Sex- and age-related variations in seasonal and circadian activity of the Nose-horned Viper *Vipera ammodytes* (Linnaeus, 1758)

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To Niki, a true friend

Abstract. The seasonal and circadian activity patterns of *Vipera ammodytes* were studied in five sites in western Bulgaria between 2014 and 2017. *Vipera ammodytes* was active from the end of February to the first half of November. In spring, adult males emerged a few weeks earlier than females and immature vipers. In autumn, the different sex/age groups started their hibernation approximately at the same time. We registered differences in the seasonal and circadian activities between the different sex/age groups. Adult males and subadults were mostly encountered during spring and autumn, and juveniles mainly in autumn, while the encounter rate of adult females was steady throughout the activity period. Females' circadian activity varied according to their reproductive status. The observed patterns might be a result of the complex effects of many factors, such as climatic conditions, differences in the reproductive behaviour and the cost of reproduction between sexes, as well as the trade-off between precise thermoregulation, predation risk and foraging needs.

Keywords. Viperidae, snakes, basking, shade, shelter.

Introduction

Snake activity is directly related to environmental conditions, especially to ambient temperatures (Gibbons & Semlitsch 1987; Nelson & Gregory 2000). In temperate zones, the snakes' activity period is interrupted by hibernation (Vitt & Caldwell 2014). European vipers usually exhibit different seasonal activity patterns depending on sex or age, this is the case for spring emergence or ingress to hibernation (Viitanen 1967; Prestt 1971; Andrén 1985; Neumeyer 1987; Baron 1992; Újvári *et al.* 2000; Lourdais *et al.* 2002; Bauwens & Claus 2019).

The Nose-horned Viper, *Vipera ammodytes* (Linnaeus, 1758) is distributed from the westernmost foothills of the Alps across the entire Balkan Peninsula, many Aegean islands, northern and northwestern Asia Minor to the Lesser Caucasus (Speybroeck *et al*. 2016). The species is usually active from March/ April to October/November, depending on the characteristics and seasonality of the particular location, and can also be encountered during exceptionally warm winter days (Biella 1983; Schweiger 1992; Heckes *et al*. 2005; Ghira 2016). In spring, *V. ammodytes* is usually active throughout the day, while in summer its activity is concentrated mainly in the morning and the afternoon, and in some regions during parts of the night (Bruno 1967; Biella 1983; Beshkov 1993; Stumpel & Hahn 2001; Crnobrnja-Isailović 2002; Ghira 2016; Zadravec & Koren 2017).

In Bulgaria, *V. ammodytes* is widely distributed, with the exception of the high mountains, urbanized areas and intensively cultivated agricultural land (Stojanov *et al*. 2011). In that country, the species' activity period ranges from the end of February or the beginning of March to November and the species exhibits predominantly diurnal activity (Beshkov 1993; Stojanov *et al*. 2011); however, crepuscular (activity during twilight) and nocturnal activity is also common in warm nights (Dyugmedzhiev *et al*. 2020a).

Despite abundant data on this snake species activity, information about the ontogenic and sex variations in activity patterns is scarce and limited to investigating differences between the periods of spring emergence (Biella 1983; Heckes *et al*. 2005; Ghira 2016), or to seasonal differences in the encounter rates of males and females (Crnobrnja-Isailović 2002; Crnobrnja-Isailović *et al*. 2007).

The aim of the current study is to evaluate the potential sex- and age-related differences in the patterns of the seasonal and circadian activity of *V. ammodytes*.

Material and methods

Fieldwork

We studied five sites in western Bulgaria: 1) near Karlukovo Village (43°10′ N, 24°3′ E); 2) near Gara Lakatnik Village (43°5′ N, 23°23′ E); 3) near Balsha Village (42°51′ N, 23°15′ E); 4) near Bosnek Village (42°29′ N, 23°11′ E); 5) in the Kresna Gorge (41°46′ N, E23°9′ E). More detailed information of the study sites including a map, photographs, sizes of the sites and habitat characteristics are provided in Dyugmedzhiev *et al*. (2020b). Each site was visited from April to September, once per month in 2014 and afterwards twice each month until 2017. In the rare occasion when a scheduled visit to a particular site could not be accomplished within a given month, it was compensated by an additional visit to the same site in the respective month of the subsequent year. Additional visits were conducted between January–March and October–December, although these were not evenly distributed across the sites (Appendix), due to variable weather, which rarely provided sufficient opportunities to conduct a visit to each site during days with favourable conditions. Therefore, most of the visits between October and March were conducted to the sites near Karlukovo and Balsha, where some exact communal hibernating dens were discovered, in which ingress and emergence from hibernation could be more easily monitored. In 2013 and 2018, several additional random visits of one day each took place at the sites near Lakatnik, Bosnek and Kresna Gorge (in 2013) and Balsha and Kresna Gorge (in 2018). In addition, areas close to the five study sites were also visited in each year of the study period; however, those visits were rare and were randomly distributed across years and seasons. Data from those additional nearby localities were used only for the analyses of circadian activity.

We visited field sites on days with favourable weather for viper activity with maximal daily temperatures above 15°C (based on local weather forecasts prior to the visits as well as by temperature measurements in the field during the visits with a quick-reading digital thermometer (TOPELEK TECP022AH; accuracy

± 0.3°C)), because *V. ammodytes* is rarely active below those temperatures (DYUGMEDZHIEV *et al*. 2021). Searches for vipers started when morning temperatures reached at least 15-16°C: usually around 12:00h in winter, at 11:00h in March, October and November, at 9:00h in April, May and September and at 8:00h during the summer months. From October to March, searches lasted until ambient temperatures dropped below 13-14°C, which was usually in the afternoon. From April to September, searches lasted until dusk, i.e., around 30 minutes before dark; however, during some days vipers were also searched throughout parts of the night, usually until 23:00–24:00h. In case of heavy rain, searches were stopped and were resumed after the rain stopped, if ambient temperatures were still favorable for vipers' activity. Due to the difference in day length of suitable weather conditions, the hours of search effort were unequal for the different months and seasons. Searches were conducted in the entire vicinity of the study sites, and the same route was followed for each visit and twice per day. Vipers were located by sight and by inspection of potential hideouts (rock crevices, under stones, etc.). Observation time as well as activity type was recorded for each viper found. Captured vipers were measured (precision 0.5 cm), weighted (precision: 0.01 g), colour marked and documented by photograph for individual identification (DYUGMEDZHIEV *et al*. 2018). Sex was determined by the body's colour pattern, the length and width of the tail, and the SVL/TL ratio (TOMOVIĆ *et al*. 2002). Vipers were gently palpated in order to determine female reproductive status. After these procedures, all animals were released at the site of capture.

