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Interpopulation Variations in Circadian Activity of the Nose-horned Viper *Vipera ammodytes* (Linnaeus, 1758) (Reptilia: Viperidae)

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To Niki, a true friend

Abstract: A detailed study on the circadian activity patterns of *Vipera ammodytes* was carried out in order to evaluate for potential interpopulation variations. Five sites along a 180 km latitudinal gradient (from north to south as follows: Karlukovo, Lakatnik, Balsha, Bosnek and Kresna) in western Bulgaria were studied in 2014–2017. In spring, differences in circadian activity patterns were present between the time intervals of the peak in the number of observations of the different populations. In summer, differences were present between catchability and activity type of the vipers from different populations, as well as between peaks of observations. In autumn, the patterns of circadian activity were similar for each of the vipers' population. The observed variations in activity patterns might be attributed to the physico-geographical, climatic and habitat characteristics of the different regions on the one hand and the evolutionary adaptations of the populations on the other.

Key words: Serpentes, snakes, ecology, Balkan Peninsula

Introduction

The Nose-horned Viper *Vipera ammodytes* (Linnaeus, 1758) is a medium-sized viper distributed from the westernmost foothills of the Alps throughout the Balkan Peninsula and many Aegean islands to northern and north-western Asia Minor and the Lesser Caucasus (Speybroeck et al. 2016). Molecular studies show that the species is of high genetic diversity throughout its range and the current taxonomy, based solely on morphological traits, is in need of a major revision (Ursenbacher et al. 2008, Čubrić et al. 2019, Freitas et al. 2020). Depending on the characteristics of the particular location, *V. ammodytes* is usually active from March/April to October/November, although in warm days, especially in more southern populations, it may also be active during parts of the winter (Sochurek 1958, Biella 1983, Schweiger 1992, Heckes et al. 2005, Plasinger et al. 2014, Ghira 2016). The species is predominantly diurnally active, although in warm nights it could also be active during parts of the night (Bruno 1967, Beshkov 1978, 1993, Biella 1983, Crnobrnja-Isailović 2002, Crnobrnja-Isailović et al. 2007, Ghira 2016, Zadravec & Koren 2017, Dyugmedzhiev et al. 2020a). The circadian activity depend on the environmental conditions and the species exhibits seasonal variations in its activity patterns. Because of the variable ambient temperatures, in spring and autumn vipers usually concen-

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trate their activity in the warmest middle parts of the day, when ambient temperatures are the most favourable for basking and successful thermoregulation. In summer, due to the high temperatures, vipers usually bask only in the morning and in the late afternoon, while during the warmest parts of the day they are hidden in the shade or in shelters (Biella 1983, Biella & Blättler 1989, Beshkov 1993, Crnobrnja-Isailović 2002, Crnobrnja-Isailović et al. 2007, Ghira 2016, Dyugmedzhiev 2020, Dyugmedzhiev et al. 2021).

In Bulgaria, *V. ammodytes* is distributed throughout the country but is absent in the high mountains, urbanised areas and intensively cultivated agricultural land (Stojanov et al. 2011). Two separate clades occur within the country – north-eastern (NE) and south-eastern (SE) (Ursenbacher et al. 2008), which represent the subspecies *V. a. ammodyte*s Linnaeus, 1758 and *V. a. montandoni* Boulenger, 1904, respectively (Tomović 2006). Two distinct subclades, eastern and southern have been established within the SE clade. The eastern subclade represents the distribution of *V. a. montandoni* in the eastern part of Bulgaria. The southern subclade is found in northern Greece and the western part of North Macedonia, in immediate proximity to the south-western border of Bulgaria (Ursenbacher et al. 2008). Although the authors did not sample specimens from south-western Bulgaria, Tzankov et al. (2017) stated that those populations most probably belong to the southern subclade.

