

Published by the British
Herpetological Society

Patterns of spatial and temporal association between *Zootoca vivipara*, *Anguis fragilis*, *Vipera berus* and *Natrix helvetica* at artificial refuges

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A 15-year data set of reptile observations at corrugated iron refuges was analysed to describe the spatial and temporal associations between species pairs of viviparous lizards *Zootoca vivipara*, slow worms *Anguis fragilis*, northern vipers *Vipera berus* and grass snakes *Natrix helvetica*. Of the two snake species, only the viper is known as a routine lizard predator. We analysed two variables expressing pairwise reptile associations at refuges. The first analysis was of monthly spatial overlap assessed as the proportion of unique refuge positions used in common, but not necessarily used simultaneously. The second analysis was of a more precise spatial and temporal assessment based on counts of reptile pairs cohabitating at the refuges (i.e. using the same refuges simultaneously). Apart from viviparous lizards paired with either of the two snake species, the frequencies for both variables were either as expected or significantly greater than expected by chance; in particular grass snakes cohabited much more frequently than expected with both vipers (+327%) and slow worms (+218%). In contrast, for the viviparous lizard/viper pair both variables were statistically significantly less frequent than expected by chance - monthly overlap (-35%) and cohabitation (-87%). As viviparous lizards are preyed upon by vipers, cohabiting would be much reduced but the significantly lowered monthly spatial overlap may indicate active avoidance. For the viviparous lizard/grass snake pair the spatial overlap was as expected by chance but, as with vipers, the frequency of cohabiting was significantly less than expected by chance (-75%). These observations are discussed in relation to the known kairomonal responses of this lizard to viper and grass snake deposits. Viper deposits are also believed to act as a kairomone for slow worms, but we found no evidence that they avoided vipers, supporting existing literature showing that *V. berus* is unlikely to be an important slow worm predator.

Keywords: species associations, cohabitation, corrugated iron refuges, viper kairomone, chalk grassland

INTRODUCTION

Artificial refuges of galvanized corrugated iron are commonly used for monitoring reptiles that may be found beneath or on them (Dodd, 2016). These refuges give both a suitable fixed reference point and a location where reptiles may be observed singly or in combination. Consequently, observations at refuges are a convenient way to investigate the temporal and spatial overlap between species leading to possible insights into the relationships between species and between conspecifics. For example, the relationship between adult and juvenile smooth snakes *Coronella austriaca* was observed at arrays of refuges where the juveniles appeared to confine themselves to the periphery of the population, which has been interpreted as their avoidance of the cannibalistic adults (Kolanek et al., 2019). Laboratory studies in which potential prey species such as the viviparous lizard *Zootoca vivipara* (Thoen et al., 1986; Van Damme et al., 1995) and slow worm *Anguis fragilis* (Cabido et al., 2004) were exposed to chemical deposits from lizard predators such as the smooth snake and northern viper or adder

Vipera berus have demonstrated clear responses that suggest the chemicals involved are a kairomone used by these lizards to avoid predation. In the case of *Z. vivipara*, the observed responses were changes from normal behaviour, which involved an alternation of activity bouts and basking, to long periods of immobility, interrupted by jerky, hesitant walks, behaviours that would reduce their mobility and hence chances of detection. There appears to have been only a single study outside the laboratory on the behaviours induced by this kairomone. This investigated the associations between viviparous lizards and slow worms with their predator the smooth snake. In this case, records from iron refuges suggested that there was no evidence that either lizard species avoided shelters regularly used by smooth snakes and it was concluded that old chemical cues from smooth snakes apparently did not deter its potential prey from using the same shelters (Ceirans & Nikolajeva, 2017).

