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Crepuscular and nocturnal activity of the Nose-horned viper, *Vipera ammodytes* (Linnaeus, 1758) is more common than previously reported

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Abstract

Different snake species may be active at various times of the day. In Europe, most snake species are predominantly diurnal, but about a third are partially or principally crepuscular and/or nocturnal. Here, we report the first instance of multiple *in situ* observations of the crepuscular and nocturnal activity of *V. ammodytes* in Bulgaria. Overall, usually as a result of general herpetological surveys and chance observations between 2001–2020, we recorded crepuscular/nocturnal activity of twenty-seven individuals from both sexes and all age classes (juvenile to adult), observed from April to September, following warm (maximum daily T_{air} = 20–28 °C) and hot (T_{air} > 28 °C) days. These records represent less than 1.5% of all our personal viper observations. However, given that our observations occurred throughout the country, within five different climatic zones, we hypothesise that nocturnal activity of *V. ammodytes* is more common than previously reported.

Key Words

behavior, ecology, snake, temperature, Viperidae

Introduction

Nocturnal activity in ectotherms might lead to suboptimal performance due to depressed body temperature (T_{body}) compared to preferred temperature ($T_{preferred}$), potentially incurring costs such as slower digestion. However, changes in activity timing might lower predation risk and increase prey availability (Vitt and Caldwell 2014). Different snake species may be active at various times of the day and can modify their behavior according to current environmental and biotic conditions (Vitt and Caldwell 2014). Based on the predominant time of activity, European snakes can be classified into three groups: 1) nocturnal (ca. 17% of the European species, e.g. *Eryx jaculus* (Linnaeus, 1758), *Telescopus fallax* Fleischmann, 1831, etc.); 2) diurnal and nocturnal (ca. 15% of the European species, e.g., *Natrix* sp.); 3) diurnal, with limited or no crepuscular activity (ca. 68% of the European species, e.g., *Hierophis* sp., *Dolichophis caspius* (Gmelin, 1789), *Malpolon* sp.) (Speybroeck et al. 2016). European vipers from the genus *Vipera* are usually active during the day, but nocturnal activity has been observed for some species, e.g. *V. aspis* (Linnaeus, 1758) (Naulleau 1975; Mattea and Allain 2020), *V. berus* (Linnaeus, 1758) (Wareham 1998), *V. latastei* Bosca, 1878 (Brito 2003).

Throughout its range (NE Italy and S Austria, most of the the Balkan Peninsula, Anatolia, and the Transcaucasia), the Nose-horned viper, *V. ammodytes* (Linnaeus, 1758) may exhibit diverse diurnal activity patterns based on the particular location's characteristics and seasonality (Heckes et al. 2005; Ghira 2016; Dyugmedzhiev 2020). Similarly, its activity during darkness can be highly variable: partially to highly crepuscular/nocturnal, especially on warm nights (e.g. Schreiber 1912; Boulenger 1913; Calinescu 1926 in Beshkov 1993; Karaman 1939; Bruno 1967; Muschelischvili 1970; Bannikov et al. 1971; Biella 1983; Zadravec and Koren 2017) or without nocturnal activity detected during active searches even when other snake species have been active (Biella and Blättler 1989; Schweiger 1992; Crnobrnja-Isailović 2002; Crnobrnja-Isailović et al. 2007).

In Bulgaria, the species' activity has been described succinctly as 'almost exclusively diurnal' (Beshkov and Nanev 2002) and 'diurnal, with some crepuscular/nocturnal activity following warm summer days' (Naumov 2007; Stojanov et al. 2011). Specific data on the times of activity of *V. ammodytes* have been published only in Beshkov (1977) and extended in Beshkov (1993). Overall, 154 individuals were collected using general and targeted day and night surveys between 1953–1990 from throughout the country. Observations were made under natural light conditions, between 5:30 h and 21:00 h, except for a single individual found after dark at 21:30 h on 6 September in SE Bulgaria (Lesovo Village, Haskovsko) after a very hot day. Concurrently, other snake species were found active at night. Here, we report multiple observations of the crepuscular and nocturnal activity of *V. ammodytes* in Bulgaria.