Although several studies with data on the species activity exist, information about the intraspecific variations in the activity patterns is very limited and is focused mainly on intersexual differences (Sochurek 1958, Biella 1983, Heckes et al. 2005, Ghira 2016, Crnobrnja-Isailović 2002, Crnobrnja-Isailović et al. 2007). To our knowledge, there are no studies that compare the activity patterns between different subspecies and populations.

The aim of the current study was to evaluate the potential variations in the patterns of circadian activity of *V. ammodytes* between populations, located in areas with different physico-geographical or climatic conditions. We also discuss on the potential role of the phylogenetical specifications on the behaviour of the vipers.

Materials and Methods

Study sites

Five sites along the latitudinal gradient in western Bulgaria were studied. The straight line distance between the northern- and the southernmost sites is about 180 km and their exact locations from north to south are as follows: (1) near Karlukovo Village (N43°10' E24°3'; 111–250 m a.s.l.); (2) near Gara Lakatnik Village (N43°5'; E23°23'; 352–733 m a.s.l.); (3) near Balsha Village (N42°51'; E23°15'; 652–853 m a.s.l.); (4) near Bosnek Village (N42°29' E23°11'; 942–1332 m a.s.l.); (5) the Gabrovitsa site in the Kresna Gorge (N41°46' E23°9'; 165–488 m a.s.l.; presented as "Kresna" in the table and figures); all coordinates were coded according WGS 84 mercator. Sites 1 and 2 are karst valleys along the Iskar River, with steep rock terraces and patches of deciduous forests. Site 3 is an abandoned quarry, with surrounding fields, bare hills and deciduous forests. Site 4 is a middle-mountain karst valley along the upper reaches of the Struma River, with stony slopes, covered with shrubs and sparse deciduous forests. Site 5 is a plain along the middle reaches of the Struma River, covered with scattered shrubs and abandoned vineyards. It is surrounded by steep stony slopes, overgrown with forest vegetation (for more detailes, including map and photographs of the five sites, see Dyugmedzhiev et al. 2020b). The first four sites fall in the temperate-continental climate zone and the fifth is in the continental-Mediterranean zone (Kopralev 2002).

Fieldwork

Fieldwork was conducted mainly between April and September from 2014 to 2017. During this period, each site was visited once per month in 2014 and twice per month from 2015 onwards. Some additional visits were also made between January and March and October and December, however they were unevenly distributed across the sites. Each visit lasted one day. The field effort at each site was as follows: Karlukovo – 59 visits with a total of 516.5 field hours; Lakatnik – 58 visits with a total of 528.4 field hours; Balsha – 57 visits with a total of 451.4 field hours; Bosnek – 52 visits with a total of 459.15 field hours; Kresna Gorge – 54 visits with a total of 472.3 field hours.

Field visits were in days, in which activity of the vipers was feasible (maximal daily temperatures above 15°C). The investigations were performed from early morning to dusk (night monitoring was sporadical). The search was throughout the entire vicinity of the targeted sites, with the exception of some physically inaccessible areas (e.g. too thick patches of shrubs or very steep rock walls). The same route pattern was followed in each visit. The vipers were localised by sight during the active search and by inspection of potential hideouts (holes, burrows, rock crevices, under stones and logs). The time of

observation and the activity types were recorded for each viper specimen. Captured vipers were measured (precision 0.5 cm), weighted (precision: 0.01 g), colour marked and photographed for individual identification (see Dyugmedzhiev et al. 2018) and then released at the site of capture.

Data processing

The active period was divided into three seasons: spring (March–May), summer (June–August) and autumn (September–November). The day was divided into four time intervals: morning (8–12 h), noon (12–16 h), afternoon (16–20 h) and evening (20–22 h). Three types of activity were distinguished in the studied vipers: 1) basking in the open; 2) resting in the shade (of bushes, trees, etc.); 3) hiding in shelters. Taxonomic division was based on Ursenbacher et al. (2008) and Tzankov et al. (2017). Vipers from site 1 (Karlukovo) were attributed to the eastern subclade, or *V. a. montandoni* (E); vipers from sites 2 and 3 (Lakatnik and Balsha) to the northeastern clade, or *V. a. ammodytes*; vipers from sites 4 and 5 (Bosnek and Kresna Gorge) to the southern subclade, or *V. a. montandoni* (S).

