Emigration and seasonal migration of the northern viper (*Vipera berus*) in a chalk grassland reserve

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ABSTRACT - Long-term monitoring of individually recognisable northern vipers (*Vipera berus*) has provided new evidence concerning emigration and seasonal migration. Northern vipers are well known to migrate from their wintering areas in springtime to forage and/or reproduce and then eventually return to the same wintering areas to hibernate. Less well known is their capacity to emigrate and in this study we suggest that this can be recognised when a viper selects a new wintering area at least 150 m from that used previously. Evidence is provided showing that there are two significant opportunities for emigration. First, neonates may wander considerable distances from their place of birth before selecting their hibernacula. Second, in the following spring some of the emergent juveniles disperse from the neonate-selected wintering areas but lack the homing ability to return to them and are consequently obliged to select new hibernacula. The sub-adults and adults developing from them have sufficient homing abilities to return to the wintering areas they occupied as juveniles. Only 45 % of males and 23 % of females showed signs of emigration and, interestingly, males emigrated over significantly greater distances than females. The direction of viper displacements in springtime varied considerably being influenced by the position of the sun, topography, weather, barriers to movement, and corridors of cover. Irrespective of migration direction, the sub-adults and adults appeared to make accurate returns to their wintering areas. The return of many adult males to these areas was commonly prior to their second moult and close to mid-summer; much earlier than reported previously. This is interpreted as an opportunity to occupy a warmer area to facilitate repopulation of the testes with spermatocytes prior to hibernation and is equivalent to the behaviour of gravid females that remain in the wintering area to promote the development of their embryos. But unlike females the males remain hidden from view until the autumn. The significance of neonates and juveniles as the life stages that emigrate is discussed in relation to viper reintroduction programmes.

INTRODUCTION

In springtime, northern vipers (*Viper berus*) may make seasonal migrations away from their established wintering areas for foraging and/or reproduction and eventually return to the same wintering area to select a hibernaculum. Wintering areas are typically warmer, drier habitats receiving extended periods of sunlight (Viitanen, 1967; Prestt, 1971). The seasonal migrations are distinct from emigration that can be recognised by the selection of new, distant, wintering areas. Emigration is an important feature of viper behaviour enabling the formation of new sub-populations and the maintenance of healthy metapopulations (Madsen et al., 1999). Unlike migration, to date emigration has been poorly documented.

The seasonal movements of *V. berus* across the landscape have been reported in several studies (Saint Girons, 1952; Viitanen, 1967; Prestt, 1971; Neumeyer, 1987) which are in general agreement with each other but differ in certain specifics. Northern vipers emerge from hibernation in springtime (usually March and April). Adult males are more tolerant of cold conditions and break hibernation a week or two before the adult females and immatures. Their early emergence allows them to bask in the spring sunshine consequently accelerating spermiogenesis (Viitanen, 1967; Herczeg et al., 2007). They are ready to mate following their first moult, after which they seek out reproductively active females, often over considerable distances from the wintering area (Viitanen, 1967; Hand, 2018). After a period of searching, the males may be guided to their mates if they encounter the scent trails left by the reproductively active females. Following the period of sexual activity the males are reported to seek out places to forage, referred to as the 'summer areas'. Likewise non-reproductive adult females and the immatures of both genders also seek out the summer areas to forage. The foraging vipers generally disappear from view so that they are difficult for humans to detect without aids such as telemetry or artificial refuges. It has been demonstrated recently that they tend to take up positions in deep cover, effectively below ground (Hand, 2018). Following mating, reproductive females seek out good basking locations in the wintering areas to advance the development of the embryos they carry. After giving birth in late summer (August or early September) these females begin to forage, although if food is available then some females may feed whilst they are still gravid (Bauwens

& Claus, 2019). In the autumn (September and October) the vipers move close to their wintering areas and subsequently select a hibernaculum. The vipers may hibernate singly or in groups but Viitanen (1967) noted that some 25 % of the snakes winter separately, many of these being neonates.

How the vipers manage to navigate the landscape remains poorly known but there are some clues. In southern Finland, Viitanen (1967) observed that on trend the vipers travelled south-west in the spring and in the opposite direction, north-east, in the autumn so that they return to the proximity of their previous wintering area. He speculated that they do this by following the sun from mid-day onwards in the spring (photo-positive) and the opposite in the autumn (photo-negative).