A 15-year reptile monitoring project in a chalk grassland reserve in south-eastern England offered an opportunity to document potential spatial and temporal associations between viviparous lizards *Z. vivipara*, slow worms *A.*

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fragilis, northern vipers *V. berus* and grass snakes *Natrix helvetica* at corrugated iron refuges; the two lizard species are potential prey of the viper (Prestt, 1971; Beebee & Griffiths, 2000), while the grass snake is not known as a lizard predator, especially in Britain (Gregory & Isaac, 2004). The associations between the species were examined by comparing differences between the observed and expected overlaps in monthly use of refuge positions and between observed and expected rates of cohabitation at refuges.

MATERIALS & METHODS

The data presented here were collected over 15 years (2008 to 2022) during visits to a chalk grassland reserve (open area of about 10 ha) south-east England (51° 19' N, 000° 11' E), in the reptile active period from March to October (8 months). The number of annual visits varied from 56 to 79, which were mostly undertaken from 09:00 h to 12:00 h. Each visit followed a standard survey path (3 km) and at intervals along the path there were refuge positions where artificial refuges of galvanised corrugated iron (dimensions - 50 cm x 60 cm, 0.5 mm thick, 0.5 g/cm²) were laid. The refuges were placed on the slopes of this reserve in similar habitat with more or less equal representation of south, south-west and west facing aspects. In 2008, there was a total of 31 refuge positions. The number of refuge positions was gradually increased at the beginning of each year until it reached 50 positions in 2016 and remained constant thereafter. According to anecdotal experience of surveying this site, the two snake species were frequently found at refuges when digesting food or sloughing, the viviparous lizards were typically basking on refuges or beneath them sloughing or just sheltering, and slow worms were more permanent residents. Occasionally, viper cadavers were encountered and the stomach contents of these was examined to give some information on the diet of this species.

Records were made of the reptiles at refuges, overwhelmingly under the refuges but occasionally on them. This investigation was part of a much more detailed study where reptiles were also recorded along the survey path and at refuges made from roofing felt, we have only reported reptile observations from the corrugated iron refuges. This is because we wished to make comparisons between all four reptile species and, apart from slow worms, corrugated iron refuges provided considerably more data.

Statistical analyses

Three main analyses were conducted using the collected data. The first analysis explored the relationship between the number of each reptile species at refuges and the number of available refuges. To give a measure of the spatial and temporal distribution of reptile species, their use of refuges was then subject to two further different analyses. The first analysis considered monthly overlap of species pairs in their use of refuge positions (use of same refuge positions irrespective of whether animals were found together or not). The second analysis concerned

the degree to which individuals of pairwise species combinations were cohabiting (species present together at refuges at the same time).

Correlation of reptile encounters and refuge numbers

Variation in the monthly rate at which the four reptile species were found at corrugated iron refuges was compared using a plot of log₁₀ transformed monthly means with their standard deviations. The relationship between this encounter rate at refuges and the number of different refuges occupied monthly by each species was then examined by preparing a log/log plot of these two variables and the strength of this relationship tested using the non-parametric Spearman's rank correlation on the transformed data set. The Spearman's rank test was used as data, even when log-transformed, did not meet the assumption of Normal distribution required for parametric analysis.

Monthly spatial overlap of refuge occupancy by species pairs

The first analysis was designed to answer the question - 'To what extent do the species pairs overlap in their choice of refuge positions?'. This was assessed by comparing the observed frequency of monthly overlap for each species pair with the expected frequency of overlap. The analysis was initiated by making a count of the number of unique refuge positions that each species had occupied in each of the 120 months of the study. Then a count was made of the number of unique refuge positions that had been occupied at some time during the month by each of the six pairwise species combinations (Table 1). As an illustration, if we were operating 50 refuge positions then the maximum 'overlap' would be 50 and the minimum would be 0, i.e. there was no attempt to quantify the number of overlaps at the same refuge position. The total count of unique refuge positions (number refuge positions x number months, summed over 15 years) was 5264 or 658 for each of the eight study-months (March to October) across the 15 years of study.