Statistical analyses

All statistical analyses were carried out with Statistica 10.0 (StatSoft, Inc. 2011). Statistical significance was accepted at $p < 0.05$. Individuals that were found multiple times throughout the day, were included in the analyses only with the data from the first observation, due to the potential change in behaviour caused by the capture and measuring procedures. A χ^2 test was used for the analyses of the circadian activity of the different populations. In these analyses, we compared the number of observations of the vipers during the different parts of the day, as well as between the different activity types for each season separately. Due to the irregular character of the nocturnal monitoring and the insufficient data about the evening hours (20–22 h), the latter were removed from the analyses. Cluster analysis (through UPGMA based on the Euclidean distance) was used to express the similarity between studied populations with respect to circadian activity.

Results

A total of 672 observations of *Vipera ammodytes* were made in the five study sites: 226 from Karlukovo, 161 from Lakatnik, 145 from Balsha, 58 from Bosnek and 82 from Kresna Gorge. Active vipers on the surface were found between 8 and 23 h. The earliest observation was at 8:03 h in summer at the site around Lakatnik. The latest observations were at 22:06 h in autumn at the site around Karlukovo and at 22:48 h in summer at the site in Kresna Gorge.

In spring, the number of observations throughout the day differed significantly for each population, except Bosnek, where the result was close to significance ($p = 0.07$) (Table 1). In regards to activity types, significant differences were observed in each population (Table 1). The majority of vipers from each taxa and population were detected basking in the open in the middle part of the day. However, small differences were present between the intervals of the peak in observations in the different populations. In *V. a. montandoni* (E) from Karlukovo, the peak was in the intervals 14–16 and 16–18 h (Fig. 1a). Some differences between the peaks in the number of observations were present between the different populations of *V. a. ammodytes* and *V. a. montandoni* (S). In the southern population of *V. a. ammodytes* (around Balsha), the peak was highest between 12–14 and 14–16 h, but still remained high in the interval 16–18 h. In contrast, in the northern population (around Lakatnik, distanced approximately 30 km from Balsha), the number of observations sharply decreased after the peak from 12–14 to 14–16 h. In the northern population of *V. a. montandoni* (S) (around Bosnek), the peak was similar to the peak detected in the Balsha population (the distance between the two populations is approximately 40 km), and differed from the peak of the southern population (in Kresna Gorge, approximately 90 km from Bosnek). In the population in Kresna Gorge, the peak was between 14–16 h and the activity remained high in the interval 16–18 h (Fig. 1a).

In the summer, the number of observations throughout the day differed significantly only for the populations from Karlukovo and Balsha, while in regards to activity type, significant differences were observed in each of the four populations that were analysed statistically; sample size from the population around Bosnek for this season was insufficient for testing statistically (Table 1). The majority of *V. a. montandoni* (E) from Karlukovo were detected hiding in shelters in the midday (see Fig. 1b), while a lower number of vipers were found basking in the open (mainly in the morning, the late afternoon and the early evening) or laying in the shade (in the noon and afternoon). During this season, some differences were present between the circadian activities of the two populations of *V. a. ammodytes* (Balsha and Lakatnik). In the population around Balsha, vipers were detected in the open from 8–10 to 12–14 h, while in the population around Lakatnik – from 8–10 to 10–12 h. In the latter population, after those

hours, the vipers were found mainly in the shade, while at the Balsha population the vipers were found in the shade or in shelters rather rare (Fig. 4). The population around Lakatnik showed a second peak of viper's activity in the open, between 18–20 h, while such peak was absent in the population around Balsha. During the summer, detection of the vipers in both populations of *V. a. montandoni* (S) was low throughout the day and vipers were detected mainly in the shade (Fig. 1b).

