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Population Estimates of the Nose-horned Viper *Vipera ammodytes* (Linnaeus, 1758) (Reptilia: Viperidae) from Five Populations in Bulgaria

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To Niki, a true friend

Abstract: Five populations of *Vipera ammodytes* in Western Bulgaria located along a latitudinal gradient were studied using the Capture-Mark-Recapture method. Sex ratio among subadults and juveniles was approximately 1:1 but it was difficult to be determined in adults due to methodological biases caused by differences in catchability of males and females during the active season. The marked individuals had high survival rate, but capture probability was low. From north to south, the established numbers and densities of the species in the studied areas were as follows: Karlukovo – 796 individuals, with density 5.78 ind./ha, Lakatnik – 319 individuals, with density 1.59 ind./ha, Balsha – 635 individuals, with density 4.12 ind./ha, Bosnek – 296 individuals, with density 0.73 ind./ha, Kresna Gorge – 245 individuals, with density 2.07 ind./ha. Differences in movement rate between sexes were observed, with adult males being more mobile than females. During gestation, pregnant females became very static and usually kept close to the hibernating areas. After parturition, the neonates stayed close to these areas until the beginning of hibernation.

Key words: density, movement rate, home range, Capture-Mark-Recapture, Balkans

Introduction

The species from the genus *Vipera* Laurenti, 1768 are sedentary and usually use the same territory (home range) each year, usually with limited movements within it (Saint Girons 1952, 1997, Neumayer 1987, Naulleau 1966, Naulleau et al. 1996, Baron 1997, Brito 2003, Thomas 2004, Weinmann et al. 2004, Graitson 2008). Typically, representatives of the genus, for which data are available, are characterised by high survival rate (Neumayer 1987, Baron et al. 1996, Saint Girons 1996). These traits make them useful model species for conducting population studies based on the Cap-

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ture-Mark-Recapture method. Such studies among European vipers usually are dealing with *Vipera berus* (L., 1758) (Viitanen 1967, Andrén 1982, Völkl, 1986, 1989, Neumeyer 1987, Ursenbacher & Monney 2003, Phelps 2004, 2007, Thomas 2004, Weinmann et al. 2004, Wollesen & Schwartz 2004), *Vipera aspis* (L., 1758) (Saint Girons 1952, 1981,1996, Naulleau 1966, Monney 1992, Naulleau & Bonnet 1995, Naullaeu et al. 1996, Lourdais et al. 2002), *Vipera ursinii* (Bonaparte, 1835) (Baron et al. 1996, 2010, Újvári & Korsós 1997) and *Vipera latastai* (Bosca, 1878) (Brito 2003). In contrast, the Nose-horned Viper *Vipera ammodytes* (L., 1758) is poorly studied, with no published data based on the CMR method and only scarce population data available (Künzl 1954, Muschelischvili 1970, Beshkov 1977, Dushkov 1978, Bozhanskii & Kudryavcev 1986, Schweiger 1992, Luiselli 1996, Christov 2002, Plasinger et al. 2014, Mebert et al. 2015, Ghira 2016).

In Bulgaria, the Nose-horned Viper is distributed throughout the country with the exception of the high mountains. The species exhibits markedly high genetic diversity in Bulgaria, with at least two well-differentiated clades in the northwest–southeast alternate (Ursenbacher et al. 2008, Stojanov et al. 2011).

The aim of the present study was to obtain basic population estimates from different populations such as sex ratio, survival rate, population size and density and movement rates based on a multi-year study using the Capture-Mark-Recapture method.

Materials and Methods

Five sites along a latitudinal gradient of the species distribution in western Bulgaria were chosen for the field studies (Fig. 1). The locations, surface area and habitat characteristics of the study sites are as follows: (1) near Karlukovo Village (111-250 m a.s.l., 10.38 ha) – a karst valley with steep rocks and terraces as well as patches of deciduous forests; (2) near Gara Lakatnik Village (352-733 m a.s.l., 10.18 ha) – a karst valley with the land cover similar to the first site; (3) near Balsha Village (652-853 m a.s.l., 5.34 to 21.86 ha) – an abandoned quarry surrounded by fields, bare hills and a deciduous forest (initially, the study in this site covered only the abandoned quarry with an area of 5.34 ha but, since 2016, the adjacent territories were also sampled, so the total area became 21.86 ha); (4) near Bosnek Village (942-1332 m a.s.l., 19.29 ha) – a middle-mountain karst valley with stony slopes covered with shrubs and thin deciduous forests; (5) the Gabrovitsa area in the Kresna Gorge (165-488 m a.s.l., 15.17 ha) – a plain area with scattered shrubs and abandoned vineyards surrounded by steep stony slopes with forest vegetation (Fig. 2). The sizes of the studied sites were

