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# Age and reproductive status determine spatial niche utilization in *Vipera ammodytes* (Linnaeus, 1758)

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***To Niki, a true friend***

**Abstract.** While data on habitat use of *Vipera ammodytes* are abundant, most studies are purely descriptive and only list the typical habitats in which the species is found. The intraspecific variations (i.e., ontogenetic and intersexual) in habitat and microhabitat utilization remain very poorly studied. In order to assess those intraspecific variations, we studied five different populations in western Bulgaria between 2014–2017, searching for vipers from early spring to late autumn in 24 different habitat types. The ontogenetic and intersexual variations in spatial niche breadth were analysed using several ecological diversity indices, and microhabitat characteristics were estimated by the presence of trees/shrubs, grasses and stones/rocks within a 5 m diameter of each viper's location. Vipers were found in 17 habitat types. Habitat and microhabitat selection of *Vipera ammodytes* were age-dependent, with juveniles having the narrowest spatial niche and preferring more open microhabitats. The breadth of the spatial niche gradually increased with age, along with the tendency to inhabit microhabitats with more shrubs. During gestation, female's spatial niche narrowed significantly and pregnant vipers again tended to use more open microhabitats, known as rookery. The observed results could be explained by a combination of factors, such as 1) the ontogenetic differences in the trophic niche and feeding patterns, 2) different prey type abundance in distinct habitats and microhabitats, 3) the size differences between age groups with all benefits and limitations that come with them, 4) distinct behavioural patterns differing between sex/age groups or 5) a size-related bias in detection probabilities.

**Key words.** Habitat, microhabitat, vipers, snakes, ontogenetic.

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## Introduction

Snakes have low dispersal habits and their distribution usually depends on both the climatic and habitat characteristics of the environment. The microclimatic conditions and microhabitat characteristics highly influence snakes' habitat selection (Vitt & Caldwell 2014) and the presence of stony microhabitats is often of key importance for spatial niche utilization (Reinert 1993; Kurek *et al*. 2018). These microhabitats provide snakes with suitable thermal conditions for thermoregulation and easy access to shelter from unfavourable weather or predators. Factors such as locality and season, as well as some individual traits such as age, reproductive status or even colour pattern, also might influence snakes' habitat (Reinert 1984, 1993; Sweet 1985; Shine 1986; Seigel 1986; Burger & Zappalorti 1989; Luiselli *et al*. 1994; Charland & Gregory 1995; Webb & Shine 1998) or microhabitat (Neumeyer 1987; Brito 2003; Martínez-Freiría *et al*. 2010; Strugariu *et al*. 2011) utilization.

European vipers are generally sedentary snakes, with usually small to medium sized home range territories that they reside within throughout most of their lives (Naulleau *et al*. 1996; Saint Girons 1997; Brito 2003; Weinmann *et al*. 2004; Graitson 2008; Plasinger *et al*. 2014; Dyugmedzhiev *et al*. 2020). This home range usually includes suitable hibernating sites, thermoregulation sites, shelters from unfavourable climatic conditions or predators and a sufficient food base. If all of these factors are present within a given small territory, vipers can inhabit it throughout the activity period (Saint Girons 1980; Neumeyer 1987; Naulleau *et al*. 1998; Thomas 2004; Wollesen & Schwartze 2004). However, when suitable hibernation spots are not situated close to the areas with rich food base, or with suitable summer' microclimatic conditions, vipers conduct yearly seasonal migrations, leaving the hibernating areas in the spring and returning in the autumn (Duguy 1963; Viitanen 1967; Prestt 1971; Saint Girons 1980; Anderson 2003; Wollesen & Schwartze 2004). The distance of these migrations varies to a great extent and depends on individual locality. The longest registered seasonal migration in a European viper species is documented for *Vipera berus* (Linnaeus, 1758), in which some individuals from England and Finland are known to travel up to 1.5–2 km from the hibernating areas to the summer habitats (Viitanen 1967; Prestt 1971).

The Nose-horned Viper *Vipera ammodytes* (Linnaeus, 1758) is distributed from the western foothills of the Alps across the entire Balkan Peninsula and many Aegean islands to north-western and northern Asia Minor and the Lesser Caucasus (Speybroeck *et al*. 2016), and occurs in a wide variety of habitats. It usually inhabits different types of sunny open stony or rocky habitats with shrubs and grasses, although it is not uncommon to be found in various types of light deciduous forests as well (Tuleshkov 1959; Bruno 1967; Beshkov 1978, 1993; Ioannidis & Bousbouras 1997; Stumpel & Hahn 2001; Heckes *et al*. 2005; Crnobrnja-Isailović *et al*. 2007; Ghira 2016). Within this wide variety of habitats, the species usually demonstrates clear affinity to stony and rocky microhabitats, which provide access to shelter and a richer food base (Beshkov 1978, 1993; Mebert *et al*. 2015; Ghira 2016). In Bulgaria, *V. ammodytes* is widespread throughout the country, except in the high mountains, intensively cultivated agricultural and urbanized land (Stojanov *et al*. 2011).

Despite the abundant data on *V. ammodytes* habitat use, most studies are purely descriptive and merely list the habitats in which the species is most often found. The various aspects of intraspecific variations (i.e. interpopulation, taxonomic, seasonal, intersexual and ontogenetic) in habitat and microhabitat use remain very poorly studied. The very few studies that briefly deal with this topic provide some insights on the taxonomic (Ghira 2016), interpopulation (Dyugmedzhiev *et al*. 2024), seasonal (Beshkov 1993; Crnobrnja-Isailović *et al.* 2007; Dyugmedzhiev *et al*. 2024) and intersexual variations in habitat and microhabitat use (Crnobrnja-Isailović *et al.* 2007). Crnobrnja-Isailović *et al.* (2007) state that in Serbia, Montenegro and Northern Macedonia, females are detected most often in summer, mainly in rocky habitats with eastern and southern exposure, while males are detected mainly in spring, in open deciduous forests with southwestern exposure. To date there are no studies focused on potential ontogenetic variations in habitat/microhabitat utilization of *V. ammodytes*.