Data processing

The potential activity period was divided into three seasons: spring (March–May), summer (June–August) and autumn (September–November); due to the insufficient sample size (only two observations, both in February, see Appendix), data from the winter period (December–February) were not included in the analyses. We distinguished three types of viper activity: 1) basking in the open; 2) laying in the shade (of bushes, trees, etc.); 3) hiding in shelters. Based on the total length, vipers were considered as juveniles (juv: up to 28cm), subadults (sub: 28–46 cm for females and 28–49 cm for males) or adults (ad: over 46 and 49 cm for females and males, respectively) (DYUGMEDZHIEV *et al*. 2020b). Three groups of adults were defined: 1) adult males (mad); 2) adult females, not participating in the current breeding period (non-pregnant; fad); 3) pregnant females (fadP).

Statistical analyses

All statistical analyses were carried out with Statistica 10.0 (StatSoft, Inc. 2011). Due to the disproportionateness of the sample sizes by sex and age, statistical significance was accepted at $p < 0.01$. When an individual was found more than once throughout the day, only the data from the first observation were included in the analyses, because of the possible effect of capture and measuring procedures on viper behaviour and activity. Since the overall recapture rate was low (around 20%, see DYUGMEDZHIEV *et al*. 2020b) and recaptures during two consecutive visits were very rare, pseudo-replication was not considered to have any major effect on the data. Hence, the only recapture data excluded from the statistical analyses were those happening during the same day.

A χ^2 test was used to statistically compare the number of observations between males and females throughout the seasons and between pregnant and non-pregnant females during summer (sex/reproductive status as groups; number of observations in each season as conditions). Since search effort in different seasons was the same for each group, this test is unaffected by a potential bias in search effort between seasons. In order to avoid the effect of this bias in search effort when analyzing the occurrence of each sex/age group between different seasons, we calculated the encounter rate, an index of catchability as the ratio of the number of observations (N) to the search time in hours (H). This index was calculated separately for the different seasons each year and for each of the sex/age groups. Since data were not normally distributed (Kolmogorov-Smirnov & Lilliefors test, $p < 0.05$), a Kruskal-Wallis H test was used

TABLE 1

Dates of early spring- and late autumn observations of the different sex/age groups from the populations near Balsha and Karlukovo, where ingress and emergence from hibernation could be monitored at previously discovered hibernating dens. The hibernaculum near Balsha was discovered in spring 2015, so data for this population are presented from this point onwards; the hibernaculum near Karlukovo was discovered in autumn 2015, so data from this populations are presented from that month onward.

sex/ age	Date of first observation					Date of last observation					
	Balsha			Karlukovo		Balsha			Karlukovo		
	2015	2016	2017	2016	2017	2015	2016	2017	2015	2016	2017
mad	26.03	22.03	28.02	18.03	24.02	18.10	11.11	11.10	06.11	24.10	17.10
fad	27.04	–	24.03	08.04	22.03	–	23.10	06.10	11.11	07.11	04.10
sub	–	22.03	24.03	08.04	22.03	03.11	27.10	11.10	17.10	09.10	27.10
juv	–	16.04	–	21.04	25.04	13.11	27.10	–	02.10	07.11	12.11

to compare the seasonal encounter rates. Because the χ^2 test indicated a lack of significant differences between the number of observations of males and females for both subadults and juveniles, as well as between pregnant and non-pregnant females in summer (see Results), in the Kruskal-Wallis H test, no sex distinction was made for subadults and juveniles, nor were pregnant and non-pregnant adult females differentiated. Due to the low sample size, data about the seasonal activity of the different populations could not be compared statistically.

Results

Seasonal activity

A total of 688 *Vipera ammodytes* were observed during the study; data of 636 encounters were used for the analyses of seasonal activity. The earliest and the latest dates on which active vipers were observed were 24 February (Karlukovo) and 14 November (Lakatnik), respectively. The start and the end of the activity period varied across years (Table 1).

In spring, adult male vipers emerged from hibernation a few weeks before the adult females and subadults, usually at the beginning or the second half of March, depending on the year (Table 1). Adult females and subadults usually emerged at the same time – by the second part of March or the beginning of April, depending on the year. Juvenile vipers were the last to emerge, mostly by the end of April. At the end of autumn, vipers from the different sex/age groups started their hibernation approximately at the same moment, between the second half of October and the first half of November, depending on the year (Table 1).

The number of observations between males and females during the activity period differed significantly only in adults (ad: $\chi^2 = 49.38$, $p < 0.0001$; sub: $\chi^2 = 0.95$, $p = 0.62$; juv: $\chi^2 = 1.3$, $p = 0.52$; in each test df = 2). The number of observations of pregnant and non-pregnant female vipers during the summer did not differ significantly ($\chi^2 = 1.58$, df = 1, $p = 0.47$), although the latter were found more frequently than the first (Fig. 1).