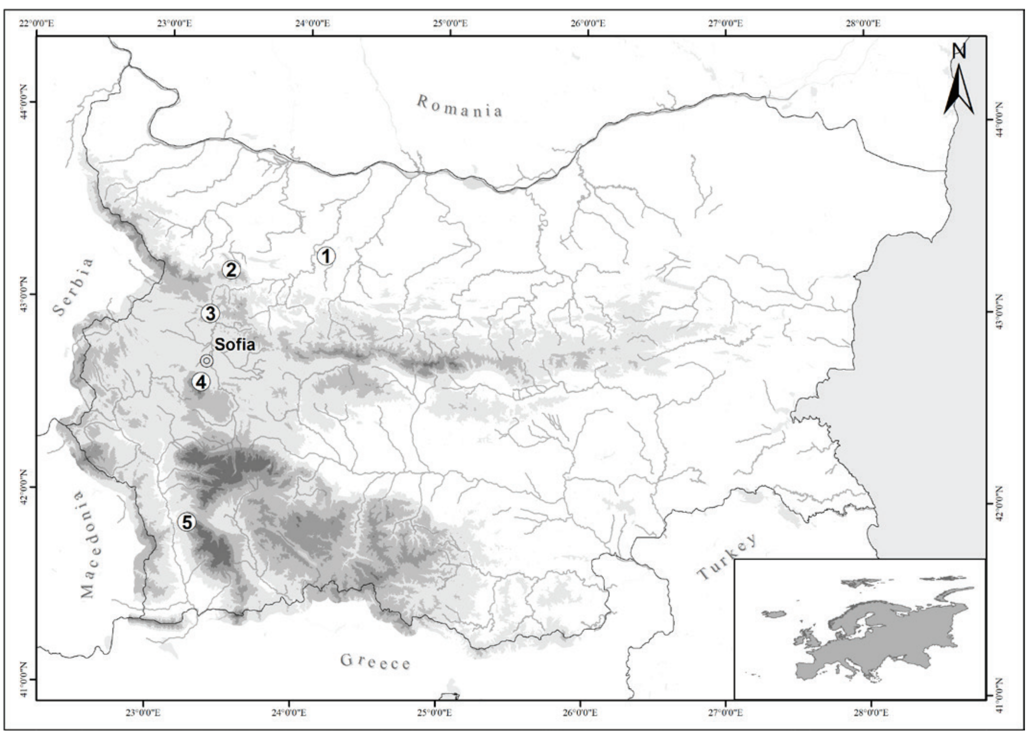

Fig. 1. Location of the study sites: 1. Karlukovo Village (*V. a. montandoni* N). 2. Lakatnik Village (*V. a. ammodytes*). 3. Balsha Village (*V. a. ammodytes*). 4. Bosnek Village (*V. a. montandoni* SW). 5. Kresna Gorge (*V. a. montandoni* SW).

calculated using ArcGIS 10.4.1.; they represent the area in which search effort was regular.

The main part of the field work was conducted in the period 2014-2017. During this period, each site was visited monthly between April and September. In 2014, the visits were made once per month and, since 2015 onwards, twice per month. Additional visits were carried out also in January-March and October-November but not evenly across the sites. Several random visits of the sites around Lakatnik, Balsha, Bosnek and Kresna Gorge were conducted in 2013 and 2018. The numbers of visits and the hours spend in the field at each study site are as follows: Karlukovo – 59 visits (total of 516.5 hours), Lakatnik – 58 visits (528.4 hours), Balsha – 57 visits (451.4 hours),