The aim of the current study was to assess the ontogenetic and intersexual patterns of habitat and microhabitat use of *V. ammodytes*. We tested the hypothesis that habitat use, spatial niche breadth and microhabitat preferences depend on individuals' sex, age and reproductive status.

## Material and methods

### Study sites

Five sites in western Bulgaria were studied: 1) near Karlukovo Village, north-western Bulgaria (43°10′ N, 24°3′ E; 111–250 m a.s.l.); 2) near Gara Lakatnik Village, north-western Bulgaria (43°5′ N, 23°23′ E; 352–733 m a.s.l.); 3) near Balsha Village, the central parts of western Bulgaria (42°51′ N, 23°15′ E; 652–853 m a.s.l.); 4) near Bosnek Village, the central parts of western Bulgaria (42°29′ N, 23°11′ E; 942–1332 m a.s.l.); 5) the "Gabrovitsa" area in the Kresna Gorge, south-western Bulgaria (41°46′ N, 23°9′ E; 165–488 m a.s.l.). Sites 1 and 2 are karst valleys along the Iskar River, with steep rock cliffs interspersed with patches of deciduous forests. Site 3 is an abandoned quarry, surrounded by bare hills, fields and deciduous forests. Site 4 is a middle-mountain karst valley along the upper reaches of the Struma River, with rocky slopes, covered with shrubs and sparse deciduous forests. Site 5 is a plain along the middle reaches of the Struma River, vegetated with grass, scattered trees, shrubs and abandoned vineyards, and surrounded by steep stony slopes, vegetated with deciduous forests. Map and photographs of the sites are presented in Dyugmedzhiev *et al*. (2020).

### Fieldwork

Fieldwork was conducted mainly between April and September from 2014 to 2017, when each site was visited regularly once per month in 2014 and twice per month from 2015 onwards. Additional visits were also made between January–March and October–December; however, they were irregular and unevenly distributed among sites. Visits were made in days with daily temperatures above 15°C, on which vipers' activity was expected (Dyugmedzhiev *et al*. 2021), and each visit lasted one day. Vipers were searched from morning to dusk and in some days (between May and September) throughout parts of the night. The entire area of the respective study site was searched, except for some physically inaccessible parts (e.g., very dense shrubs and steep rock cliffs, etc.). During each visit, we followed the same route, covering all of the different habitat types in the particular site. However, due to the size differences of the different habitat types, the search effort was not equal across habitats. Vipers were located by sight and by inspection of potential hideouts (i.e., under stones, inside rock crevices, etc.). Coordinates (Garmin eTrex 20; precision: 10 m), habitat and microhabitat characteristics of the location for each detected viper were recorded. Habitat types were categorized visually based on a list of habitats generated from the mobile application SmartBirds Pro (Popgeorgiev *et al*. 2015). A total of 24 different habitat types were derived (Table 1). Microhabitat characteristics of each viper's location were categorized according to the percentage of areas with trees/shrubs, grasses, stones/rocks, water surfaces and roads (combined total of 100%) within a radius of 2.5 m from the snake's location. Captured vipers were measured (snout to vent (SVL) and tail length (TL); precision 0.5 cm), weighted (precision: 0.01 g), colour marked and thoroughly photo documented for individual identification (Dyugmedzhiev *et al*. 2018). Sex was determined by vipers' colour pattern, tail length, tail base width and the SVL/TL ratio (Tomović *et al*. 2002). Females' reproductive status was determined by gentle palpation. All animals were then released at the site of capture.

### Data processing

The activity period was divided into three seasons: spring (March–May), summer (June–August), autumn (September–November). Vipers were divided into three age groups, based on the combination of individual total length (SVL + TL) and body length (SVL): 1) juveniles/new-borns (juv: up to 28 cm total length or 24.7 cm SVL); 2) subadults (sub: 28 – 46 cm total length for females and 49 cm total length for males, or 24.7 – 41 cm and 42.5 cm SVL, respectively); 3) adults (ad: over 46/49 cm total length for females and males, respectively, or 41/42.5 cm SVL, respectively) (Dyugmedzhiev *et al*. 2020). Adults were divided into three groups: 1) adult males (mad); 2) adult females, not participating in the current breeding period (non-reproductive; fad); 3) pregnant females (fadP).

### Statistical analyses

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 overall low recapture rate (around 20%, Dyugmedzhiev *et al.* 2020), 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 from the same day. Dead animals were also excluded from the analyses, as it is impossible to objectively assess whether they died while passing through the habitat in their way to a neighbouring, more suitable one, or whether they actually stayed in this particular habitat prior to their death. Due to the low number of pregnant females from spring/autumn ($n = 2$), they were not included in the analyses for this period.