The encounter rate of adult males differed significantly between spring and summer, was close to a significant difference between summer and autumn (p = 0.03) and did not differ significantly between spring and autumn (Table 2). Adult males had two distinct peaks in their encounter rate. The first, which

TABLE 2

Results of Kruskal-Wallis H tests between (first row) encounter rates across the three seasons and (last three rows) the p values from the post-hoc tests testing for differences in encounter rates of different sex/age groups of *V. ammodytes* between the different seasons. n refers to samples size (i.e., the sum of each separate encounter rate per season for each study site in each year).

	mad: H = 24.93, p < 0,0001, n = 66	fad: H = 3.51, p = 0.17, n = 66	sub: H = 7.57, p = 0,02, n = 66	juv: H = 13.35, p = 0,001, n = 66
spring vs summer	p < 0.0001	p = 1	p = 0.09	p = 0.92
spring vs autumn	p = 0.07	p = 0.22	p = 1	p = 0.004
summer vs autumn	p = 0.03	p = 0.54	p = 0.04	p = 0.09

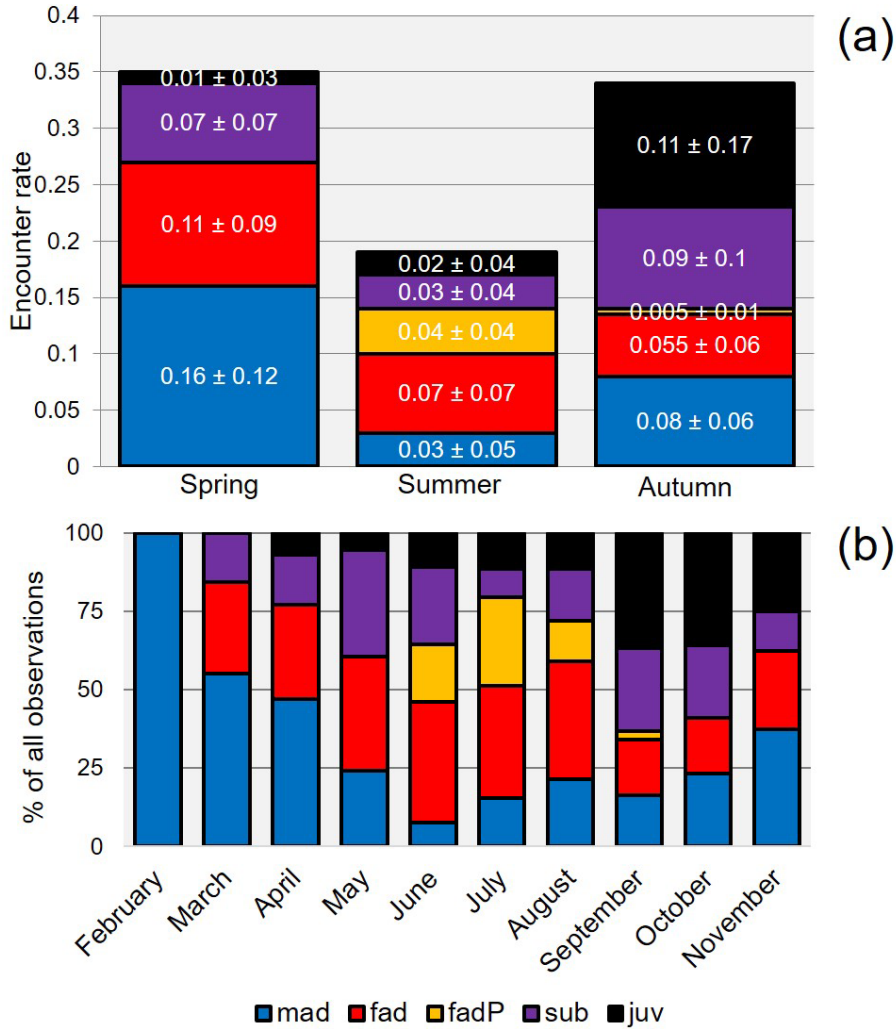Figure 1 – Encounter rate of *V. ammodytes*, calculated across all years of the study according to sex/age throughout the activity period. (a) mean values (± SD) of the seasonal encounter rate (white text inside the bars). (b) monthly encounter rate in % during the activity period. Abbreviations: fad = non-reproductive adult females; fadP = pregnant adult females; juv = juveniles; mad = adult males; sub = subadults.

was more pronounced, occurred in spring, with peak in April. The male encounter rate then started to decrease from May to September, reaching its lowest value in June. After the end of September, a second and more restricted peak in the encounter rate was observed (Fig. 1). The encounter rate of adult females did not differ significantly across seasons (Table 2). Adult females were equally encountered throughout most of the activity period, with a slight decrease in their encounter rate in autumn (Fig. 1). The encounter rate of subadult vipers also did not differ significantly between the different seasons, however between summer and autumn the difference was almost significant ($p=0.04$, see Table 2). Subadults also had two peaks in their encounter rate in May/June and in September/October, although these were not as distinct as in adult males (Fig. 1). Statistically significant differences between the encounter rates of juvenile vipers were only found between spring and autumn (Table 2). Juveniles had a clear peak in their encounter rate in autumn, mainly between September and October, while their encounter rate was low during the other months of the activity period (Fig. 1). These tendencies were valid for all studied populations, with only small deviations for adult females from Lakatnik and subadults from Karlukovo. The first were encountered less frequently in autumn than in spring and summer while the latter had relatively high encounter rate throughout the entire activity period (Fig. 2).