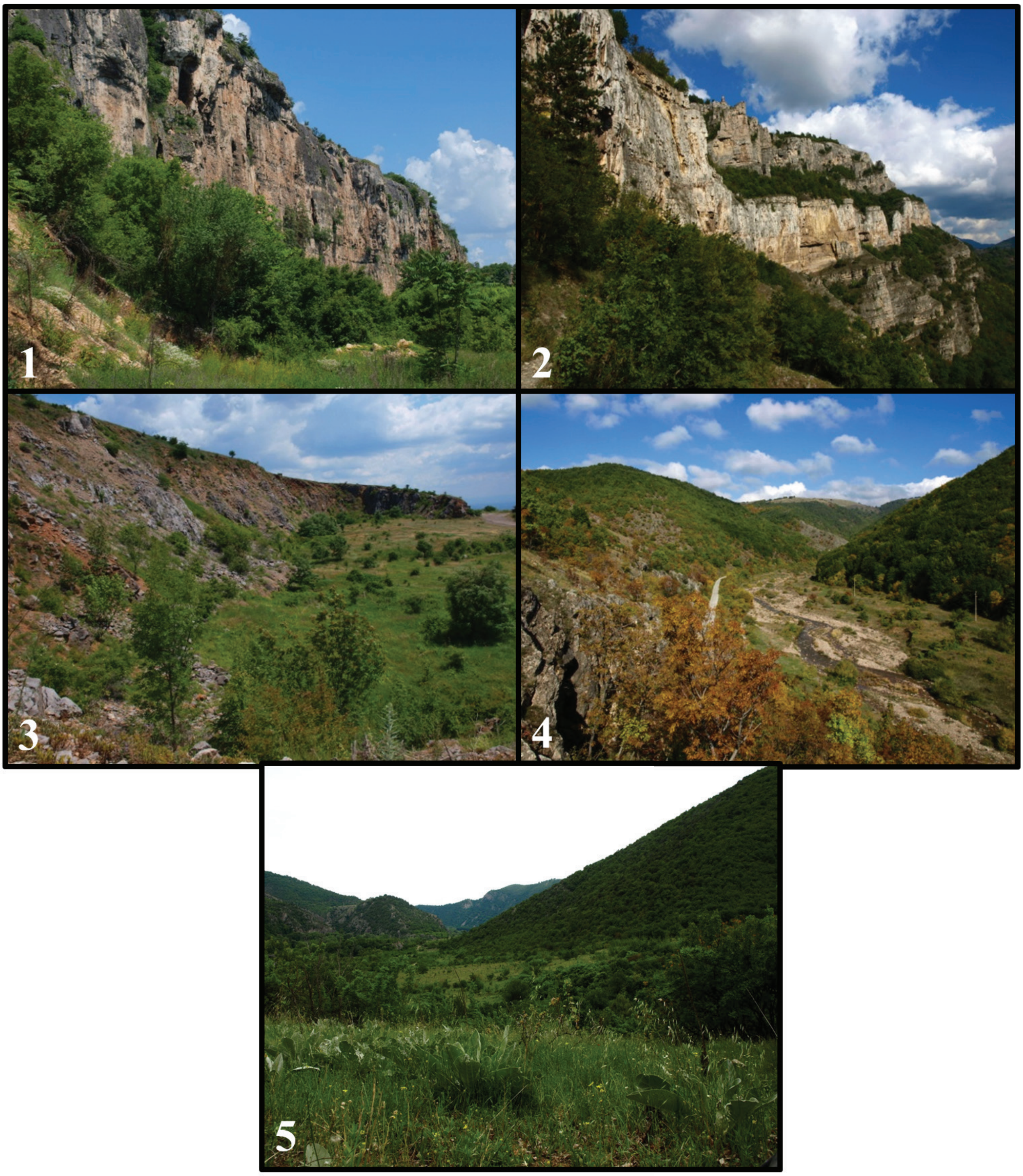

Fig. 2. View of the study sites: 1. Karlukovo Village (*V. a. montandoni* N). 2. Lakatnik Village (*V. a. ammodytes*). 3. Balsha Village (*V. a. ammodytes*). 4. Bosnek Village (*V. a. montandoni* SW). 5. Kresna Gorge (*V. a. montandoni* SW).

Bosnek – 52 visits (459.15 hours) and Kresna Gorge – 54 visits (472.3 hours).

The search for vipers was conducted in days, in which activity of the snakes was feasible (daily temperatures above 15°C). Vipers were searched from early morning to dusk (and, in hot days, throughout parts of the night) in the entire vicinity of the study sites, with the exception of certain stretches, where search was not physically possible (too thick patches of shrubs or very steep rock walls). For repeatability and comparability of the results in each site, the same route scheme was followed for each visit. Snakes were located by visual observation during active search, along with inspection of potential hideouts, e.g. holes, burrows and rock crevices as well as turning over stones and logs. Coordinates for each viper found were taken with a hand held GPS device (Garmin eTrex 20, with accuracy to ± 5 m). All captured specimens were measured and weighted. On the basis of the total length of the snakes, three age groups were derived: juveniles (juv) – up to 28 cm, subadults (sub) – between 28 and 46 cm, adults (ad) – over 46 cm. Juveniles were derived on the basis of the maximal sizes of neonates, which were born in the current year (both in the laboratory and found in the field after their birth) and measured in the field before the start of their first hibernation. Adults were derived on the basis of minimum sizes of snakes for which a sexual maturity was certain (by observing a mating behaviour or gestation). The size threshold for this group is derived from the individuals captured during this study as well as from literature data for Bulgaria (Dushkov 1978).The group of subadults is comprised by the vipers with sizes between the limits of the other two groups. The sex of the snakes was determined by inspecting the colour pattern of the body and the tail morphology (the length and the width of the tailroot as well as the ratio between the snout-vent length and tail length). For each captured viper, photographs of the dorsal and ventral sides of the body and the tail as well as all sides of the head (including the anterior side of the horn) were taken. After all procedures were carried out, the snakes were released on the site of capture. Gravid females from the beginning of August to the second half of September were brought to the laboratory until parturition. Neonates were measured, weighted, photographed and their sex was determined. Then both neonates and adult females were released at the site of capture.