In the current study, *V. berus* populations were monitored on a chalk grassland reserve for twelve-years. Data on viper movements were collected by observing them along survey paths and at artificial refuges. The results are presented first as a series of four illustrative case studies of landscape movements by individual vipers, and then analysed to provide summaries of emigration by a larger number of males and females.

MATERIALS AND METHODS

Survey site

The study site was a chalk grassland nature reserve at about 51˚N, 0˚E. The reserve is managed by Kent Wildlife Trust and comprises three distinct areas of grassland totalling 11.1 ha separated from each other by dense woodland (Fig. 1). These three areas have margins and islands of low scrub and generally slope at 10˚ to 15˚ and each area has a different aspect: Area 1 slopes west into a relatively narrow valley, Area 2 slopes predominantly to the south-west, and Area 3 slopes predominantly southwards; the last two areas face into a wide open vale. The grassland is managed by extensive cattle grazing, usually from August to November, and scrub clearance by hand.

In addition to the grassland, there is a further 17 ha of sheep-grazed pasture to the west with hedgerows (Fig. 1)
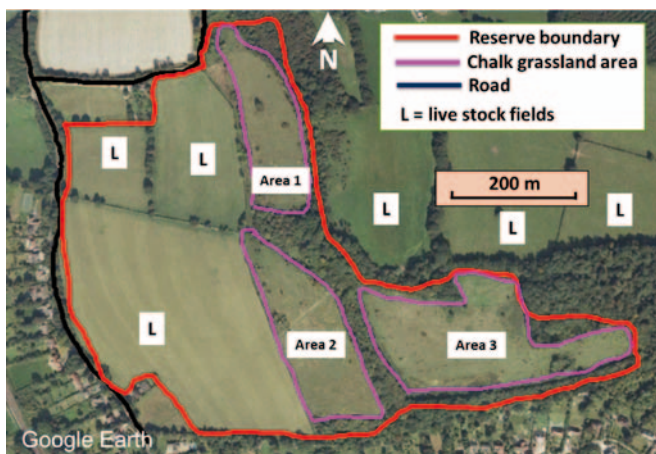

Figure 1. Map of the reserve showing three areas of chalk grassland, livestock fields, housing to the south and west, road to the west and north

along which viper observations are made. Otherwise, the reserve is bordered by open farmland, housing, woodland, and roads. It seems to offer few prospects of connection with other viper populations.

Monitoring methodology

A detailed account of the monitoring methodology is presented by Hodges & Seabrook (2018). The data presented here were collected from 2008 to 2018 during visits to the whole site in the reptile active period from February to October. The number of annual visits varied from 59 to 77. For each visit, the survey followed standard survey paths (total 6 km) and at intervals along the paths there are refuge positions where paired artificial refuges of corrugated iron and roofing felt (each 50 cm x 60 cm) are placed. At the start there were 31 refuge positions, increasing to 50 positions from 2016 onwards; vipers were recorded at refuge locations and along the survey paths. In this study, the advantage of using refuges is that they increase the numbers of observations on immature stages (Hodges & Seabrook, 2016), particularly in the vicinity of the wintering areas selected by neonates and juveniles, as well as on adults that are moulting or digesting food. To facilitate individual recognition, close-up photographs were taken of head-scale patterns (Benson, 1999) when the vipers were located under refuges or, by using a long-focus lens, when they were basking in the open; the patterns were coded and then entered into a database. As of 2018 the database held records of 505 individual vipers but only in the case of 52 individuals (10.3 %) was there sufficient data to contribute to this study. The study involved no animal handling in order to minimise disturbance and stress.

Different life stages were defined as follows: neonates had not yet hibernated; juveniles had hibernated only once; and, the sub-adult stages in the case of males were completed in two years and in females three years. Adults were recognised by having completed a total at least 4 hibernations in the case of males and, normally, a minimum of five in the case of females. In this study, assigning age class to individuals was relatively easy as nearly all vipers had been observed initially as neonates or juveniles, and in a few cases only as fully mature adults. The gender of adults and sub-adults was determined by colouration and body proportions (Smith, 1951; Beebee & Griffiths, 2000) while that of juveniles was assigned by colour and confirmed when they had developed to later stages.