In autumn, the number of observations throughout the day differed significantly for each of the four populations that were analysed statistically (Table 1). In regards to activity type, significant differences were observed in each of the populations, except Lakatnik. In Lakatnik, the result was close to significance ($p = 0.08$) (Table 1). The majority of vipers from each population were found basking in the open in the middle part of the day. Peak of the detectability was between 14–16 h with the exception of the population in Kresna Gorge, where it appeared later (between 16–18 h). In the population around Lakatnik, in the interval between 16–18 h (Fig. 1c), was a second peak of vipers detected in the shade.

The cluster analysis showed a different grouping of the populations for each of the seasons (Fig. 2). No clear pattern of grouping based on taxonomic affiliation or latitude could be observed.

Discussion

The results from the cluster analysis can be interpreted as evidence that in the studied populations, the circadian activity does not depend directly on the taxonomic affiliation or latitude, but is determined mainly by the locally specific features of the habitat and the populations' structures and dynamics.

The observed differences in the peaks of the circadian activity between the different taxa and populations in spring might be attributed to two factors – the physico-geographical and climatic characteristics of the different localities on the one hand, and the evolutionary adaptations of the taxa on the other. Both population of the red-tailed clade, *Vipera ammodytes ammodytes*, had an earlier peak of activity, compared to almost all populations of the green-tailed subclades, *V. a. montandoni* (E) and (S). In Bulgaria, the green-tailed subclades inhabit much warmer and drier areas than the red-tailed clade, and their ranges are expanding at the expense of the shrinking range of the red-tailed clade (Dyugmedzhiev 2020). Thus, it may be speculated that the green-tailed subclades are more heat-tolerant than the red-tailed clade. This is probably the reason why they leave their night shelters later, when ambient temperatures are higher, compensating for this with later cessation of their activity. In the population around Bosnek, however, *V. a. montandoni* (S) had more similar circadian activity in spring with the closely situated *V. a. ammodytes* population around Balsha, than with the more distanced *V. a. montandoni* (S) population in Kresna Gorge. This indicates the variability in circadian activity of the taxa in regards to the climatic and physico-geographical characteristics of the area. The Bosnek population inhabits a mid-mountain area with an altitude close to the vertical distribution limit of the species (Stojanov et al. 2011, Tzankov et al. 2014). In spring, sunlight ceases earlier and afternoon temperatures are lower than those in Kresna Gorge, which probably necessitates the transition to earlier activity in the morning hours. The different duration of the activ-

Table 1. Results from the χ^2 test for the differences between number of observations during the separate day parts and activity types for the different populations in each season (in all cases df = 2; n/a denotes cases when sample size was adopted as insufficient for testing).

	Population	Spring		Summer		Autumn	
		χ^2	p	χ^2	p	χ^2	p
Day parts	Karlukovo	8.77	0.01	6.34	0.04	38.93	< 0.001
	Lakatnik	24.02	< 0.001	4	0.14	8.91	0.01
	Balsha	23.68	< 0.001	7.8	0.02	36.88	< 0.001
	Bosnek	5.25	0.07	n/a	n/a	9.89	0.007
	Kresna	12.82	0.002	2.23	0.33	n/a	n/a
Activity type	Karlukovo	75.27	< 0.001	11.07	0.004	43.87	< 0.001
	Lakatnik	72.98	< 0.001	12	0.002	5.09	0.08
	Balsha	91.68	< 0.001	23.45	< 0.001	23.59	< 0.001
	Bosnek	19	< 0.001	n/a	n/a	7.16	0.03
	Kresna	55.18	< 0.001	7.87	0.02	n/a	n/a