For short-term identification, the vipers were marked with a non-toxic, alcohol-free red colour pen (Faber-Castell Multimark 1525 permanent). Individual numbers were painted onto the mid-dorsal section of the body with size 2.5-3 cm for adults and subadults and 1-1.5 cm for juveniles (except for the neonates because they were still in process of shedding). For long-term identification, the number, shape and arrangement of the scales of the anterior part of the horn as well as the pholidosis (arrangement of the scales) and colour patterns of the head and the body were used (see Dyugmedzhiev et al. 2018a).

The sex ratio at each site was analysed for each age class with χ^2-test. Due to the low number of subadults in some study sites, this group was combined together with the group of juvenile vipers in the analysis.

For determining the number and density of the vipers in each studied site, the Capture-Mark-Recapture (CMR) method was used. Due to the relatively low recapture rate, the data for the sexes and the age groups were analysed together for the entire population. Marked individuals from individual visits were grouped by seasons for each year of the study. The seasons were categorised as follows: spring – end of February till May, summer – June-August, and autumn – September-November. For the analysis we applied the Cormack-Jolly-Saber (CJS) model for open population of the program MARK v.9.0 (White & Burnham 1999). This model calculates the survival rate (Phi) and the capture probability (p) of the individuals to estimate the approximate size of the population. From the generated models, the one with the lowest Akaike's Information Criterion (Akaike 1973) was chosen. Since the boundaries of the studied sites were conditional and the sites could not be physically restricted from the surrounding territories, it was impossible to estimate the extend of the whole population. For the calculation of the density of the species at each site, a buffer of 338 m was added to the area, in which regular searches were carried out. This buffer was based on the maximum linear movement (over two years) of an individual estimated in the current study (see Results). The estimated areas used for calculating the densities of the species were as follow: Karlukovo – 137.7 ha, Lakatnik – 200.13 ha, Balsha – 154.11 ha, Bosnek – 407.61 ha and Kresna Gorge – 118.36 ha.

The individual movement distances and the home range of the individuals were calculated using the program Garmin BaseCamp v. 4.7.0 (c). To measure the movement distances, we used line distance. Each recapture of an individual was treated as a separate observation (measured as the distance in meters from the previous location). Individual movements within the same day were excluded from the analysis because of the high dependence of these movements on our interference. The vipers were grouped in five groups based on sex, age and reproductive status: (1) sexually immature vipers (sub/juv), (2) adult males (mad), (3) adult females not participating in the current breeding season (fad), (4) pregnant females (fadP), a group representing only the movements of pregnant females during the period of gestation (June-September), (5) adult females immediately before or after gestation (fadb/aP), a group representing the movements of individuals with pregnancy confirmed in the relevant year, with those movements covering the period just before the pregnancy (the end of autumn in the previous year and the spring in relevant year) and shortly after parturition (the autumn, immediately after parturition and the beginning of spring of the next year). Not all of the individuals in group 4 were present in group 5 because a big portion of females were captured and recaptured only during the period of pregnancy. Data for the movement distance of individuals, which belonged to two different groups in two consecutive recaptures (e.g. subadults in the previous capture and adults in the following recapture or pregnant females, recaptured several years later, when they were non-reproductive) were excluded from the analyses. Since the data were not normally distributed (Kolmogorov-Smirnov & Liliefors test, $p < 0.01$), Kruskal-Wallis ANOVA test was used. The statistical analyses were performed with Statistica 10.0 (StatSoft, Inc. 2011).

Results

During the field surveys, a total of 539 viper individuals were captured and marked (Table 1). Ninety-eight (18.18%) of them (58 females and 40 males) were recaptured and identified at least once. The maximum number of recaptures for an individual was eight times. A total of 142 recaptures of those 98 individuals were made, excluding daily recaptures.

The sex ratio among immature vipers (juv and sub) was approximately equal in each of the populations ($\chi^2 = 1.353$, df = 4, $p = 0.85$). A statistically significant difference between the sex ratio of the adult vipers was found ($\chi^2 = 15.18$, df = 4, $p < 0.01$), with the females prevailing in the populations around Karlukovo, Lakatnik and Bosnek but, in Kresna Gorge, the opposite trend was observed. In the population around Balsha, the sex ratio remained approximately equal among the adult vipers (Table 2).