To analyse spatial niche breadth of each sex/age group, two ecological diversity indices were used: Shannon (H) and Simpson (1-D). They can vary from 0 to 5 and the higher the value is, the wider the species' spatial niche is (i.e., the species occurs in more diverse habitats). The Shannon index gives higher weight to rare habitats, while the Simpson index – to more abundant habitats (Krebs 1999). The diversity indices were calculated based on a frequency matrix representing the number of observations of vipers from each sex/age group in each habitat type (with the combined data for all seasons, Table 1). Because *V. ammodytes* seasonal activity patterns and encounter rates vary depending on age, sex and reproductive status (Dyugmedzhiev *et al.* 2022), the combined data for all seasons were used for the calculation of the indices, in order to reduce potential bias in seasonal encounter rates between different groups. For ordering sex/age groups according to habitat diversity, Rényi's index family (diversity profiles) was used, based on the same frequency matrix. When acceptable (i.e., diversity profiles did not intersect), the significant differences of the two indices between the different sex/age groups were assessed by a permutation test. A correspondence analysis, based on the same frequency matrix, was used to evaluate the seasonal patterns of habitat use in regards to vipers' sex/age. Nose-horned vipers are known to use similar habitats during spring and autumn, which often differ from those used during summer (Dyugmedzhiev *et al.* 2024), so two separate analyses were conducted – one for summer and one for the combined data from spring and autumn. The combined data for the latter two seasons allowed increasing the sample size for some of the groups (i.e., juveniles). Habitat types in which vipers were never observed were excluded from the analyses.

Since normal distribution of the data could not be achieved (Kolmogorov-Smirnov & Liliefors, $p < 0.05$), a Kruskal-Wallis H test was used to analyse the microhabitat characteristics of different sex/age groups' locations. Due to the low percentage of water surfaces and roads, only the data for trees/shrubs, grasses and stones/rocks were used as groups in the analyses. Due to seasonal vegetation growth, microhabitat measurements conducted in different seasons could lead to some bias. However, due to the high number of vipers for which the microhabitat characteristics were estimated within a 5 m diameter of each individual's observation point (which cannot be measured with the GPS device having a 10 m resolution), conducting measurements in a limited period was not possible. To account for such a bias due to differences in seasonal vegetation growth, the cover of the three microhabitat categories was compared separately between vipers' sex/age groups during summer (when vegetation is at its highest) and spring/autumn combined (when vegetation is lower).

All statistical analyses were conducted with Statistica 10.0 (StatSoft Inc. 2011). Shannon and Simpson indices were calculated in Past 3.25 (Hammer *et al.* 2001). Statistical significance was accepted at $p < 0.05$.

## Results

### Habitat use

A total of 648 records of *Vipera ammodytes* were used to analyse the habitat preferences of the different sex/age groups: 160 adult males (129 in spring/autumn; 31 in summer), 188 non-reproductive adult females (108 in spring/autumn; 80 in summer), 54 pregnant females (2 in spring/autumn; 52 in summer), 142 subadults (102 in spring/autumn; 40 in summer) and 105 juveniles (79 in spring/autumn; 26 in summer). Vipers were found in 17 of all 24 available habitat types (Table 1).

Pregnant females and juvenile vipers had the narrowest niche breadth (i.e., the lowest values for Shannon and Simpson indices), followed by subadults, while non-reproductive adult females and adult males had the widest niche breadth (Fig. 1a). According to the Rényi's profiles, there was a high overlap between the spatial niches of juveniles and pregnant females, and a partial overlap between these two groups and subadults (Fig. 1b). There was also a partial overlap between spatial niches of adult males and non-reproductive adult females (Fig. 1b). Taking these niche overlaps into account, the permutation test was only applied to compare adult males and non-reproductive adult females to the other three groups. Statistically significant differences were found for the values of both indices between each of the compared groups (Table 2).

The first two dimensions of the correspondence analysis with data from spring/autumn explained 88% of the variance. The first dimension separated subadults from the other sex/age groups, while the second dimension separated juveniles from the other three groups. Most of the habitat types were grouped close to the adult males and females. Only two habitat types were grouped closer to subadults (H1 – rocks + shrubs + trees and H8 – stony road scarps + grass + shrubs) while each of the two habitat types closest to juveniles (H2 – quarries + grass + shrubs and H7 – stony areas + grass + shrubs) were closer to adult females and males than to juveniles (Fig 2a).

The first two dimensions of the correspondence analysis with data from the summer explained 84% of the variance. The first dimension clearly separated males from pregnant females, while the second dimension separated non-reproductive adult females, subadults and juveniles from the first two groups. The latter three groups were grouped close to six habitat types (H1 – rocks + shrubs + trees, H7 – stony areas + grass + shrubs, H8 – stony road scarps + grass + shrubs, H9 – highly sparse forests + shrubs +