Circadian activity

The data for all 688 observations of *V. ammodytes* were used for the analyses of their circadian activity. The earliest and the latest observations occurred at 8:03 h (in summer at Lakatnik) and at 22:06 h and at 22:48 h (in autumn at Karlukovo and in summer at Kresna Gorge), respectively.
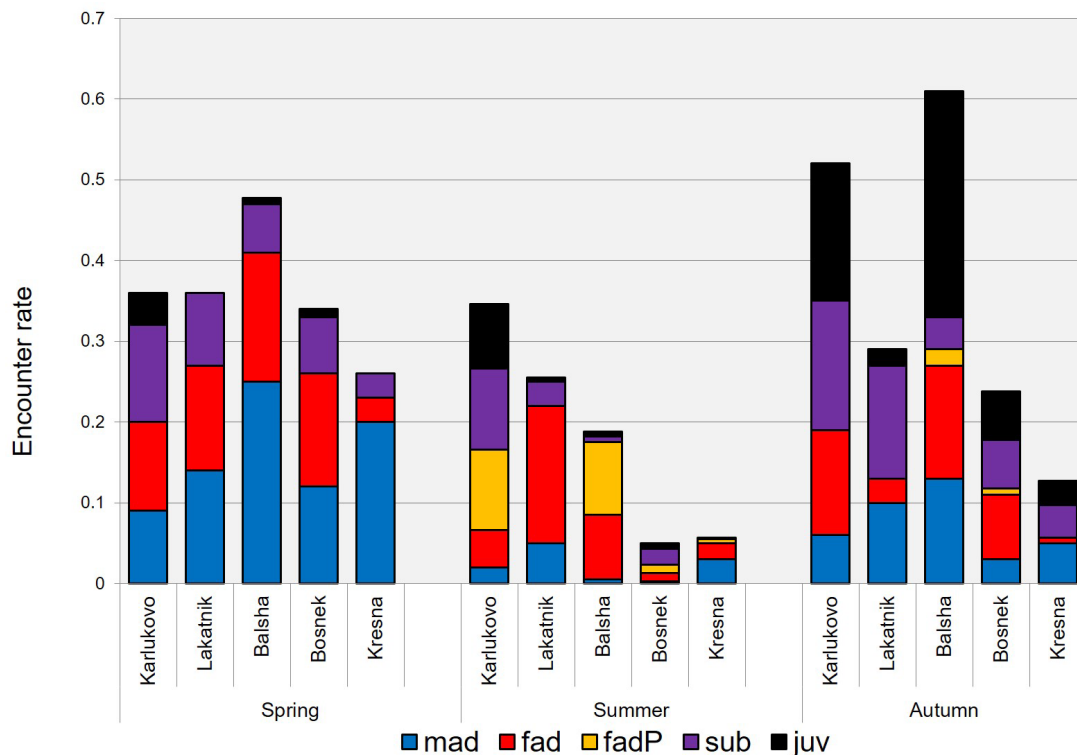

Figure 2 – Mean values of the seasonal encounter rate of *V. ammodytes* according to sex/age for each population. Abbreviations: fad = non-reproductive adult females; fadP = pregnant adult females; juv = juveniles; mad = adult males; sub = subadults.

In spring, adults and subadults were mostly found basking in the open in the middle part of the day, while few vipers were found in the shade or in shelters. Juveniles were detected throughout the day, in the open, in the shade and in shelters (Fig. 3a).

In summer, adult male and non-pregnant female vipers were found throughout the day. In the morning, late afternoon, and evening, we observed them mainly in the open, and in the middle part of the day mostly in the shade. A low number of non-pregnant female vipers were found in shelters, while the number of males detected in shelters was negligible. In contrast, the majority of pregnant females was found hiding in shelters in the middle part of the day, and to a lesser extent basking in the open in the morning. The number of pregnant females being active on the surface in the afternoon was very low and no pregnant vipers were observed to be active in the evening or during the night, which differs as compared to all other sex/age groups. Subadults and juveniles were found equally frequent throughout the day; more specifically in the morning, late afternoon and evening basking in the open, and at noon and the afternoon in the shade or in shelters (Fig. 3b).

In autumn, each group was mostly encountered basking in the open in the middle part of the day (Fig. 3c).
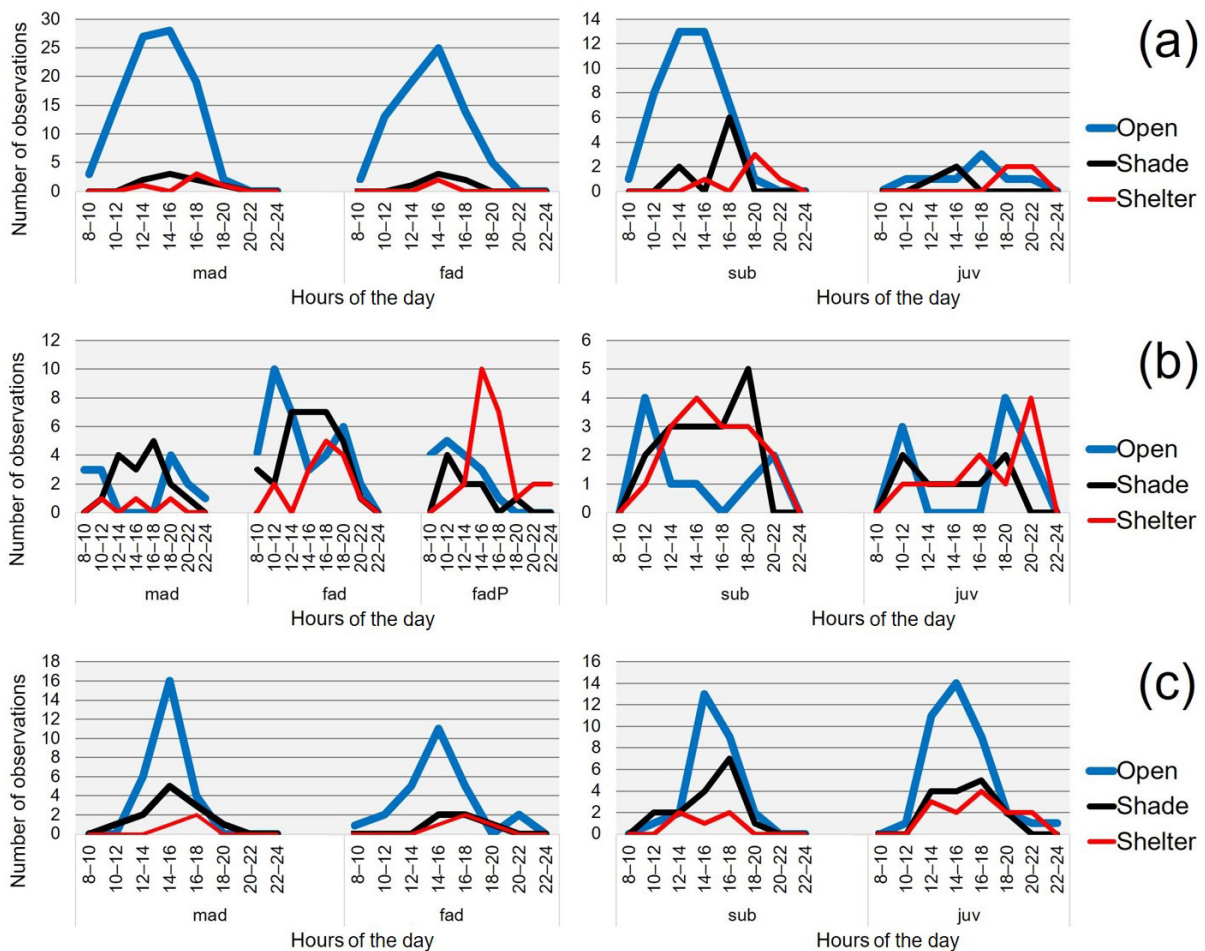
Figure 3 – Circadian activity of *V. ammodytes* according to sex/age in spring (a), summer (b) and autumn (c). Open = vipers basking in the open; Shade = vipers laying in the shade; Shelter = vipers, hiding in shelters. Abbreviations: fad = non-reproductive adult females; fadP = pregnant adult females; juv = juveniles; mad = adult males; sub = subadults.