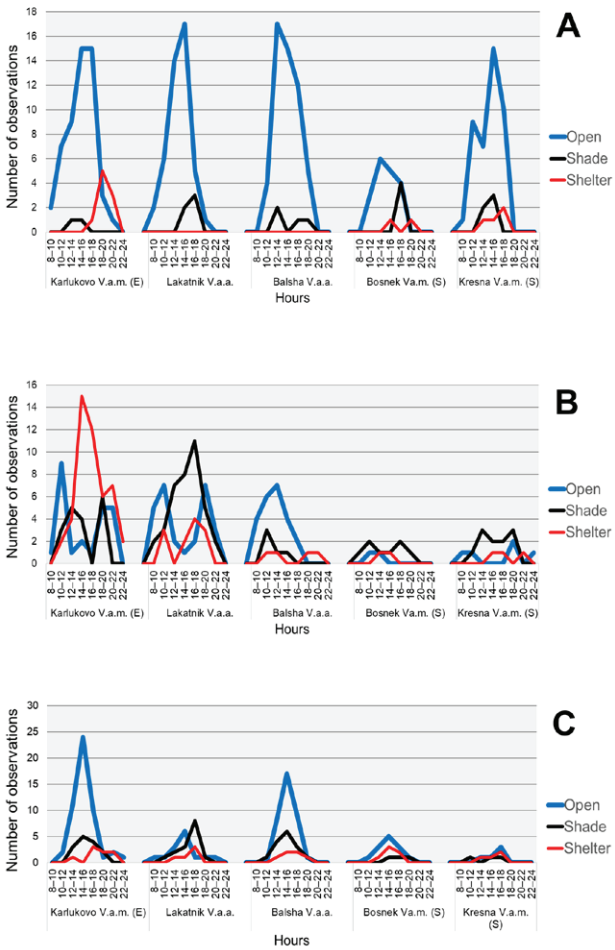

Fig. 1. Circadian activity of *Vipera ammodytes* in regards to taxa and respective populations in spring (A), summer (B) and autumn (C). Open – vipers basking in the open; Shade – vipers standing in shade; Shelter – vipers, hiding in shelters; V. a. a. – *V. a. ammodytes*; V. a. m. (E) and (S) – eastern and southern subclades of *V. a. montandoni*, respectively.

ity peaks in the two populations of *V. a. ammodytes* (Balsha and Lakatnik) may also be attributed to the physico-geographical characteristics of the two areas. The Lakatik population inhabits an area with vertical cliff walls, which block the sunlight in the afternoon, thus ending it earlier than in the quarry inhabited by the Balsha population. This leads to lower afternoon temperatures in the first population, leading to an earlier decrease in vipers' activity.

The high catchability in the Karlukovo population in summer could be attributed to the physical characteristics of this site, as well as with the populations' demographic dynamics. During the season, most vipers were found in shelters in the middle, hottest part of the day. In Karlukovo site, there was a large amount of small and medium-sized stones, which were easy to flip off and to detect snakes hiding underneath them. In the other sites, there were mostly large stones and formidable stone piles, which made the detection of snakes underneath them practically impossible. Furthermore, almost half of the vipers from Karlukovo, that were found in midday, were pregnant females (48 % of all observations at midday). Pregnant females need to maintain higher and more constant temperatures during gestation (Naulleau 1979, Ladyman et al. 2003, Weinmann et al. 2004, Baron et al. 2012, Lorioux et al. 2013, Lourdais et al. 2013, Dyugmedzhiev et al. 2021). They achieve that by basking until noon and then spending the rest of the day in shelters with optimal thermal qualities where they can maintain „preferred" temperatures for longer periods (Dyugmedzhiev et al. 2021, Dyugmedzhiev et al., 2022). The differences in the circadian activity of the two populations of *V. a. ammodytes* (Balsha and