Material and methods

We compiled the author's personal records of *V. ammodytes*, collected during viper-specific and general herpetological surveys carried throughout Bulgaria in 2001–2020 and during the species active season (mostly April to September). Most searches were non-systematic, varied in time and intensity, and occurred throughout the country. However, between 2014 and 2019, some of the search effort was systematic, with viper-specific surveys conducted monthly during the active season of the species in five different localities, as part of an ongoing ecological study on the species (for more details see Dyugmedzhiev et al. in press).

We considered an individual as active if it was found on the surface and not utilizing cover. When possible, immediately after hand-capturing an active viper, we used a quick-reading digital thermometer (precision: 0.1 °C) to measure the snake's body temperature at the cloaca (T_{body}), temperature of the substrate ($T_{substrate}$) and air temperature (T_{air}) at 15 cm above the ground. We estimated temperature of the microhabitat ($T_{microhabitat}$) as the average of $T_{substrate}$ and T_{air} (Dyugmedzhiev et al. 2019; Dyugmedzhiev 2020). When possible, we measured an individual's snout to venth length (SVL) and tail length using a flexible ruler (precision: 0.5 cm). We identified its respective age class and sex based on the total body length (juveniles < 28 cm, subadults > 28 cm, adult females > 46 cm, adult males > 49 cm) (Dushkov 1978; Dyugmedzhiev et al. in press), the ratio of the SVL and tail length, and coloration patterns (Tomović et al. 2002). Captured vipers were then released on site.

For each observation, we recorded the geographical coordinates (GCS WGS 84), the date and time, and subsequently identified the astronomical sunset time and the day length for the specific date and locality. We defined activity as crepuscular if an individual was found from 15 min before sunset to 30 min after sunset (usually finding snakes was still possible without an artificial light source) and as nocturnal if found more than 30 min after sunset and before next sunrise. In most cases at the same localities where we found crepuscular/nocturnal snakes, we also searched during the day and measured daily T_{air} throughout. Thus, we considered days as warm when T_{air} was 20–28 °C and hot when the maximum recorded daily T_{air} > 28 °C; we have identified that above 28 °C, the detectability of *V. ammodytes* decreases, as most animals retreat to shelters or in shade (Dyugmedzhiev 2020).

Using QGIS (v. 3.14), for each observation we extracted elevation data based on a 40-m Digital Elevation Model and the Köppen-Geiger climate classification based on a high-resolution (1-km pixel size) map for 1980–2016 (Beck et al. 2018). Moonrise, moonset, and % illumination were obtained with Virtual Moon Atlas (v. 7.0).

Results

Overall, we recorded 11 crepuscular and 16 nocturnally active individuals (Table 1), from ca. 2000 personal observations. We observed two individuals on each of three dates: 2 April 2017, adult females seen next to each other; 14 July 2018, adult males; 7 September 2016, adult female and juvenile male. The remaining observations were of single individuals per day. Most (78%) of the observations of crepuscular and nocturnally active vipers were made after 2014 when search effort increased and became more systematic (χ^2 = 8.33, df = 1, p = 0.004). Except for the latest recorded activity (252 min after sunset), the rest were up to 160 min, with 59% of all observations occurring up to 45 min after sunset. Active individuals included 12 males, 14 females and 1 individual whose sex was not determined, from all age classes (6 juveniles, 3 subadults and 18 adults).

We recorded active snakes from 2 April to 15 September. Activity seems to shift slightly to later hours of the night with the increase in the daily temperature; in April and May we only observed crepuscular activity.

Most (70%) of the crepuscular and nocturnally active vipers were recorded on hot days and the remaining on warm days (χ^2 = 4.48, df = 1, p = 0.034). Mean T_{body} (± SD) was

Table 1. Observations of crepuscular/nocturnally active *Vipera ammodytes*. Time – local time (UTC +3); Ss – minutes after sunset; M% – percent of moon illuminated, numbers in parentheses denote cases when the moon rise was after Time, question mark denotes cases when the moon rise was 7–9 h after Time; A/S – age class (J – juvenile, S – subadult, A – adult) and sex (F – female; M – male); L – total body length (cm); T_{body} – snake temperature (°C); T_{mh} – microhabitat temperature (°C); D_{len} – day length in hh:mm; T_d – warm (W) or hot (H) day; KG – Köppen-Geiger class; Elev – elevation. See the text for details.