Discussion

In the study sites, the activity period of *V. ammodytes* lasted from the end of February to the first half of November, which fits the data of BESHKOV (1993) for Bulgaria, as well as for the other parts of the species' distribution range in general (BIELLA 1983; SCHWEIGER 1992; HECKES *et al*. 2005; PLASINGER *et al*. 2014; GHIRA 2016). The year-to-year variation of the start and the end of the activity period depended on the weather conditions of each individual year. In spring, different sex/age groups seemed to emerge from hibernation at different moments while ingress to hibernation seems to occur approximately at the same time. This pattern is well documented for *V. ammodytes* (BIELLA 1983; HECKES *et al*. 2005; GHIRA 2016), as well as for the genus *Vipera* in general (VIITANEN 1967; PRESTT 1971; DUGUY 1972; BARON *et al*. 1996; ÚJVÁRI *et al*. 2001; PHELPS 2004; WEINMANN *et al*. 2004; GRAITSON 2008).

Adults' seasonal and circadian activity patterns

There was a clear difference between genders in the seasonal encounter rates of adult *V. ammodytes*. Similarly, in Serbia and Montenegro, adult males and females exhibited different seasonal activity patterns with adult males being mostly encountered in spring and adult females later, in summer (CRNOBRNJA-ISAILOVIĆ 2002; CRNOBRNJA-ISAILOVIĆ *et al*. 2007). Similar patterns were documented in other species of the genus (ANDRÉN 1985; NEUMEYER 1987; BARON *et al*. 1996; BONNET & NAULLEAU 1996; LOURDAIS *et al*. 2002; GRAITSON 2008; BAUWENS & CLAUS 2019). It seems that reproduction influences activity patterns, since these sex-specific differences were only observed in adults and might be due to different reproductive behaviour and reproduction-associated energy losses of males and females. In spring, adult males emerged from hibernation earlier than the other sex/age groups. This timing can most likely be explained by the need of male vipers for intensive basking after spring emergence for the maturation of the spermatozoa (ANDRÉN 1985; HERCZEG *et al*. 2007). This prolonged basking often makes adult males easily detectable in early spring. During the mating period, adult males spent most of their time searching for females, or in combat with other males, so they often travelled longer distances (VIITANEN 1967; PRESTT 1971; ANDRÉN 1985; PHELPS 2004; GRAITSON 2008; HAND 2018; DYUGMEDZHIEV *et al*. 2020b). During searches for females and combats, males were often less careful, which might increase their detectability. In addition, due to the more variable ambient temperatures in spring, vipers must spend more time basking for successful thermoregulation, mainly in the middle part of the day, when temperatures are the most favourable (DYUGMEDZHIEV *et al*. 2021). In summer, due to the high temperatures, male *V. ammodytes* spent most of the day hidden in the shade and to a lesser extend in shelters, where they were often difficult to detect. Compared to females, males encounter a much lower reproduction-associated depletion of reserves, which are easily restored after the mating period (DYUGMEDZHIEV 2020). Hence, in summer, males could minimize their activity, which also reduced their encounter rate. In addition, it is possible that at least some of the males shifted their activity hours outside of the present study's search period, and extended their activity to dusk and the night, or even until dawn. This is indicated by the fact that some adult males were found to be already active at the start of the search at 8:00h, and still active at the end of the search at night. The decrease of ambient temperatures in autumn again required a longer basking in the open during the warmest parts of the day for thermoregulation (DYUGMEDZHIEV *et al*. 2021), which led to the second peak in their encounter rate, mainly during the warmest parts of the day. Due to the absence of reproductive behaviour in autumn, however, the encounter rate of males was not as high as in spring.