Recording viper positions

The positions of vipers were recorded either at refuges or if along the survey paths then as the distance and direction from the nearest refuge. Observations of vipers emerging in early spring (February to early April) and/or those about to enter hibernation in autumn (September to early October) indicate the wintering areas chosen and the approximate location of their hibernacula (Viitanen, 1967; Prestt, 1971; Neumeyer, 1987); in this study the wintering areas typically had diameters of 20 - 30 m. To observe approximate distances between wintering areas, their locations were plotted on Google Earth and the straight line distance

between them in subsequent years was measured by creating a path on Google Earth (Path Tool). The lengths of paths were estimated using 'KML Path Measurer' (available for free download). If a viper was within 10 m either way of the previous year's position then its movement was treated as the selection of a basking site and not emigration or migration, i.e. recorded as zero. If the location of successive wintering areas was more than 150 m apart this was treated as evidence of emigration.

Statistical analysis

Data on the distances between the wintering areas selected by neonates and those selected by the same individuals in the last sub-adult stage, and the distances between these areas selected by the same individuals as adults in their first or second years, had high values of kurtosis and skewness (>0.8). This indicated that that they did not conform to a normal distribution. Consequently, paired comparisons were made using the Mann Whitney 'U' test (Siegel, 1956), applied as the more conservative two-tailed test. Differences were treated as statistically significant when the probability of them occurring by chance was 5 % or less (p≤0.05). With large sample sizes the data were approximated to a normal distribution (z), while smaller samples were assessed against the Mann Whitney 'U' distribution.

RESULTS

Case studies

The case studies reported below have been chosen as good examples of vipers making long displacements across the landscape of the reserve. They are intended to indicate the potential for emigration and/or seasonal migration, giving details of net directions and annual timings. Such lengthy displacements were observed in few of 505 vipers known to the project but there may perhaps have been many more cases of this if circumstances had permitted greater frequency of observation on these vipers.

Case Study 1 - Emigration and seasonal migration of a male viper (M100) in immature and adult stages

In the four years before M100 became sexually mature, all net displacements across the reserve were to the west of its site of birth (1, Fig. 2). M100 was first observed as a neonate under a refuge tin on 12th September 2012 (1, in Fig. 2) but, in a warm autumn when the snakes were still active even in October, it subsequently selected a hibernaculum about 200 m to the north-west (2, in Fig. 2) where it emerged in early April 2013. The juvenile viper was seen again three months later (July 2013) when it had moved beneath a refuge tin 275 m to the south-west (3, in Fig. 2). M100 was not seen during the two sub-adult stages (2014 & 2015) but the wintering area selected by the second stage sub-adult was evident when in April 2016 the newly emerged adult male was detected 200 m further west (4, in Fig. 2). There is no indication of the path travelled by this snake as a sub-adult but the net displacement between wintering area of the neonate and that of the last sub-adult was 713 m. In 2016 and 2017 the mature M100 dispersed in search of females resulting in net displacements to the north of the wintering area (5 & 7, in Fig. 2) where on both occasions M100 was found with a reproductive female. In both years M100 eventually returned south to the same wintering area (♣ in Fig. 2).

The pattern of emigration shown by M100 was a net westward movement starting with the neonate and continued by the juvenile. The last observation of the
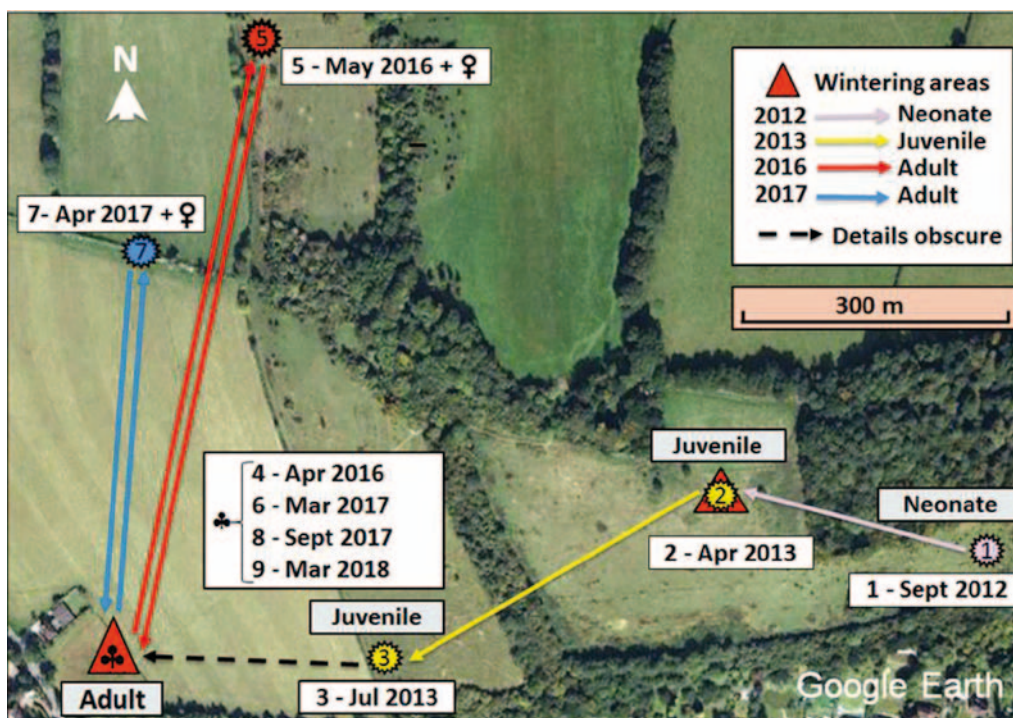