Time	Ss	M%	A/S	L	T_{body}	T_{mh}	D_{len}	T_d	KG	Elev	Latitude and Longitude	Date
19:38	-15	?38	A/F	76.1	17.7	15.3	12:44	W	Dfb	709	42.8553, 23.2529	02.04.17
19:38	-15	?38	A/F	75.2	22.7	15.1	12:44	W	Dfb	709	42.8553, 23.2529	02.04.17
20:55	-11	98	A/F	58.6	25.1	23.9	15:10	W	Dfb	520	43.0889, 23.3820	07.07.17
20:56	-9	100	J/F	27.2	28.2	26.9	15:20	H	Dfa	165	43.1796, 24.0603	20.06.16
20:25	1	99	A/M	62.3	30.4	26.4	13:48	H	Dfb	508	43.0896, 23.3860	17.08.16
21:00	1	(4)	A/M	~55	–	–	14:53	H	BSk	222	41.7631, 23.1562	14.07.18
20:11	6	(23)	S/M	33.3	28.5	24.6	13:21	H	Dfa	165	43.1795, 24.0604	27.08.16
20:58	8	(58)	S/F	36.9	22.6	21.4	15:18	H	Dfb	543	43.0895, 23.3848	16.06.17
20:39	12	67	J/M	25	22.7	17.2	14:13	H	Dfa	170	43.1801, 24.0575	04.05.17
21:02	24	100	A/F	62.8	27.1	24.5	14:13	H	Dfb	521	43.0895, 23.3836	07.08.17
20:13	27	?34	J/M	26.4	24	20.3	12:50	W	Dfa	209	43.1803, 24.0562	07.09.16
20:47	31	(1)	A/F	52.9	20.7	19.1	13:35	W	Dfb	447	43.0888, 23.3819	22.08.17
21:30	31	(4)	A/M	~63	–	–	14:53	H	BSk	214	41.7618, 23.1560	14.07.18
21:38	32	(27)	A/M	58.8	26.1	23.8	15:18	H	Dfa	167	43.1801, 24.0571	28.06.17
20:09	34	(24)	A/F	52.8	23.9	22.9	12:28	H	Dfb	521	43.0895, 23.3836	15.09.17
21:39	42	(28)	A/M	59.8	24.7	19.8	14:56	H	Dfa	170	43.1801, 24.0577	18.07.17
21:54	52	97	S/F	41.9	26.3	24.9	15:09	H	BSk	212	41.7662, 23.1554	15.06.19
21:10	69	(59)	A/F	–	–	–	13:24	H	Csa	322	41.4282, 26.0670	25.08.05
21:21	85	(66)	J/M	~20	–	–	13:31	H	BSk	9	42.7373, 27.8923	23.08.16
21:22	96	?34	A/F	61.1	21.5	19.6	12:50	W	Dfa	303	43.1516, 24.1013	07.09.16
22:48	104	84	A/M	49.4	27.6	26.4	15:06	H	BSk	210	41.7662, 23.1554	04.07.17
22:40	112	?76	A/M	–	–	–	15:04	W	Cfa	438	41.9328, 25.2894	06.06.06
22:06	135	98	J/F	24.6	27.9	14.8	13:00	H	Dfa	166	43.1799, 24.0549	04.09.17
23:10	144	(61)	A/F	–	–	–	15:03	W	Cfa	296	41.7034, 25.9668	08.06.04
23:00	149	(0)	A/F	–	–	–	14:16	H	Cfa	380	41.8677, 25.3264	04.08.05
22:25	158	94	J/–	–	–	–	12:45	H	BSk	92	41.4130, 23.3174	09.09.11
1:00	252	(17)	A/M	–	–	–	14:56	H	Csa	333	41.5975, 26.0507	11.07.05

24.66 ± 3.89 °C (range: 17.7–30.4, *N* = 9) for the crepuscular vipers and 25.09 ± 2.61 °C (20.7–27.9, *N* = 9) for the nocturnal individuals. Mean $T_{microhabitat}$ (± SD) was 21.23 ± 4.57 °C (15.1–26.9, *N* = 9) for the crepuscular vipers and 21.76 ± 3.68 °C (14.8–26.4, *N* = 9) for the nocturnal vipers.