The probability of each species alone occupying a refuge was determined by dividing the occupancy frequency (number of unique refuge positions occupied each month) by the total number of unique refuges inspected each month for the 15-year study (658). Then the probability of any two species pair using the same refuge position during a given month (P_{overlap}) was estimated as the product of the two single species probabilities. Data were then analysed using simulation under the null hypothesis that species distributions are independent of one another. This approach, which does not require assumptions of independence to be met (Dugard et al., 2012), has been taken as in our data repeated measures from the same population violates the assumption of independence of data points made by more conventional statistical methods. The analysis was undertaken using base R (version 4.2.0) in RStudio (version 2022.2.02) (R Core Team, 2022). For each species pair, for each observation (i.e. for each month for each year, or 120 observations), the expected number of overlaps was drawn from a binomial distribution with

the number of observations set to the number of unique refuges present that month and the probability of overlap set to P_{overlap} . The mean number of simulated overlaps was then calculated. This process was repeated 9,999 times to generate a frequency distribution of simulated observed counts under the null hypothesis, against which the observed mean overlap (representing the 10,000th repeat) was compared. The proportion of this distribution more or less than (whichever was less) the observed mean was then used to calculate two-tailed p-values by doubling the 1-tailed p-value. As calculations were made individually for each observation (i.e. each month for each year), variation driven by year and month is accounted for and the analysis considers overall trends across the dataset. Two-tailed tests were used as there was no *a priori* prediction of direction of any effect. Probability values were treated as statistically significant if $p_{2\text{-tailed}} < 0.05$.

Cohabitation at refuges by species pairs

The second analysis was designed to answer the question, 'Do the reptiles tolerate the presence of each other under the same refuges?'. We counted instances where pairs of the four reptile species were observed actually cohabiting. There was a total of 44,536 refuge observations (number refuge positions x number site visits, summed over 15 years) during the study. To assess the statistical significance of the extent to which different species pairs were observed cohabiting, the observed total monthly counts for species pairs were compared with expected counts. We determined the frequency at which each species alone was found at refuges by dividing the observed numbers of refuges occupied by each species over 15 years (slow worm: 3802 refuges, viviparous lizard: 1661 refuges, viper: 1478 refuges, and grass snake: 330 refuges) by the total number of refuge inspections (44,536). The probability of any two species cohabiting (P_{cohabit}) was the product of the two refuge use rates. These data were analysed in the same manner as overlap data, using simulation, but with the binomial distribution probability parameter set at P_{cohabit} .

The data for the monthly spatial overlap and cohabitation analyses can be found in Supplementary Material on the BHS website and the R code at <https://github.com/CJMichaels/Hodges-et-al-2024.-Spatial-and-temporal-association>.

RESULTS

Variation in encounter rates at refuges

All four reptile species were encountered at corrugated iron refuges during the reptile active season of March to October (Fig. 1). The mean encounter rate of slow worms, however, was generally greater than the other three species, while grass snakes were always encountered at much lower rates than the other three taxa.

Monthly spatial overlap in refuge occupancy

The total 15-year monthly counts of different refuge positions used individually by the four reptile species show that the greatest number of different positions

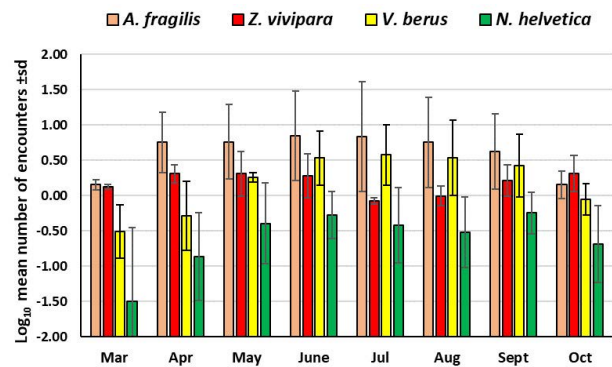


Figure 1. Mean monthly encounter rate (log scale) \pm standard deviation for four reptile species on a chalk grassland reserve recorded from corrugated iron refuges, 2008 to 2022