The high encounter rate of adult females *V. ammodytes* in spring and autumn might also be attributed to their thermoregulatory activity during variable ambient temperatures. Explaining the high encounter rate of females during summer seemed to be more complex, since the circadian activity seemed to vary according to the females' reproductive status. The two strategies for avoiding heat (hiding in shelters or staying in the shade on the surface) probably provided different opportunities for the vipers. Therefore,

the observed female activity patterns might be explained by a trade-off between precise thermoregulation, risk of predation and need for feeding. Pregnant females were mostly found while hiding in shelters at noon. During gestation, female vipers need more precise thermoregulation for embryo development (BONNET & NAULLEAU 1996; LORIOUX *et al.* 2013; DYUGMEDZHIEV *et al.* 2021). Spending much of the day in shelters with optimal thermal conditions allows pregnant *V. ammodytes* to maintain 'preferred' temperatures longer than vipers retreating to the shade (DYUGMEDZHIEV *et al.* 2021). Additionally, in these shelters, pregnant females would be less exposed to predation than vipers staying on the surface. Non-pregnant females, on the other hand, were equally frequently encountered throughout the day, mostly basking in the morning, the late afternoon, and the early evening, while usually spending the noon in the shade and, more rarely, in shelters. Reproduction is a very energy-dependent process for female vipers, and needs a high amount of energy reserves (BONNET *et al.* 1994; BONNET & NAULLEAU 1995; NAULLEAU & BONNET 1996; BARON *et al.* 2012; BAUWENS & CLAUS 2019). After giving birth, female *V. ammodytes* are very emaciated and with depleted reserves, which need to be replenished to start the next reproductive cycle (LUISELLI & ZUFFI 2002; DYUGMEDZHIEV 2020). Because of this, non-pregnant females needed to feed more intensively than the other sex/age groups in the subsequent one or two years, which resulted in their increased activity throughout the activity period. However, the females' feeding period is relatively limited, mainly during summer and autumn (DYUGMEDZHIEV 2020), so non-pregnant females need to be more active in summer than the other sex/age groups. Staying on the surface in the shade during the hottest hours of the day in summer might benefit non-pregnant females by prolonging their hunting opportunities, and thus increasing their chances for capturing prey. Snakes on the surface would be more likely to encounter diurnally active prey, such as lizards (which were a substantial part of the diet of each age group (DYUGMEDZHIEV 2020)), than those hidden in shelters. However, snakes on the surface were more likely to be encountered than those in shelters, which explained the fact that non-pregnant females were found more often than pregnant ones. No pregnant females were observed to be active at night, in contrast to the other sex/age groups. Snakes being nocturnally active move at suboptimal temperatures for the potential benefit to increase their feeding opportunities (VITT & CALDWELL 2014; DYUGMEDZHIEV *et al.* 2020a). It appears that pregnant *V. ammodytes* choose the safety of their shelters over the risk of suboptimal temperatures.

Subadults' seasonal and circadian activity patterns

The higher encounter rate of subadult *V. ammodytes* in spring and autumn compared to summer might be explained by the thermal characteristics of the three seasons, i.e. because of the variable ambient temperatures in spring and autumn, vipers needed to bask longer for successful thermoregulation. Additionally, subadults fed relatively regularly from spring to autumn, and as a result, they maintained a relatively constant amount of body reserves throughout the entire activity period (DYUGMEDZHIEV 2020). So perhaps, a large number of subadults could afford to reduce their activity on the surface during summer days and by doing so decreased the risk for predation. During the warmest parts of the day, subadults that still needed to feed stayed in the shade where they could hunt, while others with already ingested prey retreated to shelters. This might explain the equal encounter rates of subadults in the shade and in shelters during the middle part of day.

Juveniles' seasonal and circadian activity patterns

The high encounter rate of juvenile *V. ammodytes'* in autumn should be attributed to the fact that immediately after their birth, which usually takes place between the second half of August and the first half of September (LUISELLI & ZUFFI 2002; DYUGMEDZHIEV 2020), they need to feed more intensively to build up a sufficient amount of reserves to survive their first hibernation (VÖLKL 1989; DYUGMEDZHIEV 2020). Thus, juveniles are expected to spend more time on the surface during the warmest parts of the day. The reduced encounter rate of juveniles in spring and summer might be attributed to several

factors. First of all, juveniles that have not been able to gain enough reserves in autumn might suffer higher winter mortality than the other sex/age groups, especially during long winters (VÖLKL 1989). Furthermore, juvenile *V. ammodytes* emerge from hibernation later in spring than the other sex/age groups. Because those vipers are most vulnerable to predators (HOUSTON & SHINE 1994; MADSEN & SHINE 1994; BONNET & NAULLEAU 1996; LOURDAIS *et al*. 2002; WEBB & WHITING 2005), they might wait for more stable climatic conditions to emerge from hibernation as well as live a more secretive and cautious life in general. However, assumptions about juveniles' higher mortality often lack empirical support, and long-term capture-recapture studies on *Vipera ursinii* (Bonaparte, 1835) and *Vipera berus* (Linnaeus, 1758) question these statements (BARON *et al*. 2010; BAUWENS & CLAUS 2018). On the other hand, the smaller size of juveniles allows for a faster rise of their body temperatures, reducing the time required for basking (BONNET & NAULLEAU 1996; LOURDAIS *et al*. 2002; WEBB & WHITING 2005). This probably explains the equal encounter rates of juveniles in the open, in the shade and in shelters throughout the day. It should be noted however that the distinction between juveniles and subadults in the present study is somewhat arbitrary and is only based on the size of individuals. It is possible that after an intensive feeding prior to their first hibernation, new-borns could grow rapidly in size and in the following spring and summer would already fall into the size limit of subadults, which could explain the rapid decrease in the encounter rate of juveniles during spring and summer.

Conclusions

Vipera ammodytes exhibited different seasonal and circadian activity patterns depending on sex and age. Adult males and subadults were encountered mainly in spring and autumn, and juveniles mainly in autumn, while adult females were observed throughout the entire activity period. Females' reproductive status seemed to influence their circadian activity. The observed intergender and ontogenetic differences might be a result of the complex effect of many factors, such as climatic conditions, differences in the reproductive behaviour and the cost of reproduction between sexes, as well as the trade-off between precise thermoregulation, risk of predation and feeding needs.

Acknowledgements

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Appendix

Number of observations of *V. ammodytes* according to sex/age and field effort during the different months for each study site.