Vipera ammodytes occurs throughout the country at elevations below 1450 m; crepuscular/nocturnally active individuals were found across both N-S and E-W gradients, at ~0–700 m a.s.l. (Fig. 1). The crepuscular/nocturnally active individuals occurred in five classes of the Köppen-Geiger climate classification: *Dfa* (N = 8) and *Dfb* (N = 8) (Cold, no dry season; with hot or warm summer, respectively), *BSk* (N = 6; Arid, steppe, cold), and *Cfa* (N = 3) and *Csa* (N = 2) (Temperate, hot summer; without a dry season or with dry summer, respectively).

In seven cases, when it could have potentially influenced snakes' activity, the moon's illumination was approaching full moon (>90%); in four of the five cases when the moonrise was 7–9 h before the time of observation, illumination was 34–38%. In 13 cases, regardless of the illumination percentage, the moon was likely not visible due to rising after the observation or setting beforehand; these cases also tend to have low illumination percentages.

Discussion

Nocturnal activity has been demonstrated for several species of European vipers (Naulleau 1975; Wareham 1998; Brito 2003; Mattea and Allain 2020). However, vipers are notoriously difficult to find even during the day due to their less-active lifestyle, often low densities, and camouflage coloration; even if active, observing them at night under artificial light is complicated and likely further decreases detectability. In addition, in Bulgaria nocturnal surveys tend to focus less on squamates (especially vipers), and instead usually focus on amphibians with well-known nocturnal activity. All of these reasons expectedly lead to low chances of nocturnal observations. Our results suggest that increased effort specifically for viper nocturnal searches will reveal that this is more widespread than previously reported in Bulgaria, as has been demonstrated for other localities (e.g. Schreiber 1912; Boulenger 1913; Calinescu 1926 in Beshkov 1993; Karaman 1939; Bruno 1967; Muschelischvili 1970; Bannikov et al. 1971; Beshkov 1977, 1993; Biella 1983; Zadravec and Koren 2017) and would provide higher-quality quantifiable data to aid in understanding the ecology and physiology of *V. ammodytes* further.