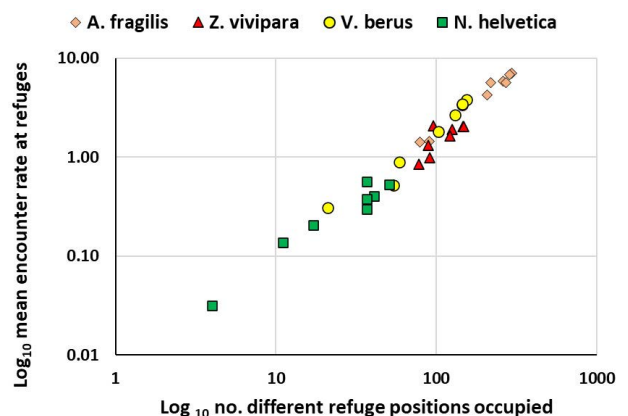


Figure 2. A log/log plot of the mean monthly encounter rate of four reptile species against the monthly total number of different refuge positions occupied during the eight-month reptile active season from 2008 to 2022

was occupied by slow worms (1708, 32% of total). While viviparous lizards (896, 17% of total) and vipers (812, 15% of total) were similar and grass snakes much lower (235, 4% of total). When the monthly encounter rates for each species (Fig. 1) are plotted against the monthly totals for the number of different refuge positions occupied (Fig. 2) the two are strongly correlated ($r_s = 0.98$, $n = 32$, $p < 0.001$). This suggests that for all four species, the number of different refuges at which the species were found is a function of their encounter rates (potentially a proxy for abundance).

When the observed and expected numbers of spatial overlaps of species pairs at different refuge positions were compared, those for the viviparous lizard/viper pair were significantly lower than would be expected by chance (Zv/Vb , Table 1), i.e. there was less overlap in the use of the same refuge positions than would be expected if refuge use by each species was independent of the other. The counts of refuge positions used by viviparous lizards with either grass snakes or slow worms were no different from those expected by chance (Zv/Nh , Zv/Af , Table 1). In the case of the three other pairwise species combinations, observed counts of shared refuge positions were all greater than expected by chance (Af/Vb , Af/Nh & Vb/Nh , Table 1).

Table 1. Pairwise comparisons of the observed and expected degree of spatial overlap between four reptiles species (*Vb* = *Vipera berus*, *Zv* = *Zootoca vivipara*, *Nh* = *Natrix helvetica*, *Af* = *Anguis fragilis*) expressed as counts of the same refuge positions occupied by both species at some time during any given month (over 15 years), and the statistical probability of the difference between observed and expected values occurring by chance, significant p values are in bold.

Species Pair	Observed	Expected	p _{2-tailed}	Direction
ZV/VB	0.733	1.132	< 0.0001	Lower by -35%
ZV/NH	0.35	0.337	0.857	-
ZV/AF	2.65	2.460	0.178	-
AF/NH	1.192	0.733	< 0.0001	Higher by +63%
AF/VB	3.2	2.505	< 0.0001	Higher by +28%
VB/NH	0.85	0.367	< 0.0001	Higher by +132%

Table 2. Pairwise comparisons of the monthly (for 15 years) observed and expected count of cohabitation by four reptile species (*Vb* = *Vipera berus*, *Zv* = *Zootoca vivipara*, *Nh* = *Natrix helvetica*, *Af* = *Anguis fragilis*), at corrugated iron refuges and the probability of the difference between observed and expected values occurring by chance, significant p values are in bold.