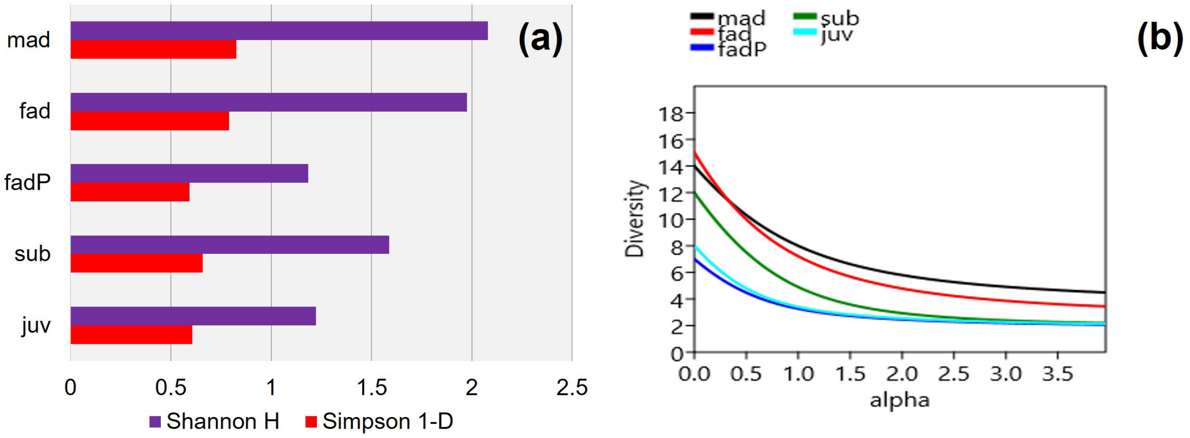

Figure 1 – Comparison between the spatial niche of the different sex/age groups of *V. ammodytes*. (a) niche breadth of the different sex/age groups, based on the values of Shannon and Simpson indices; (b) diversity profiles of the niche breadth of the different sex/age groups. Abbreviations: mad = adult males; fad = non-reproductive adult females; fadP = pregnant adult females; sub = subadults; juv = juveniles.

TABLE 1

Habitat types and number of observations (n) of individuals from the different sex/age groups during spring+autumn and summer.

| **HABITAT TYPE** | **Sex/age<br>n Spring+Autumn/Summer** | | | | |
|---|---|---|---|---|---|
| | **mad** | **fad** | **fadP** | **sub** | **juv** |
| Rocks / screes with scattered shrubs and trees (H1) | 2/4 | 3/12 | 0/0 | 4/2 | 1/1 |
| Abandoned quarries overgrown with grasses and shrubs (H2) | 34/0 | 23/4 | 1/13 | 8/3 | 27/0 |
| Abandoned buildings and ruins (H3) | 0/0 | 0/0 | 0/0 | 3/0 | 0/0 |
| Stone piles / stone walls (man-made) overgrown with grass and scattered shrubs (H4) | 3/0 | 1/0 | 0/1 | 0/0 | 0/1 |
| Stone piles / stone walls (man-made) overgrown with shrubs (H5) | 15/3 | 6/6 | 0/5 | 6/1 | 0/0 |
| Stone piles / stone walls (man-made) overgrown with trees and shrubs (H6) | 5/5 | 3/2 | 0/0 | 2/1 | 0/0 |
| Rocky/ stony areas overgrown with grass and shrubs (H7) | 39/10 | 37/37 | 1/30 | 52/27 | 40/19 |
| Rocky /stony road scarps overgrown with grass and bushes (H8) | 4/1 | 7/5 | 0/0 | 10/2 | 0/1 |
| Highly sparse deciduous forests with shrubs growing on rocky / stony areas (H9) | 1/0 | 2/1 | 0/0 | 0/0 | 0/0 |
| Rivers (H10) | 0/0 | 1/0 | 0/0 | 0/0 | 0/0 |
| Rocky / stony areas overgrown with shrubs (H11) | 2/1 | 2/0 | 0/1 | 1/0 | 0/0 |
| Light deciduous forests with shrubs growing on rocky/stony areas (H12) | 16/1 | 18/6 | 0/0 | 13/3 | 8/3 |
| Rocks / screes with very sparse vegetation (H13) | 0/2 | 0/6 | 0/1 | 0/1 | 1/1 |
| Dirt roads (H14) | 1/0 | 1/0 | 0/0 | 0/0 | 0/0 |
| Ecotone (H15) | 4/2 | 1/0 | 0/0 | 0/0 | 0/0 |
| Shrubbery without or with very few stones/rocks (H16) | 0/0 | 0/0 | 0/0 | 2/0 | 0/0 |
| Meadows / pastures with scattered shrubs and no or very few stones /rocks (H17) | 3/2 | 3/1 | 0/1 | 1/0 | 2/0 |
| Asphalt roads (H18) | 0/0 | 0/0 | 0/0 | 0/0 | 0/0 |
| Abandoned quarries with very scarce vegetation (H19) | 0/0 | 0/0 | 0/0 | 0/0 | 0/0 |
| Ravines with dark deciduous forests (H20) | 0/0 | 0/0 | 0/0 | 0/0 | 0/0 |
| Grassy road scarps without rocks / stones (H21) | 0/0 | 0/0 | 0/0 | 0/0 | 0/0 |
| Mud / dirt / muck (H22) | 0/0 | 0/0 | 0/0 | 0/0 | 0/0 |
| Bare sand screes (H23) | 0/0 | 0/0 | 0/0 | 0/0 | 0/0 |
| Abandoned gardens / vineyards / pastures (H24) | 0/0 | 0/0 | 0/0 | 0/0 | 0/0 |

rocks, H12 – light forests + shrubs + rocks and H13 – sparsely vegetated rocks), with non-reproductive adult females grouping much closer than subadults and juveniles. Adult males were grouped close to two habitat types (H6 – stone piles + trees + shrubs and H17 – madows + shrubs) and pregnant females to one (H2 – quarries + grass + shrubs) (Fig 2b).