Based on the lowest AIC values, for the analysis of the populations around Karlukovo and Lakatnik was chosen a model with time-dependent survival rate (Phi) and constant capture probability (p), whereas for the populations from the other sites a model was chosen in which both Phi and p were constant. The estimated numbers of individuals in the study sites varied from 245 to 796 and the population density ranged from 0.73 to 5.78 ind./ha (Table 3).

The distances of movements differed significantly between the separate sex/age groups in general (Kruskal-Wallis ANOVA: $H = 16.52$, $p < 0.01$, $n = 127$). However, the post-hoc test showed that only the difference between the pregnant females (fadP) compared to adult males (mad) and immatures (sub/juv) were statistically significant (fadP vs. mad: $p < 0.01$, fadP vs. sub/juv: $p < 0.05$). The first group was characterised by the smallest movement distances and the other two – by the largest ones. The movement distances of the females immediately before or after gestation (fadbP/aP) were close to those of the immature vipers; those of the adult females non-participating in the reproductive season (fad) were

Table 1. Recapture rate (RR), number of recaptured individuals (RN), total number of specimens (TN), and number of positive identifications (PN) per site.

Site	RR	RN	TN	PN
Lakatnik	26.67%	28	105	48
Karlukovo	17.28%	33	191	48
Balsha	17.19%	22	128	32
Bosnek	15.09%	8	53	8
Kresna Gorge	9.68%	6	62	6

Table 2. Sex ratio of *V. ammodytes* from five populations in Bulgaria (the data represent all marked individuals, excluding recaptures).

	Karlukovo		Lakatnik		Balsha		Bosnek		Kresna Gorge	
	m/f	ratio	m/f	ratio	m/f	ratio	m/f	ratio	m/f	ratio
ad	24/40	1:1.67	24/47	1:1.96	26/31	1:1.19	10/16	1:1.6	29/13	2.23:1
sub	20/28	1:1.4	13/17	1:1.31	7/3	2.33:1	10/6	1.67:1	5/3	1.67:1
juv	44/35	1.26:1	2/2	1:1	30/31	1:1.03	4/7	1:1.75	7/5	1.4:1
sub+juv	64/63	1.02:1	15/19	1:1.27	37/34	1.09:1	14/13	1.08:1	12/8	1.5:1
Total	88/103	1:1.17	39/66	1:1.69	63/65	1:1.03	24/29	1:1.21	41/21	1:95:1

Table 3. Survival rate (Phi as mean value ± standard deviation and minimum-maximum, or as constant), capture probability (p), estimated number (N with 95% confidence interval CI), and density (D as specimen per ha, with 95% confidence interval CI) of the species per site. AIC refers to the value of Akaike's information criterion for the chosen model.

Site	Phi (A ± SD, Min-Max, n)	p	N (95 % CI)	D (95 % CI)	AIC
Karlukovo	0.9 ± 0.21, 0.48-1.00, 11	0.1	796 (257-3379)	5.78 (0.32-13.15)	286.89
Lakatnik	0.96 ± 0.15, 0.48-1.00, 13	0.09	319 (139-1272)	1.59 (0.44-9.15)	263.65
Balsha	0.99	0.07	635 (185-2097)	4.12 (0.29-11.34)	172.44
Bosnek	0.99	0.08	296 (67-1544)	0.73 (0.23-23.04)	55.25
Kresna Gorge	0.99	0.16	245 (43-1737)	2.07 (0.18-40.40)	44.44

Table 4. Descriptive statistics of the distances (in meters) between displacements of the different sex/age groups of *V. ammodytes* (mad - adult males, fad - adult females, not participating in the current breeding season, fadP - pregnant females, fadbP/aP - adult females, immediately before or after gestation, sub/juv - sexually immature vipers, N refers to the sample size).

Groups	Mean ± SD	Min-Max	N
mad	61.19 ± 72.12	0-338	33
fad	29.3 ± 38.11	0-124	45
fadP	12.93 ± 23.44	1-90	14
fadbP/aP	42.5 ± 36.06	5-113	10
sub/juv	47.04 ± 43.73	2-145	25

with intermediate values among the other groups (Table 4). The estimated area of the individual home ranges varied from 17.3 to 3406.0 m^2 (Mean ± SD 403.63 ± 758.21 m^2, n = 19). The home range of one individual usually overlapped with those of several other individuals.

A total of 72 neonates were born in the laboratory by 12 females. Five of them were recaptured after their release. Recaptures within two weeks after birth were at most 7 m away from the release point (Mean ± SD 5.00 ± 2.65, Min-Max: 2-7, n = 3). From Karlukovo, a juvenile male born on 26.08.2017 and released on 04.09.2017 was recaptured on 12.11.2017 at the entry of a communal hibernaculum that was also used by the female that had given birth to this individual; the distance between the release place and the place of recapture was 70 m. From Balsha, a juvenile male born on 10.09.2014 and released on 19.09.2014 was recaptured on the following year (04.08.2015) at 122 m from the place of release.