Species Pair	Observed	Expected	p _{2-tailed}	Direction
ZV/VB	0.058	0.46	<0.0001	Lower by -87%
ZV/NH	0.025	0.103	0.001	Lower by -75%
ZV/AF	1.05	1.183	0.165	-
AF/NH	0.742	0.236	<0.0001	Higher by +214%
AF/VB	1.317	1.052	0.008	Higher by +25%
VB/NH	0.392	0.091	<0.0001	Higher by +331%

Cohabitation at refuges by species pairs

Species pairs cohabiting at the corrugated iron refuges (Fig. 3) were not uncommon. The total 15-year counts of cohabiting species pairs were as follows *Zv/Vb* - 7, *Zv/Nh* - 3, *Zv/Af* - 126, *Af/Nh* - 89, *Af/Vb* - 158 and *Vb/Nh* - 47. The number of viviparous lizards paired with either vipers (*Zv/Vb*, Table 2) or grass snakes (*Zv/Nh*, Table 2) were statistically significantly lower than expected by chance. In contrast, vipers paired with grass snakes or with slow worm (*Vb/Nh*, *Af/Vb*, Table 2) or slow worms with grass snakes (*Af/Nh*, Table 2) and were all cohabiting significantly more than expected by chance. For the viviparous lizard/slow worm pair (*Zv/Af*, Table 2) the observed counts of cohabiting pairs were no different than expected by chance.

The only cases where species pairs were observed cohabiting less frequently than expected by chance were between the viviparous lizard and the two snake species. There were only seven occasions when a viviparous lizard and a viper were found cohabiting. These observations