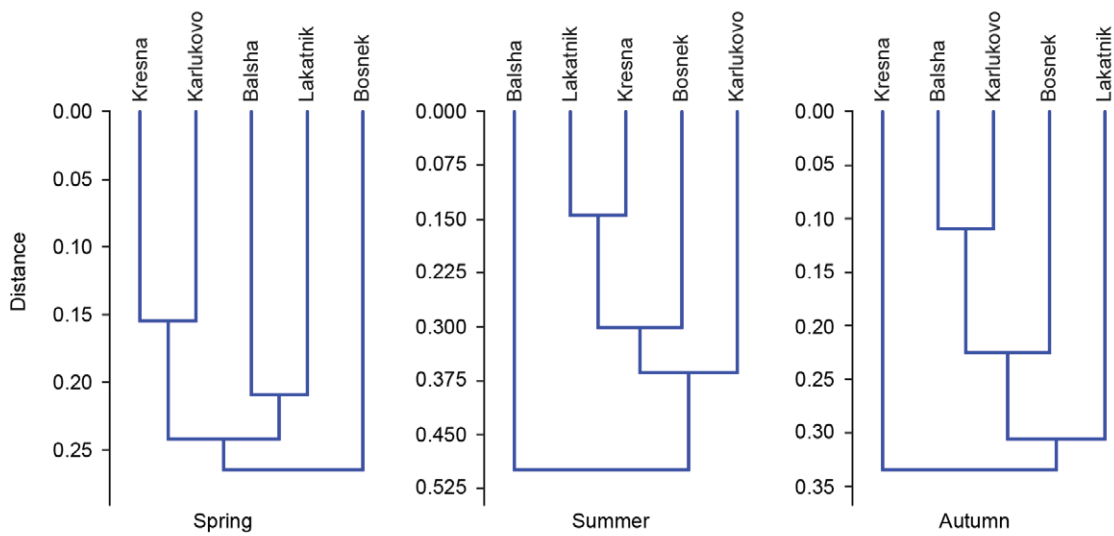

Fig. 2. Clustering of the studied populations on the basis of circadian activity data.

Lakatnik) in the summer could also be explained both by the characteristics of the sites as well as with the structure and the dynamics of the populations. The majority of vipers found in summer at the quarry around Balsha were pregnant females (69 % of the observations), which remained on its territory to give birth (Dyugmedzhiev et al. 2020b). This might explain their longer basking periods at the open sites. As mentioned earlier, at noon those vipers retreat to shelters where their detection was often impossible in this site, so catchability of vipers in the afternoon was poor. In contrast, the search effort in the site around Lakatnik covered mainly the foraging area of the population (in which no pregnant vipers were found). Vipers that spend more time on the surface would be more likely to encounter a diurnally active prey (such as lizards, which were a substantial part of vipers' diet in each population), than those hidden in shelters (Dyugmedzhiev et al. 2021, Dyugmedzhiev et al., 2022). Therefore, the benefit of prolonged hunting opportunities could explain the observed tendencies toward prolonged activity on the surface – in the shade at noon and in the open at the late afternoon. In summer, vipers from the two *V. a. montandoni* (S) populations were hard to detect and appeared mainly in the shade. This might be attributed to the very high temperatures in those sites. These temperatures do not allow the snakes to stay in the open for a long time, so the vipers spend most of the day in the shade or remained undetected, while hiding in shelters.

In autumn, the patterns of circadian activity of the different taxa and populations were similar. The small deviations in the peaks of activity in the populations around Lakatnik and Kresna Gorge might be due to the low sample size.

Conclusions

Vipera ammodytes exhibits interpopulation variations in its circadian activity patterns in a 180 km latitudinal gradient. It seems that these variations do not depend directly on the taxonomic affiliation or latitude, but are more complex and are determined mainly by the locally specific physico-geographical, climatic and habitat characteristics of the different sites and by the populations' structures and dynamics. However, phylogenetic evolutionary adaptations of the taxa might also have influence on the observed variations in circadian activity.

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