Site/ Taxa/ Visits	Month/ Year	Time spent (h.min)	sex/age (number of vipers found)						
			mad	fad	fadP	msub	fsub	mjuv	fjuv
	April 2014	5	–	1	–	1	–	–	–
	May 2014	9.3	–	–	–	–	–	–	–
	July 2014	12	–	–	1	–	–	–	–
	August 2014	10.2	–	–	–	1	1	1	–
	September 2014	9	–	1	–	–	2	1	–
	October 2014	6.2	–	–	–	3	2	–	–
	March 2015	5.3	–	2	–	–	–	–	–
	April 2015	14.45	1	2	–	–	1	–	–
	May 2015	8.1	1	2	–	–	2	–	–
	June 2015	22.2	–	3	–	–	4	–	–
	July 2015	24	–	1	–	–	1	–	1
	August 2015	23.3	1	–	2	–	1	1	–
	September 2015	21.1	1	–	–	–	–	–	–
	October 2015	13.15	–	7	–	3	–	2	1
	November 2015	8.15	2	1	–	–	–	–	–
	March 2016	3.3	1	–	–	–	–	–	–
Karlukovo *V. a. montandoni* (E) 59 visits	April 2016	16.25	3	3	–	–	1	–	1
	May 2016	20.3	1	2	–	1	4	1	1
	June 2016	25.5	1	2	–	2	4	3	2
	July 2016	27	–	–	–	–	2	1	1
	August 2016	19.2	–	3	1	1	1	–	1
	September 2016	20.2	–	1	–	2	–	4	–
	October 2016	9	3	3	–	–	1	–	–
	November 2016	4.15	–	3	–	–	–	–	1
	December 2016	2	–	–	–	–	–	–	–
	February 2017	3.3	1	–	–	–	–	–	–
	March 2017	13	4	2	–	–	1	–	–
	April 2017	17.1	2	2	–	1	–	2	–
	May 2017	25.35	2	–	–	1	5	3	–
	June 2017	29.1	2	1	9	2	1	2	1
	July 2017	22.25	1	2	9	1	1	1	3
	August 2017	19	–	–	5	1	1	3	–
	September 2017	23.55	–	–	–	–	1	6	4
	October 2017	17.4	3	3	–	1	2	3	3
	November 2017	2.5	–	–	–	–	–	2	–
	December 2017	1.2	–	–	–	–	–	–	–

Site/ Taxa/ Visits	Month/ Year	Time spent (h.min)	sex/age (number of vipers found)						
			mad	fad	fadP	msub	fsub	mjuv	fjuv
	April 2013	4.2	1	–	–	–	–	–	–
	July 2013	22.5	–	–	–	–	–	–	–
	September 2013	8.5	1	–	–	2	–	–	–
	March 2014	6	1	–	–	–	–	–	–
	May 2014	15	1	5	–	–	2	–	–
	June 2014	10	–	7	–	1	–	–	–
	July 2014	12.15	1	2	–	–	–	–	–
	August 2014	10.2	1	–	–	–	–	–	–
	September 2014	9.3	–	–	–	–	–	–	1
	October 2014	6.4	2	–	–	1	1	–	–
	April 2015	12.3	4	1	–	–	–	–	–
	May 2015	9.4	1	1	–	1	–	–	–
	June 2015	24	1	7	–	–	–	–	–
	July 2015	24.2	2	5	–	–	–	–	–
	August 2015	24.2	2	4	–	–	–	1	–
Lakatnik *V. a. ammodytes* 58 visits	September 2015	19.5	2	2	–	–	1		–
	October 2015	10.5		–	–	–	–	1	–
	November 2015	6.4	1	–	–	–	1	–	–
	April 2016	15.25	2	2	–	1	1	–	–
	May 2016	17.05	1	3	–	2	1	–	–
	June 2016	23.2	–	4	–	2	1	–	–
	July 2016	24	2	5	–	1	–	–	–
	August 2016	23.45	3	2	–	–	–	–	–
	September 2016	19.15	4	2	–	2	–	–	–
	October 2016	11.15	1	–	–	–	1	–	–
	November 2016	3.1	–	–	–	–	–	–	–
	March 2017	13.1	2	5	–	–	1	–	–
	April 2017	18	1	2	–	1	–	–	–
	May 2017	21.4	–	2	–	1	2	–	–
	June 2017	25	1	6	–	1	2	–	1
	July 2017	26.2	–	4	–	–	–	–	–
	August 2017	23.4	2	6	–	–	–	–	–
	September 2017	10.4	–	1	–	1	1	–	–
	October 2017	15	1	–	–	–	4	–	–

Site/ Taxa/ Visits	Month/ Year	Time spent (h.min)	sex/age (number of vipers found)						
			mad	fad	fadP	msub	fsub	mjuv	fjuv
	March 2014	6	3	–	–	–	–	–	–
	April 2014	5	3	–	–	1	–	–	–
	May 2014	9.3	–	1	–	–	1	–	–
	June 2014	10	–	–	2	–	–	–	–
	July 2014	7.3	–	1	3	–	–	–	–
	August 2014	11	–	–	3	–	–	–	–
	September 2014	8.2	1	1	1	–	–	–	–
	October 2014	5	1	–	–	–	–	–	–
	March 2015	5.3	4	–	–	–	–	–	–
	April 2015	10.55	4	4	–	–	–	–	–
	May 2015	10.35	2	1	–	–	–	–	–
	June 2015	14.2	–	–	–	1	–	–	–
	July 2015	23.25	–	1	–	–	–	1	–
	August 2015	21.5	–	–	–	1	–	–	–
	September 2015	17.4	–	1	–	–	–	3	2
	October 2015	11.55	1	–	–	2	–	3	2
Balsha *V. a. ammodytes* 57 visits	November 2015	6.55	1	–	–	–	1	1	–
	March 2016	3.4	1	–	–	–	1	–	–
	April 2016	15.05	2	–	–	2	–	1	–
	May 2016	17.05	1	5	–	1	–	–	–
	June 2016	10.2	–	1	1	–	–	–	–
	July 2016	23.3	–	–	4	–	–	–	–
	August 2016	18.1	–	1	–	–	–	–	–
	September 2016	17.35	1	1	–	1	–	1	1
	October 2016	8.35	5	1	–	–	1	–	1
	November 2016	2	1	–	–	–	–	–	–
	February 2017	2.45	1	–	–	–	–	–	–
	March 2017	7.1	–	1	–	1	–	–	–
	April 2017	15.4	3	5	–	–	–	–	–
	May 2017	21.1	–	3	–	–	–	–	–
	June 2017	24	–	–	3	–	–	1	–
	July 2017	26.2	–	1	4	–	–	–	–
	August 2017	24	–	–	1	–	–	–	–
	September 2017	11.4	–	1	–	–	–	2	2
	October 2017	13.1	1	2	–	–	–	6	7
	August 2018	4.2	1	1	–	–	–	–	–