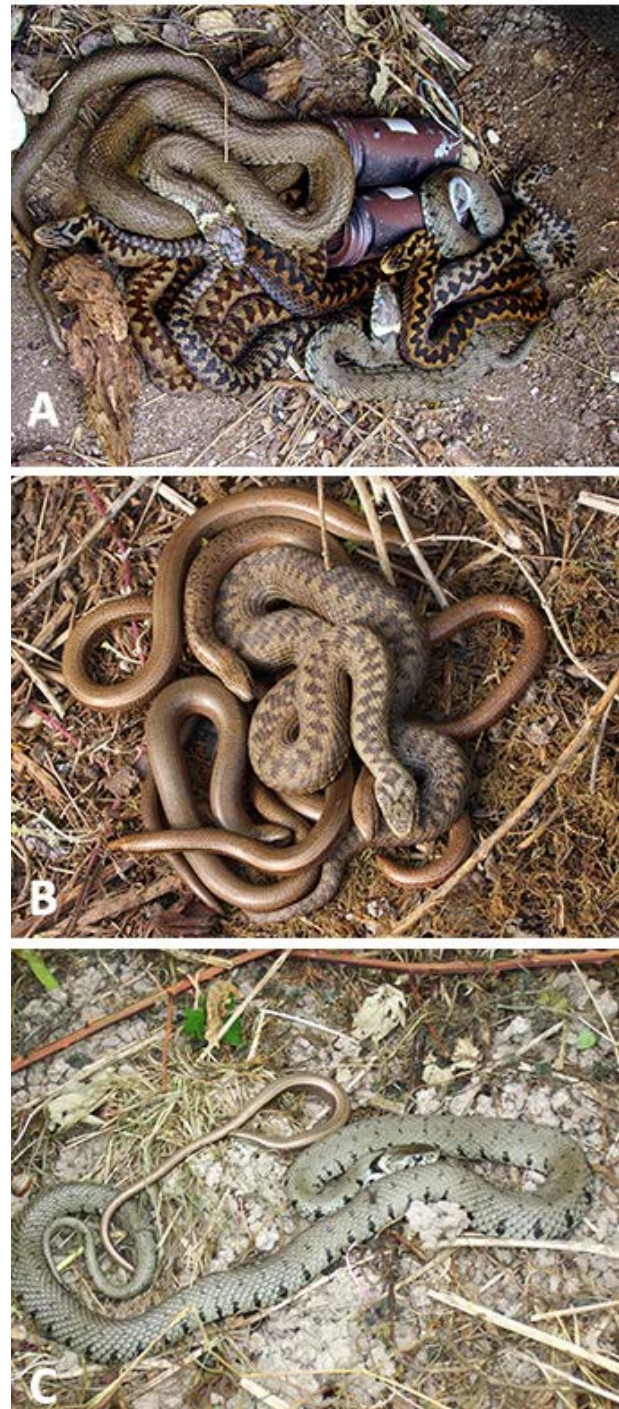


Figure 3. Reptile species pairs found together under corrugated iron refuges - **A.** Adult *Vipera berus* and *Natrix helvetica* (the canisters hold data loggers for a different study), cloudy eyes indicate that both grass snakes are soon to shed their skins, **B.** Adult female *Vipera berus* and five adult male *Anguis fragilis*, a particularly good example from a different study site nearby, and **C.** Sub adult *Anguis fragilis* with an adult female *Natrix helvetica*.

were made in the months of May to September in three years (2010 x 2, 2015 x 3, 2020 x 2), and the vipers involved were 1 adult female, 4 sub adults and 2 juveniles while the viviparous lizards were 3 adult females, 1 adult male, 1 sub adult and 2 juveniles. Likewise, there were only 3 occasions when a viviparous lizard and a grass

Table 3. Summary of the average observed/expected differences between species pairs for monthly spatial overlap in the use of the same refuge positions and cohabitation at corrugated iron refuges (Vb = *Vipera berus*, Zv = *Zootoca vivipara*, Nh = *Natrix helvetica*, Af = *Anguis fragilis*)

Reptile pair	Zv/Vb	Zv/Nh	Zv/Af	Af/Nh	Af/Vb	Vb/Nh
Spatial overlap	35% less than expected	As expected	As expected	63% more than expected	28% more than expected	132% more than expected
Cohabitation	87% less than expected	75% less than expected	As expected	214% more than expected	25% more than expected	331% more than expected

snake were found cohabiting. These observations were confined to the months of June to September in three years (2008 x 1, 2014 x 1, 2019 x 1) and the grass snakes involved were two sub adults and one adult male, while the lizards were one adult male, one adult female and one sub adult.

Observation on adder prey species

Fifteen viper cadavers were found over the course of the study. Their stomach contents included viviparous lizards, voles *Microtus* sp, wood mice *Apodemus sylvaticus* and shrews *Sorex* sp, with no slow worms despite these being a very commonly encountered species. Furthermore, there were no observations of slow worms being eaten by vipers and the two species were observed cohabiting beneath refuges more frequently than any other species combination.

DISCUSSION

All four reptile species inhabiting the chalk grassland reserve used the corrugated iron refuges throughout the reptile active period, however encounter rates varied by month across the year probably related to weather conditions and physiological and reproductive status of the individuals concerned. It was of interest to note that at the two extremes of the reptile active season, March/April and October, the two lizard species were encountered at greater rates than the two snake species suggesting a greater use of refuges in cooler weather and possibly, at least in the case of the viviparous lizard, earlier emergence from, and later entry into, hibernation (an observation made by Viitanen, 1967). For all species, the observed encounter rates, a proxy for abundance, were positively correlated with the number of different refuge positions occupied. This indicates that as the encounter rates rose more refuge positions were occupied instead of simply more reptiles appearing at the same refuges, which would instead have resulted in a sharp increase in the degree of aggregation. It also implies a relatively high degree of uniformity in the underlying physical characteristics of refuges. The degree of monthly spatial overlap between the four reptile species in their use of the same refuge positions and the extent to which these species were observed cohabiting at refuges is summarised in Table 3.

Deviations from expected values for spatial overlap and cohabitation are likely to arise from either attraction

or avoidance between species pairs and/or from a convergence between species in their preference for particular microhabitats. Predator-prey relationships would also potentially have a significant bearing on this. The northern viper is known to be a frequent predator of the viviparous lizard (Prestt, 1971; Beebee & Griffiths, 2000). In the case of slow worms, Prestt (1971) reported that *A. fragilis* amounted to only 2% of the stomach contents of *V. berus* and our own observations showed no evidence of the slow worm as a prey species. Slow worms are well protected with osteoderms in their skin (Beebee & Griffiths, 2000) and would be relatively difficult to grasp and swallow. It seems probable that they are rarely eaten by *V. berus*. Grass snakes are not known to be lizard predators but feed on fish, amphibians and small mammals (Gregory & Isaac, 2004). Our interpretations of the observed associations between the four reptile species are as follows.