## Microhabitat use

Although the individuals from all sex/age groups were found mostly in stony-rocky microhabitats with grasses and trees/shrubs, some differences were evident when comparing the microhabitat characteristics between some of the groups. In spring/autumn, a significant difference was only observed for the

TABLE 2

Results from the permutation test (p values) between the values of the diversity indices for sex/age groups with non-intersecting diversity profiles.

| | **Shannon H** | | | **Simpson** | | |
|---|---|---|---|---|---|---|
| | **fadP** | **sub** | **juv** | **fadP** | **sub** | **juv** |
| mad | 0.0001 | 0.0004 | 0.0001 | 0.0001 | 0.0001 | 0.0001 |
| fad | 0.0002 | 0.006 | 0.0001 | 0.002 | 0.003 | 0.0001 |

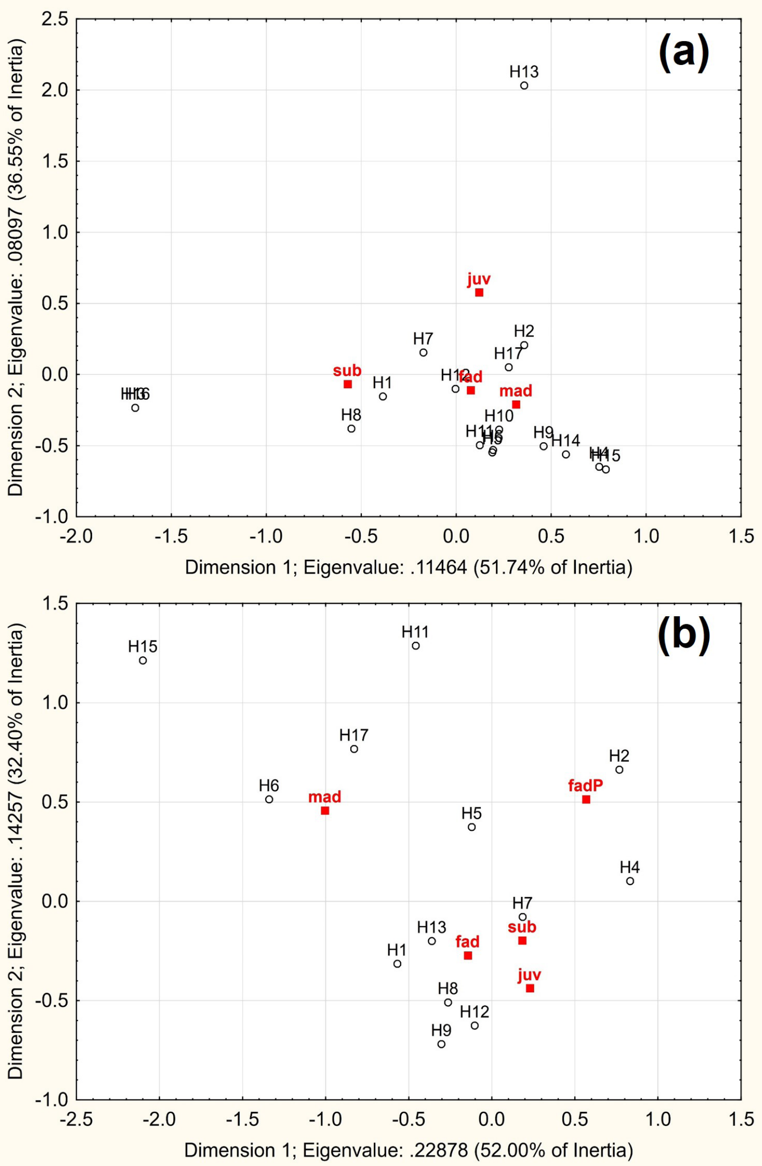

Figure 2 – Grouping between habitat types used by *V. ammodytes* and sex/age for spring/autumn (a) and summer (b), based on the results from the first two dimensions of the correspondence analysis. Abbreviations: mad = adult males; fad = non-reproductive adult females; fadP = pregnant adult females; sub = subadults; juv = juveniles; for abbreviations of the habitat types, see Table 1.

TABLE 3

Results of Kruskal-Wallis H tests between the microhabitat characteristics in the places of observations of the different sex/age groups of *V. ammodytes* during spring/autumn (first three rows) and the p values from the post-hoc tests testing for differences in the presence of trees/shrubs between sex/age groups (last four rows).

<table>
<tr><th colspan="4">Grasses: Kruskal-Wallis H test: H = 4.89, p = 0.29, n = 418</th></tr>
<tr><th colspan="4">Stones/Rocks: Kruskal-Wallis H test: H = 9.13, p = 0.06, n = 418</th></tr>
<tr><th colspan="4">Trees/Shrubs: Kruskal-Wallis H test: H = 18.73, p = 0.0009, n = 418</th></tr>
<tr><th></th><th>fad</th><th>sub</th><th>juv</th></tr>
<tr><td>mad</td><td>1</td><td>0,09</td><td>0,02</td></tr>
<tr><td>fad</td><td>–</td><td>0,07</td><td>0,02</td></tr>
<tr><td>sub</td><td>0,06</td><td>–</td><td>1</td></tr>
</table>