Discussion

The relatively low recapture rate in this study could be attributed to the fact that the sampling effort was concentrated on five different populations, which resulted in lower sampling periods for each population. Other population studies on vipers usually are concentrated on only one population, which leads to higher sampling effort and higher recapture rates respectively (Andren 1982, Völkl 1986, Neumayer 1987, Naulleau & Bonnet 1995, Saint Girons 1996, Lourdais et al. 2002, Ursenbacher & Monney 2003, Thomas 2004, Wollesen & Schwartze 2004, Baron et al. 2010).

Usually, the sex ratio in the populations of *V. ammodytes* has been reported as 1:1 (Beshkov 1977, Dushkov 1978, Christov 2002, Plasinger et al. 2014). The situation is similar in populations of other European vipers (Saint Girons 1952, Prestt 1971, Phelps 2004, Thomas 2004, Weinmann et al. 2004, Wollesen & Schwartze 2004) or close to it, with a slight predominance of females (Saint Girons 1996) or males (Phelps 2004). It appears that the sex ratio among the immature nose-horned vipers in most of the studied sites is close to 1:1. The observed changes in this ratio in the adult vipers could be attributed to several reasons. One possible hypothesis is that mortality in adult males is higher than in females due to their behaviour during the mating period. Similar pattern has been observed in *V. ursinii* (see Baron et al. 1996). During the mating period, male vipers sometimes pass long distances in search for females (see below), which probably makes them more conspicuous for predators. Moving snakes are usually easier to detect by predators (Mebert & Durso 2014, Dubey et al. 2015). This hypothesis seems, however, less likely. After parturition, females are emaciated and in bad physical condition, which results into a low rate of survival (Nilson 1981, Madsen & Shine 1993, Bonnet et al. 1994, Bonnet & Naulleau 1995, Bonnet et al. 2002, Luiselli & Zuffi 2002, Phelps 2007, Dyugmedzhiev et al. 2018b). Males, on the other hand, quickly regain their reserves lost during the mating period (Madsen & Shine 1993, Dygmedzhiev unpublished data). Due to these facts, it can be expected that the mortality is higher in adult females (e.g. Bonnet & Naulleau 1996, Lourdais et al. 2002, Phelps 2007) or at least equal to that of males (e.g. Madsen & Shine 1993). More likely, the changes in the sex ratio in adult nose-horned vipers is due to differences in catchability of the two sexes during the different parts of the active season caused by differences in their reproductive behaviour and reproductive strategies (Saint Girons 1952, Künzl 1954, Bonnet & Naulleau 1996). Males have been more catchable in spring and autumn but, in summer, their catchability has greatly declined. Female catchability, on the other hand, has been relatively equal during the entire active season. In our study, difference in this trend has been observed only in the population from Kresna Gorge, where females exhibited low catchability during the entire active season; therefore, the sex ratio in this population is skewed towards males. Due to those differences in catchability of adult vipers, the estimated sex ratio in this group could be misleading. In immature vipers, no differences in catchability of sexes have been present throughout the active season and, therefore, the sex ratio is relatively easy to be determined (Dygmedzhiev, unpublished data).

The results of the present study show that the survival rate of the individuals is very high. The fact that the values in our study are close to 1 is due to the relatively short periods between sampling sessions as well as the relatively short period of the study, in which mortality is harder to detect. The high survival rate is common for the populations of European vipers, for which data are available (Neumeyer 1987, Baron et al. 1996, Saint Girons 1996). By contrast, the capture probability of individuals is low due to the secretive life of snakes in general. According to some authors, the survival rate of young, immature snakes is lower than that of adults (Völkl 1989, Phelps 2004, Altwegg et al. 2005). According to others, however, the young have similar survival rate to that of adults and the low recapture rates are the results of low detectability of these snakes due to their small size, lower thermal requirements or migration to more remote areas (Pike et al. 2008, Bauwens & Claus 2018).

The large variation in the range of the confidence interval for the number of vipers in the studied sites is due to the relatively low recapture rate, rendering the population size estimates less reliable. It should be mentioned that all the five studied populations are open and it is not possible to determine their real spatial borders. Thus, the sampling efforts have been able to cover only a fraction of those populations. Because of that, the values for the numbers and density of the species can be accepted only as tentative, representing the numbers and densities of vipers only in the areas that have been sampled for the short period of the study and not representative for the entire populations. Some fluctuations from year to year may be present depending on prey density, climatic factors, etc. It is important to state that the higher values for the number and density of vipers in Karlukovo and Balsha are due to the fact that these values represent all age groups (adults, subadults and juveniles). In contrast, the values for Lakatnik, Bosnek and Kresna Gorge represent mainly the number and density of adults and subadults but, to a great extent, exclude juvenile snakes due to the very low detectability of the latter at these sites. Because of this as well as due to the fact that the areas of the studied sites were not equal, an objective comparison of the population estimates between the sites cannot be done. According to Ghira (2016), the density of *V. ammodytes* in Romania varies between 5 and 24 individuals per ha. Bozhanskii & Kudryavcev (1986) observed 15 individuals of this species on 10 ha studied area in June. Muschelischvili (1970) has mentioned the density of 1.5 to 20 nose-horned vipers per ha. For Northeast Italy, Luiselli (1996) has stated that the mean density of the species is 15-22 ind./ha.