Association between viviparous lizards and vipers

The association between viviparous lizards and the vipers gave significantly lower than expected values for both overlap in use of the same refuges, less by 35%, and in cohabitation less by 87% (Table 3). Viviparous lizards are a common food item of vipers so any lizards cohabiting with vipers at refuges are likely to be eaten thus reducing the chances of finding them together. Over 15 years the two species, on a monthly basis, occupied a similar number of different refuge position, viviparous lizards 17% of the total available and vipers 12%. Nevertheless, on the same monthly basis and in effectively the absence of the other species, their degree of overlap in the use of these refuge positions was significantly and substantially lower than expected by chance. This raises the possibility that some other explanation than simply predation may account for the difference. It seems reasonable to dismiss the possibility that viviparous lizards and vipers simply have different refuge preferences since there was a strong similarity between all refuge positions and the overlap of both vipers and viviparous lizards with the other two species was as expected or greater than expected suggesting that viviparous lizards and vipers would likely have similar preferences for the refuges on offer. It is known from laboratory studies that there is a kairomonal response of viviparous lizards to hexane-soluble chemical deposits from the skins of vipers (Thoen et al., 1986; Van Moorlegheem et al., 2020) that has been observed to result in a suite of behaviours that may

reduce mobility and hence the chances of detection followed by predation. However, the reduction in overlap in refuge use could be taken as evidence that viviparous lizards are avoiding those refuges that have been used by vipers, where chemical deposits from vipers may act as a kairomone. If that is the case, then the kairomone not only produces a local response that reduces mobility but leads these lizards to actively avoid those places frequented by vipers. Laboratory studies of the responses of viviparous lizards to vipers have involved confined environments where escape or avoidance have not been options. Our observations suggest that in a more natural context, where attenuated chemical signals indicate that a viper is not in the immediate proximity, it may be 'safe' to show a locomotor response that results in avoidance/escape.

Association between viviparous lizards with grass snakes

The association between viviparous lizards and grass snakes differs from that with vipers in that the overlap was as expected by chance but, as with vipers, cohabitation was less than expected (Table 3). It is known that viviparous lizards respond to grass snake chemical deposits in the laboratory, but that the response is weaker than that to vipers and the lizard is probably able to differentiate between the two species (Thoen et al., 1986). It would appear that, although they do avoid cohabiting at refuges with grass snakes, viviparous lizards do not avoid refuges that have been used by them. Whether or not they avoid grass snakes themselves is uncertain because grass snakes and vipers show a greater than expected overlap in both choice of refuge position and in cohabiting (Table 3) so that any impacts the presence of grass snakes may have had would likely be confounded with that to vipers at shared refuges. Nevertheless, the result suggests that even if grass snake deposits had some effect this would have been weaker than that of the viper kairomone. To confirm this would require a study of associations between viviparous lizards and grass snakes in a habitat without vipers.

Association between viviparous lizards and slow worms

Both the overlap in refuge use and cohabiting between viviparous lizards and slow worms were no more or less than expected by chance. It might have been expected that there would be some convergence in their choice of refuges, or at least the microhabitats represented by the refuges, so that the associations would have been greater than expected. However, as vipers were using many of the same refuges as slow worms and there is evidence that viviparous lizards avoid vipers, it is likely that this has diminished the association with slow worms. Whether or not viviparous lizards' choice of refuges converges with that of slow worms would need to be investigated in a habitat without vipers.