Site/ Taxa/ Visits	Month/ Year	Time spent (h.min)	sex/age (number of vipers found)						
			mad	fad	fadP	msub	fsub	mjuv	fjuv
Bosnek *V. a. montandoni* (S) 52 visits	May 2013	3	1	1	–	–	–	–	–
	May 2014	8.3	1	2	–	2	–	–	–
	June 2014	10.4	–	–	–	1	–	–	–
	July 2014	11	–	–	–	–	–	–	1
	August 2014	11.25	–	–	–	–	–	–	–
	September 2014	4	–	1	–	–	–	–	–
	October 2014	5	–	1	–	–	–	–	1
	April 2015	13.05	–	1	–	–	–	1	1
	May 2015	17.2	1	1	–	–	–	–	–
	June 2015	16.15	–	1	–	1	–	–	–
	July 2015	24.15	–	–	–	–	–	–	–
	August 2015	21.3	–	–	–	–	–	–	–
	September 2015	15.5	–	2	–	–	1	–	–
	October 2015	13	–	–	–	–	1	–	1
	November 2015	8.2	1	–	–	–	–	–	–
	April 2016	13.4	1	–	–	–	1	–	–
	May 2016	20.25	–	–	–	–	–	–	–
	June 2016	12	–	–	1	–	–	–	–
	July 2016	25	–	1	–	–	–	–	–
	August 2016	24.3	–	–	–	1	–	–	–
	September 2016	19.2	–	–	–	1	3	–	–
	October 2016	6	1	1	–	–	–	–	–
	March 2017	6.35	1	1	–	–	–	–	–
	April 2017	17.4	1	–	–	1	–	–	–
	May 2017	24.25	1	1	–	3	1	–	–
	June 2017	27	–	1	1	–	1	–	–
	July 2017	25.4	1	–	1	–	–	–	–
	August 2017	23.1	–	–	–	–	–	–	–
	September 2017	18.2	–	–	1	1	–	–	–
	October 2017	12.2	2	–	–	–	–	1	2
Kresna gorge *V. a. montandoni* (S) 54 visits	May 2013	4.2	1	–	–	–	–	–	–
	September 2013	11	–	–	–	–	1	–	1
	May 2014	11	2	–	–	1	–	–	–
	June 2014	20.2	1	–	–	–	–	–	–
	July 2014	11.25	–	–	–	–	–	–	–
	August 2014	11	–	–	–	–	–	–	–
	September 2014	8	–	–	–	–	–	–	–
	October 2014	3.4	1	–	–	–	–	–	–
	July 2015	12	–	–	–	–	–	–	–

Site/ Taxa/ Visits	Month/ Year	Time spent (h.min)	sex/age (number of vipers found)						
			mad	fad	fadP	msub	fsub	mjuv	fjuv
Kresna gorge *V. a. montandoni* (S) 54 visits (continued)	August 2015	13.25	–	–	–	–	–	–	–
	March 2016	3.3	1	–	–	–	–	–	–
	April 2016	14.05	2	1	–	–	–	–	–
	May 2016	19.4	1	–	–	–	–	–	–
	June 2016	12.45	–	1	–	–	–	–	–
	July 2016	26.25	2	–	1	–	–	–	–
	August 2016	24.1	1	2	–	–	–	–	–
	September 2016	18.55	1	–	–	–	1	–	–
	October 2016	5	–	–	–	–	–	–	–
	March 2017	4.4	–	–	–	2	–	–	–
	April 2017	28.1	5	1	–	1	–	–	–
	May 2017	41.2	4	2	–	–	–	–	–
	June 2017	45.3	1	2	–	–	–	–	–
	July 2017	40	3	2	–	1	–	–	–
	August 2017	32.2	1	–	–	–	–	–	–
	September 2017	18	2	1	–	–	1	–	1
	October 2017	14.4	–	–	–	–	–	–	–
	May 2018	17.1	6	1	–	–	–	–	–
Random visits outside of the studied sites 35 visits	April 2013	7	1	–	–	–	–	–	–
	May 2013	21.4	1	2	–	1	–	–	1
	June 2013	6.3	–	1	–	–	–	–	–
	March 2014	3.1	1	–	–	–	–	–	–
	April 2014	8	1	1	–	–	–	–	–
	May 2014	23.3	5	1	–	1	–	–	2
	May 2015	5	–	2	–	–	–	–	–
	August 2015	4.5	–	–	–	–	–	–	2
	April 2016	2	1	–	–	–	–	–	–
	July 2016	5	–	–	–	1	–	–	–
	September 2016	1	–	1	–	–	–	–	–
	October 2016	1.15	–	–	–	1	1	–	–
	March 2017	4.3	–	1	–	–	–	–	–
	April 2017	4	1	3	–	–	–	1	–
	July 2017	3	1	–	–	–	–	–	–
	October 2017	2.4	–	–	–	–	1	–	–
	April 2018	36.25	7	3	–	1	–	–	–
	May 2018	11.4	2	3	–	–	–	–	–
Total number of vipers from each group			176	204	54	69	75	60	50
Overal total observations of vipers				688					