Our results suggest that *V. ammodytes* is a sedentary species with low movement rates. The individuals use the same territory for long periods, adhering to it every year. Similar conclusions about the species have been stated by previous authors (Künzl 1954, Schweiger 1992, Plasinger et al. 2014). The sedentary lifestyle is typical for the entire genus *Vipera* (Saint Girons 1952, 1997, Neumeyer 1987, Naullaeu 1966, Naullaeu et al. 1996, Baron 1997, Újvári & Korsós 1997, Brito 2003, Thomas 2004, Weinmann et al. 2004, Graitson 2008). *Vipera ammodytes* does not have pronounced territoriality in which individuals defend their territory. Often several individuals can be observed basking close to each other or using the same shelter, without any signs of intolerance between them. This was most pronounced in pregnant females, in which often several individuals (3-6) could be observed on relatively small area (between 50 and 180 m^2). Similar aggregations of pregnant females are characteristic for other species of the genus *Vipera* (Viitanen 1967, Neumeyer 1987, Monney 1992). The absence of intolerance and territory defence is also common for the genus, in which the home ranges of several individuals overlap (Naulleau 1966, Prest 1971, Neumeyer 1987, Baron 1997, Phelps 2004). The estimated areas for the home range and for the linear displacements of the individuals, established in the present study, are only indicative, since due to the low recapture rate per individual, it is impossible to calculate them to full extent. Mebert et al. (2015, 2017) have stated that the registered movements in straight line of *V. ammodytes* are from 20 to 493 m. Schweiger (1992) has observed one male specimen in the period of nine years, within different seasons, on an area of about 80 m^2. Plasinger et al. (2014) have established that home ranges of two individuals of *V. ammodytes* tracked by radio telemetry are 1696.6 m^2 and 699.51 m^2, respectively. According to Ghira (2016), the size of the home range for adult specimen of the species is between 416 and 2000 m^2. The size of the home range is dependent on the physical characteristics and the resources of the environment (pray and shelter availability, suitable basking sites, etc.) as well as by the sex and seasonal cycles (Naulleau 1966, Neumeyer 1987, Naulleau & Bonnet 1995, Naullaeu et al. 1996, Baron 1997, Saint Girons 1997, Brito 2003, Thomas 2004). For *V. aspis*, various authors indicate the following home range sizes: 25,000 m^2 for males and 13900 m^2 for females (Naulleau 1966), 3,024 m^2 (Naulleau & Bonnet 1995), from 2,927 to 9,524 m^2, decreasing during the period of pregnancy and with yearly differences in the size (Naullaeu et al. 1996), 259 m^2 for males, 169 m^2 for non-reproductive and 200 m^2 for reproductive females (Saint Girons 1997). For *V. berus*, the estimated home range is as follows: 52,000 m^2 for males and 7,600 m^2 for reproductive females (Neumeyer 1987), 4,000 m^2 for males and 7,000 m^2 for females (Thomas 2004). For *V. latastei*, Brito (2003) has reported a home range of 2,400 m^2, with an increase in September to 15,200 m^2. For *V. ursinii*, Baron (1997) has estimated a home range size of 1,551 m^2 for males and 949 m^2 for females. Our data shows that the estimated areas of the home range in the present study can be underestimated and should be treated only as minimum values.

