolated at higher altitudes. Although the initial results suggest that the thermoregulatory behavior of *D. montenegrina* is similar to that of *D. mosorensis*, further studies of its distribution pattern should be conducted, along with a more detailed analysis of the thermoregulatory behavior of both species, such as thermoregulatory precision, by measuring body temperatures and exploring seasonal variation in activity patterns.

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Conflict of interest
The authors declare no conflict of interest.

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