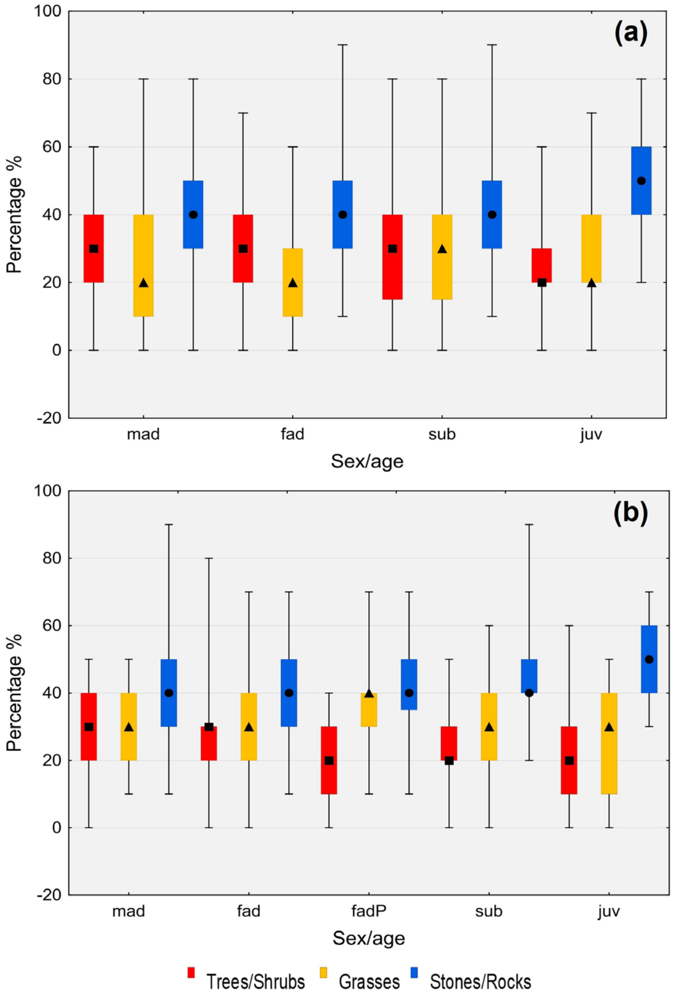

Figure 3 – Comparison of the microhabitat characteristics, presented by the percentage of trees/shrubs, grasses and stones/rocks, in the places of observations between the different sex/age groups of *V. ammodytes* during spring/autumn (a) and summer (b). The graph is presented by median (central squares, triangles and circles, respectively), 25–75 percentiles (boxes) and range (whiskers). Abbreviations: mad = adult males; fad = non-reproductive adult females; fadP = pregnant adult females; sub = subadults; juv = juveniles.

presence of trees/shrubs (Table 3). The post-hoc test revealed that these differences were significant between both adult males and females as compared to juveniles (Table 3). The presence of trees/shrubs in microhabitats of juvenile vipers was lowest and with the smallest variance, while it was highest in microhabitats of adults (Figs 3a and 4a). The values of trees/shrubs in microhabitats of subadults were situated between those of juveniles and adults and showed the highest variance (Fig 3a).

Similarly, in summer, the only differences between groups were found for the presence of trees/shrubs, where the post-hoc test revealed significances only between adult males (highest tree/shrub presence) and pregnant females (lowest tree/shrub presence) (Table 4, Figs 3b and 4). Although the presence of trees/shrubs in juveniles' microhabitats was similar to that of pregnant females (Fig 3b), no significant differences were observed when comparing juveniles and adult males (Table 4). However, juveniles' microhabitats had the highest stone/rock presence, and the p value was close to significance ($p = 0.05$) (Fig 3b).