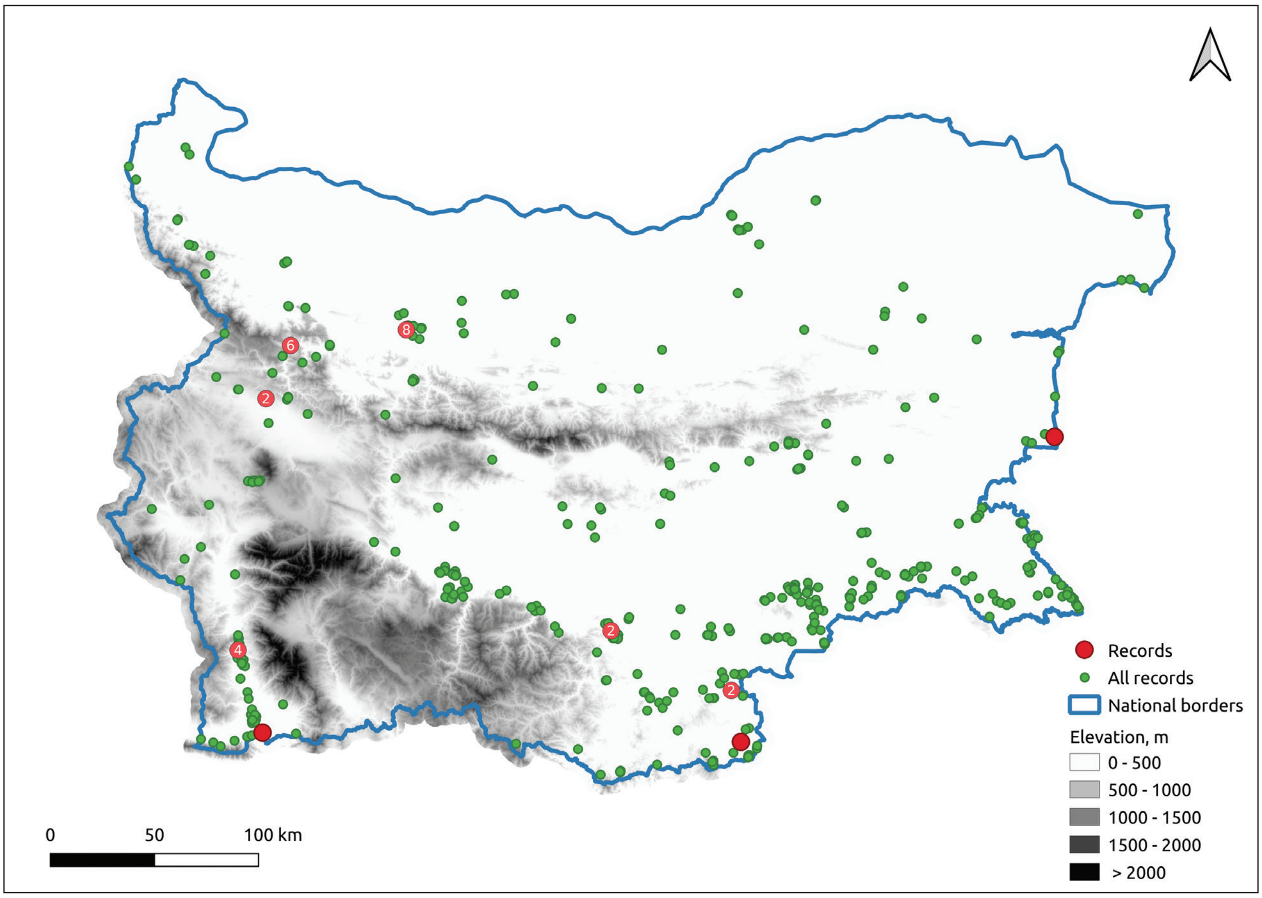

Figure 1. Indicative map of authors' personal unpublished observations of *Vipera ammodytes* in Bulgaria. Green circles – diurnally active individuals. Red circles – the crepuscular/nocturnally active individuals described in Table 1; a number indicates the count of closely situated observations.

Furthermore, the observations fall within five climatic classes which are well-represented throughout the range of the species, suggesting that environmental conditions suitable for low/no-light activity should exist for many populations; why at certain locations the species seemingly might not exhibit this behavior (e.g. Biella and Blättler 1989; Schweiger 1992; Crnobrnja-Isailović 2002; Crnobrnja-Isailović et al. 2007) should be researched further. Micro-climatic conditions are also important, demonstrated by our latest observation (1:00 h) that was made by car cruising on an asphalt road that likely stayed warmer than the surroundings and provided suitable thermal conditions to allow continued activity.

Although based on a post hoc evaluation and a low sample size, it seems that lunar illumination might play a role in the observed activity, as most of our observations were either in the close-to-full moon or no moonlight conditions. The effects of moon illumination on *V. ammodytes* behavior need to be studied further, with data related to it collected in the field. Previous research on crotaline vipers suggests a complicated relationship. The full moon visually benefits snakes in prey acquisition, while potentially increasing predation (Lillywhite and Brischoux 2012). However, moonlight avoidance has been reported for a desert species, *Crotalus viridis* Rafinesque, 1818 (Clarke et al. 1996).

It seems that the species is more likely to exhibit crepuscular or nocturnal activity mainly following hot days, substituting potentially unsuitable diurnal thermal conditions with ones optimizing physiological performance (e.g., locomotion and prey acquisition). However, snakes were also active after warm days. *Vipera ammodytes* prefers to adjust its T_{body} between 28–33 °C (Saint Girons 1978; Dyugmedzhiev 2020). Although our sample is small, we presume that the crepuscular and nocturnal individuals tend to be active with a lower T_{body} than is preferred, potentially increasing their susceptibility to predators. However, some individuals may be willing to take this risk to increase their feeding opportunities. Further studies should reveal whether this is the primary driver for this behavior.

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