Association between slow worms and vipers or grass snakes

The monthly overlap of slow worms with vipers was greater than expected (Table 3). This suggests that slow worms do not avoid vipers and that there is a convergence

in the species preferences for the microhabitats of refuge positions. Also, more vipers and slow worms were observed cohabiting than expected by chance, this is perplexing as laboratory studies have revealed that slow worms do respond to the swabs taken from the skin of either *V. berus* or *Vipera ammodytes* (Telenchev et al., 2021); in the case of *V. ammodytes* slow worms do form a significant part of the diet (Anđelković et al., 2021). It seems that although slow worms may be aware of northern vipers they do not avoid them. We did not examine the relationship between a slow worm's size and its likelihood of sharing a refuge with *V. berus*, this would be an informative area of further research. The difference between observed and expected overlap in refuge use and cohabitation of grass snakes and slow worms was even greater than for vipers and slow worms. Slow worms feed on invertebrates such as slugs and worms that favour moist habitats while a large portion of grass snake diet comprises amphibians that are also found in more moist habitats. This preference for more moist habitats may account for active selection of the same refuges in a situation where slow worms do not actively avoid grass snakes.

Association between vipers and grass snakes

The two snake species both occupied the same refuge positions and cohabited more frequently than expected by chance. In the absence of predator-prey relationships between the two snake species, it seems likely that the cryptic behaviours of both species when shedding their skins (Fig. 3) or digesting food may lead both species to select the same refuges; ones that offer more conducive environmental conditions and greater crypsis, at roughly the same times of the year. In Poland, *V. berus* and the eastern grass snake *Natrix natrix* have been documented sharing basking sites without any appearance of competition or other interference while in England during a time when male and female *V. berus* were in courtship the arrival of three *N. helvetica* at a shared site resulted in aggressive behaviour from the male vipers, this was interpreted as a behaviour specific to their reproductive condition (Dawson & Baker, 2020).

Besides cohabiting at refuges, reptiles may also cohabit at hibernacula. Viitanen (1967) lists cases from Scotland and Denmark of viviparous lizard hibernating with vipers *V. berus* and in the case of Finland mentions viviparous lizards, grass snakes and slow worms as well as the amphibians, the common frog *Rana temporaria* and common toad *Bufo bufo*, hibernating together with vipers. He comments that "joint hibernation is fairly common but the number of individuals remains low compared to the number of vipers." He also observes that "the arousal of the viviparous lizard from hibernation occurs about a week before vipers." The seeming regularity of viviparous lizards hibernating with vipers is in contrast to their apparent avoidance at refuges. If response to the viper kairomone leads to avoidance behaviour then it seem reasonable to speculate that at lower temperatures the threshold of response is raised to such an extent that that avoidance may be suppressed. This may pose no

threat to the lizards as at lower temperatures the snakes are not feeding, furthermore the lizards are expected to leave hibernacula before the vipers become active.

Our results may be interpreted as viper kairomone stimulating active avoidance by viviparous lizards rather than just a reduction in mobility as observed in laboratory studies. The kairomone would also appear to be persistent enough to remain active after a viper has moved away. To confirm this tentative avoidance response requires further study using an experimental approach to detail the behaviours involved and to quantify the relationship between response and the kairomone. Additionally, our pairwise analyses cannot account for more complex multi-species interactions in refuge choice and further research with more data from sites with different combinations of reptile species may extend these methods to further explore species interactions in a landscape.

ACKNOWLEDGEMENTS

We are very grateful to Roger Avery and Roger Meek for their advice and comments on the manuscript of this study and to three anonymous reviewers for their helpful suggestions. Jason Steel very kindly provided Fig. 3b. Thanks are due to Kent Wildlife Trust for facilitating reptile monitoring on their nature reserve and to the volunteers who help maintain these habitats.

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Accepted: 17 December 2023

Please note that the Supplementary Material for this article is available online via the Herpetological Journal website: <https://thebhs.org/publications/the-herpetological-journal/volume-34-number-3-july-2024>