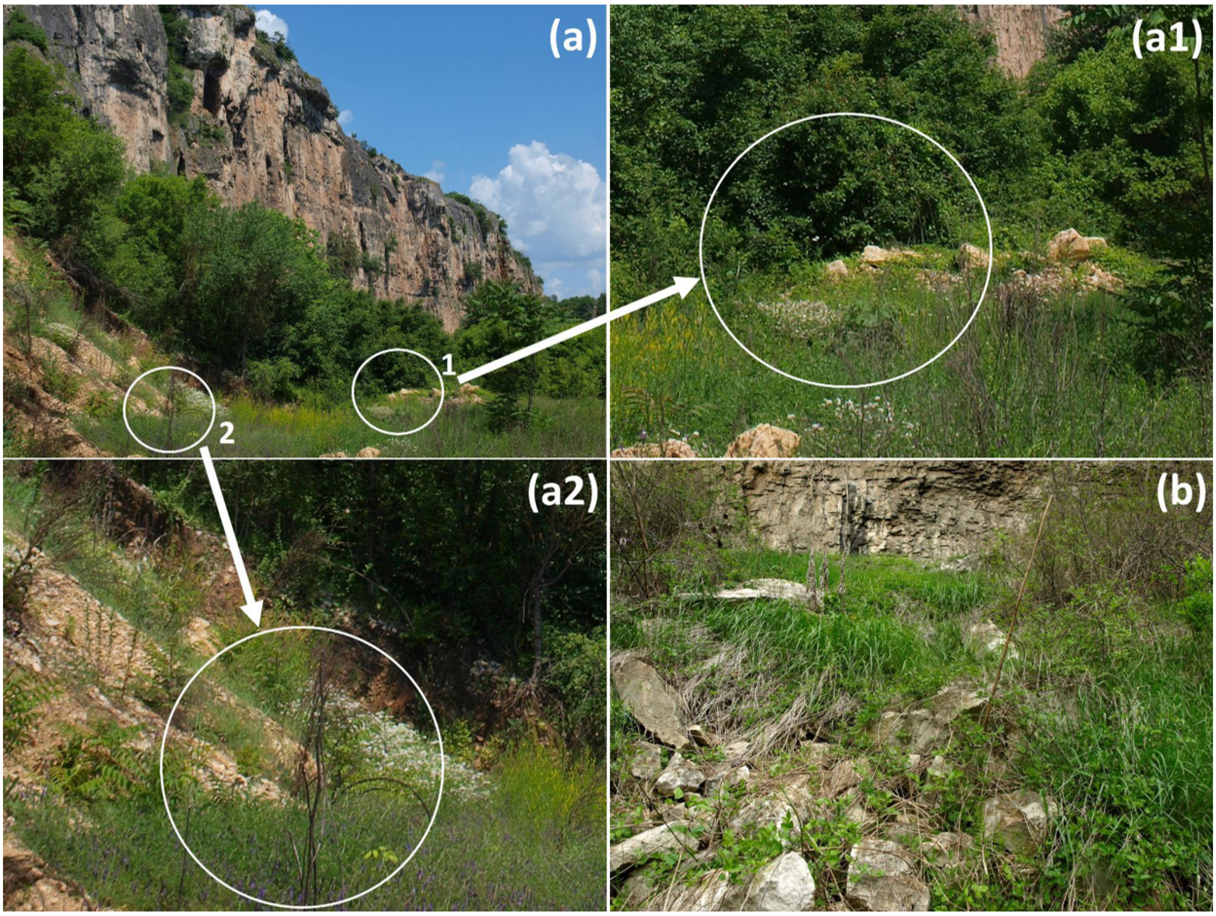

Figure 4 – View of one of the habitat types in which vipers were most often detected - rocky / stony areas overgrown with grass and shrubs (H7) in Site 1. Oval circles on (a) present an *in situ* example on the differences between the microhabitat characteristics of two locations where adult vipers (males and non-reproductive females) and juveniles were usually detected. **1**. Densely vegetated microhabitat with a combination of stones, grasses and shrubs, typical for adult vipers. **2**. Open microhabitat with combination of stones and grasses, typical for juveniles. Microhabitat characteristics are assessed on the surface within an oval circle with the viper's location being positioned in its centre. (b) shows the characteristics of the open rocky-grassy microhabitat within habitat type H7 (situated in close proximity to the hibernating area) in which most pregnant vipers from Site 1 were detected during gestation.

TABLE 4

Results of Kruskal-Wallis H tests between the microhabitat characteristics in the places of observations of the different sex/age groups of *V. ammodytes* during summer (1st, 2nd and 8th rows) and the p values from the post-hoc tests testing for differences in the presence of trees/shrubs and stones/rocks between sex/age groups (3rd–7th and 9th–13th rows).

| **Grasses: Kruskal-Wallis H test: H = 7.69, p = 0.1, n = 229**<br>**Trees/Shrubs: Kruskal-Wallis H test: H = 14.43, p = 0.006, n = 229** | | | | |
|---|---|---|---|---|
| | **fad** | **fadP** | **sub** | **juv** |
| mad | 0,89 | 0,006 | 0,25 | 0,19 |
| fad | – | 0,19 | 1 | 1 |
| fadP | 0,19 | – | 1 | 1 |
| sub | 1 | 1 | – | 1 |
| **Stones/Rocks: Kruskal-Wallis H test: H = 8.94, p = 0.06, n = 229** | | | | |
| | **fad** | **fadP** | **sub** | **juv** |
| mad | 1 | 1 | 1 | 0,05 |
| fad | – | 1 | 1 | 0,23 |
| fadP | 1 | – | 1 | 0,39 |
| sub | 1 | 1 | – | 1 |

## Discussion

Our results demonstrate that the breadth of the spatial niche of *V. ammodytes* is related to individual age and reproductive status, being most narrow in juvenile vipers and gradually increasing with age. These differences might be attributed to the age-related variations in the trophic niche of the species, as juvenile nose-horned vipers have the narrowest trophic niche, being mainly comprised of small lizards and centipedes (Beshkov 1977; Luiselli 1996; Dyugmedzhiev 2020; Anđelković *et al*. 2021; Tomović *et al*. 2022). Therefore, it can be expected that juveniles would choose habitats and microhabitats with higher abundance of these types of prey, which likely results in utilizing less other habitat types. As nose-horned vipers grow in size (and age, respectively), their ability to ingest larger prey increases, and consequently, their diet becomes more diverse, including also small mammals, snakes, birds, etc. (Beshkov 1977; Luiselli 1996; Dyugmedzhiev 2020; Anđelković *et al*. 2021; Tomović *et al*. 2022), which probably leads to a gradual use of a wider range of habitats. Interestingly, the results from the correspondence analysis indicated a shrinking in the spatial niche of adult males during summer. However, the rate of encountering males in summer is very low (Dyugmedzhiev *et al*. 2022), so these results might be due to this observational bias, and should be treated with caution. The spatial niche of gestating females also appeared to narrow sharply and the results from the correspondence analysis clearly associated the presence of pregnant females in abandoned quarries overgrown with grasses and shrubs (H2) during summer. Indeed, during this time of the year, 64% of all captured pregnant vipers, as well as few immature individuals, could be found in this habitat (in Site 3), while the other vipers migrated to another, adjacent habitats, as described in previous studies (Dyugmedzhiev *et al*. 2020, 2024). During gestation, pregnant female vipers need to thermoregulate more precisely for the development of the embryos (Bonnet & Naulleau 1996; Ladyman *et al*. 2003; Lorioux *et al*. 2013; Dyugmedzhiev *et al*. 2021). Therefore, during this period, they sharply decrease their movement rates (Dyugmedzhiev *et al*. 2020) and adjust their activity patterns in ways that facilitate thermoregulation at the expense of regular feeding (basking in the morning and spending the rest of the day in shelters with optimal thermal qualities, Dyugmedzhiev *et al*. 2021, 2022). It is possible that the abandoned quarries provide more favourable thermal conditions for thermoregulation than the adjacent habitats. This tendency of gravid female vipers as well as other snake species, to spend their gestation period in open, rocky sites, known as rookery (i.e., cliffs, rock slides or piles, etc.) is well known (Duvall *et al*. 1985; Gannon & Secoy 1985; Macartney & Gregory 1988; Reinert & Zappalorti 1988; Charland & Gregory 1995). These sites are often close to the hibernating areas, so that after their birth, the new-borns could easily find suitable hibernacula at the end of the activity period (Viitanen 1967; Neumeyer 1987; Charland & Gregory 1995; Bonnet & Naulleau 1996; Saint Girons 1997; Dyugmedzhiev *et al*. 2020). The vipers' main hibernating area was in fact located in the abandoned quarry in Site 3 (Dyugmedzhiev *et al*. 2020, 2024). Site 1 was the only other site where sufficient numbers of pregnant females were found to allow to draw some conclusions, with the majority of pregnant females (67 %) also remaining close to their hibernacula during gestation, although in a different habitat type (rocky/stony area overgrown with grass and shrubs; H7, Fig. 4b). The combination of the above-mentioned factors probably causes pregnant vipers to use fewer habitats during summer, resulting in narrowing of their spatial niche.