Values of the linear movements of the individuals exhibit a similar pattern. However, there is a clear difference between the movement rates of the individuals in relation to their sex and reproductive status. Movements of adult males observed by us are greater than those of females, and this has been shown to be typical for the whole genus (Saint Girons 1952, 1997, Viitanen 1967, Prest 1971, Neumeyer 1987, Baron 1997, Brito 2003, Phelps 2004, 2007, Weinmann et al. 2004, Wollesen & Schwartze 2004). Most studies attribute these differences to the higher mobility of males during the mating season, when they may travel long distances in search of partners. This indicates that females are somewhat more sedentary than males and the distances of displacement of the reproductive females before or shortly after gestation are similar to those of females that skip reproduction in the current year. A rapid decrease in movement rate is observed in pregnant females during the period of gestation when they become much more static and rarely make large displacements. Usually, many pregnant nose-horned vipers stay close to the hibernating places. This is most pronounced in two of the study sites where specific communal hibernation sites are detected. At Karlukovo, two such sites were established – rock blocks situated in a forest-shrub area, in the base of which nose-horned vipers hibernate together with other species of snakes, i.e. *Natrix tessellata* (Laurenti, 1768) and *Dolichophis caspius* (Gmelin, 1789). At least 20 individuals used those two sites for hibernation; however, the number of vipers hibernating there is probably higher. Individuals tend to use the same hibernating site throughout the years. In the summer months, only pregnant females (at least 67 % of all pregnant vipers are found in this site) and few immature vipers can be found close to those sites, at distances between 20 and 50 m from there. As mentioned above, several aggregations of pregnant vipers have been observed. These aggregations always occur in two particular areas of rocky slopes with shrubs and rare grasses. At the study site at Balsha, the abandoned quarry is used as hibernating place for the population. After the end of the mating period, only the majority of the pregnant females (at least 64% of all pregnant vipers at this site) as well as few immature vipers can be found in the quarry; the remaining individuals return to this area in the second half of September or early October. The decreased mobility of females during gestation as well as their adherence close to the hibernating sites is well documented among vipers (Künzl 1954, Neumeyer 1987, Charland & Gregory 1995, Bonnet & Naulleau 1996, Naullaeu et al. 1996, Baron 1997, Saint Girons 1997, Phelps 2004, 2007, Graitson 2008). A probable cause is their limited locomotion abilities during this period (Charland & Gregory 1995). It is possible, however, that the limited movements of those vipers are due to their specific thermoregulatory needs, leading to their adherence to certain habitats with optimal thermal qualities (Charland & Gregory 1995, Crane & Greene 2008). Differences in movement rate could also be influenced by local habitat. However our sample size does not allow comparisons between the populations.

Little is known in regards to movements of immature vipers. Saint Girons (1996) states that immatures are more wandering then adults. According to Phelps (2004), in a population of *V. berus*, young immature animals disperse randomly, often joining subpopulations other than their parental. High dispersal rates in immatures are documented in other snake species (Secor 1994, Dubey et al. 2008, 2011, Howze et al. 2012, Rugiero et al. 2012). The linear movement distances of immatures in our study are relatively small; however, the number of recaptures is not sufficient for clear conclusions. According to Saint Girons (1981), neonate vipers, born early in the season (July and August), disperse immediately after birth and tend to travel large daily distances. Those born later in the season (September-October) stay in the places of their birth until the start of hibernation and only in the following spring start to disperse. Neumayer (1987) and Baron (1997) also state that, after birth, neonates from populations of *V. berus* and *V. ursinii* stay close to those sites until the start of hibernation. Baron (1997) and Baron et al. (2010) point out that only in the following year they disperse but not far off and keep close to the territory of their mothers in the first years of their lives. Viitanen (1967) also mentions that, in *V. berus*, neonates stay close to the hibernating sites and, with age, the distance travelled away from those sites increases. Our observations on neonates born in the laboratory and recaptured after their release are consistent with the observations of these authors. Those vipers, born in the end of August and the first half of September, stay close to their release sites, which are close to the hibernating areas. The only specimen recaptured almost a year after its first hibernation has been found again in the quarry, in which the population hibernates, with a movement distance of only 122 m. According to Viitanen (1967), pregnant females stay close to the hibernating areas to give birth there so that the newborns can easily find the hibernacula, which are scarce in this site. In our study sites, pregnant females also tend to stay close to the hibernating areas and to give birth there. Selection of the appropriate hibernaculum is crucial for the winter survival of snakes (Viitanen 1967, Prestt 1971, Gregory 1977, Altwegg et al. 2005). An interesting observation is the movement of a juvenile specimen from Karlukovo to the hibernating site of its mother. According to a number of authors, newborn use chemical cues to find hibernating sites, emanating from adult snakes that move towards those sites (Brown & Maclean 1983, Reinert & Zappalorti 1988, Cobb et al. 2005, Howze et al. 2012). Further experimental studies are needed to confirm this hypothesis.

Conclusions

The sex ratio among immature individuals in the populations of *V. ammodytes* is close to 1:1. In adults, the sex ratio is difficult to determine as there are methodological biases related to the differences in catchability of the sexes due to the specifics of reproductive behaviour and reproductive strategies. The nose-horned vipers have high survival rate but capture probability is low. *Vipera ammodytes* is a sedentary species, with comparatively small individual home range, which often is overlapped by the ranges of other individuals. There are differences in mobility between the sexes, related to the reproductive behaviour or to differences in habitat use. After parturition, the neonates stay close to the hibernating areas.

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