Our results indicate that also microhabitat preference changes with age and depends on the vipers' reproductive status. It appears that adult vipers prefer to adhere close to trees and especially shrubs, in contrast to juveniles, which inhabit more open stony-grassy microhabitats. This pattern seems to be more obvious in spring and autumn than in summer, and the underlying reasons for these differences might be a combination of factors. First, the size difference between the age groups as well as their distinct behavioural patterns, might affect their microhabitat selection. Similar to other viper species and because of their larger size, adult *V. ammodytes* need to spend more time basking for successful thermoregulation than juveniles, especially during spring and autumn when ambient temperatures vary greatly (Herczeg *et al*. 2007; Bauwens & Claus 2018; Dyugmedzhiev *et al*. 2021, 2022). In case of a predator attack (especially an avian attack), it would be very difficult for a large adult viper to hide in an open microhabitat. By staying in the immediate proximity of shrubs during basking, adults would be better protected against predation. Juveniles with their small size should easily be able to hide and disappear between stones in the open microhabitats, as well as to apply thigothermy, i.e., basking while being in touch with the surface underneath the stones, where they are invisible to birds. Smaller subadults would also be able to find safety in the open microhabitats, while larger subadults should be safer from predatation closer to shrubs, which might explain the high variation in the values for tree/shrub-presence in their microhabitats. Because of the high ambient temperatures in summer, far less basking time is required for successful thermoregulation, even for large adult vipers, and to avoid high temperatures, vipers might need to hide in the shade or in shelters during most of the day (Dyugmedzhiev *et al*. 2021, 2022). This might be one of the reasons why the age-differences in microhabitat use are less clear during summer.

Additionally, ontogenetic differences in trophic niches and feeding periods might also affect the respective variation in microhabitat selection. The feeding patterns in *V. ammodytes* show ontogenetic differences not only regarding the breadth of the trophic niche (as mentioned above), but also in the duration of the feeding periods. Immature vipers (both juveniles and subadults) feed intensively throughout the entire activity period, in contrast to adults, which have much shorter feeding period (mainly during summer for males, and summer and autumn for non-reproductive females) (Dyugmedzhiev 2020). It could be speculated that in the open rocky/stony microhabitats lizards and centipedes are more abundant then in the densely vegetated shrub microhabitats (Beshkov & Dushkov 1981). Therefore, juveniles might inhabit them more often than adults in order to optimize their foraging opportunities. In contrast, microhabitats with more shrubs might be richer on small mammals (Beshkov & Dushkov 1981). As subadults prey on centipedes, lizards and small mammals, they might use both the shrub and the open microhabitats and this might also explain the high variation in the values for tree/shrub-presence of their microhabitats. During summer, when adults start to feed more intensively, they also might use both microhabitat types in order to increase their feeding opportunities by preying on both lizards and small mammals. This might also explain the less clear differences of age-related microhabitat selection during summer. It should also be noted that the sample size of juveniles was with the smallest number of all sex/

age groups (only 26 observations) and this might also attribute to the lack of significant differences as compared to adults. Although values for trees/shrubs were similarly low for both juvenile and pregnant vipers, only those of the latter (with higher sample size, n = 52) differed significantly from those of adult males. The observed patters could also be due to different detection probabilities, related to the size of the respective age groups (Mazerolle *et al*. 2007; Pike *et al*. 2008; Steen 2010; Durso & Seigel 2015; Bauwens & Claus 2018). For instance, due to their small size, juveniles might be much more difficult to be spotted in densely vegetated shrub microhabitats than males or juveniles occurring in open microhabitats, especially during summer when the grass is at its highest (Bauwens & Claus 2018).

Pregnant females might prefer more open microhabitats because of their need for precise thermoregulation; these habitats would increase exposure to sunlight, and temperatures below stones or in rock crevices should be much higher and more constant as compared to microhabitats in the shade of trees or shrubs. In such microhabitats females can even bask during cloudy or rainy weather, as rocks would still absorb and provide more heat for thermoregulation than shrublands and other densely vegetated areas. Choosing shelters in open microhabitats should allow pregnant females to maintain preferred temperatures longer than if they would hide in the shade, a pattern that is known for pregnant female *V. ammodytes* (Dyugmedzhiev *et al*. 2021).

## Conclusion

*Vipera ammodytes* inhabits a wide variety of habitats and microhabitats. Habitat and microhabitat selection however, depend on individual age, size and reproductive status. Juvenile vipers and pregnant females have the narrowest spatial niches and they inhabit more open microhabitats. The breadth of the spatial niche gradually increases with age/size, and so does the number of vipers occupying microhabitats with more shrubs. These patterns might be explained by a combination of factors, such as ontogenetic variations in the trophic niche and feeding patterns of this viper species, differences in prey type abundance in distinct habitats and microhabitats, the size differences between age groups (with all benefits and limitations that come with them), distinct behavioural patterns varying between sex/age groups, or a size-related bias in detection probabilities.

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