Figure 2. Net displacements across the landscape and the wintering area used by a male *V. berus* (M100) observed as a neonate in 2012, juvenile in 2013, and then as an adult (2016 – 2018). No information is available on the sub-adult stages.

juvenile was in July so that further displacement was still likely that year and indeed may have been to the location that was later observed to be the adult wintering area (♣, in Fig. 2). Further westward movement would not have been possible as this was blocked by a wide, busy road. It is not clear why as an adult M100 moved northwards although the same direction of seasonal migration has been recorded for other males in this locality. The very busy road to the west and housing and open gardens to the south would present significant barriers. The main linear features on the reserve are hedgerows and those that M100 would contact first run north-south (Fig. 2). Open pasture in the area would place reliance on the use of these hedgerows for cover. As movement south along the hedgerow was faced with the barrier of shaded woodland and housing the only option may have been to head north.

Case Study 2 - Emigration and seasonal migration of the immature stages of a male viper (M40)

M40 was observed as a juvenile and in its two sub-adult stages. In this time it demonstrated both emigration and seasonal migrations (Fig. 3). The adult M40 was not observed.

It is not known where M40 was born but as a juvenile it was seen in March 2007 in the wintering area that would have been selected by the neonate (1, in Fig. 3). The juvenile moved 180 m south-west where it was observed beneath a refuge tin (2, in Fig. 3). It seems likely that M40 then moved from here to select a wintering area 215 m to the north-east (3, in Fig. 3). This was not observed directly but has been assumed since M40 in both the first and second sub-adult stages also used this as its wintering area (♣, in Fig. 3) and undertook routine foraging migrations back to the same feeding area used by the juvenile in the south-west

(♠, in Fig. 3). In this example, it appears that the juvenile was responsible for the selection of the wintering area and hence for emigration.

Case study 3 - Seasonal migration of an adult male viper (M39)

The wintering area of adult M39 was at the top of the slope in Area 3 in a very warm sunny but otherwise exposed location. From 2012 to 2014, M39 made springtime migrations and on each occasion located at least one reproductive female. These migrations were made despite there being at least one reproductive female in the vicinity of his own wintering area (2 in both 2012 and 2014, 1 in 2013). These females were eventually paired with males that had hibernated further down the slope and had moved in a north-westerly direction to find them.

The directions of M39's springtime migrations in 2012 and 2014 were similar (Fig. 4 & Table 1). Following the first moult of the year, M39 moved in a westerly direction to the same location in both years (♥, in Fig. 4). In 2012, he was found competing with another male for access to a female while in 2014 he was observed mating with and, the following day, mate-guarding the same female. Subsequently, in both years M39 headed north where in 2012 he was found under a refuge tin (3, in Fig. 4), while in 2014 he was detected somewhat further north in the open (10, in Fig. 4). In both years, this male then returned to the wintering area (♣, in Fig. 4) to be found under a refuge tin undergoing a second moult. In both these years there was a third moult in August.

In the spring of 2013, M39 behaved differently. This viper was first detected in the wintering area on 8th April, somewhat later than usual due to the cool damp weather
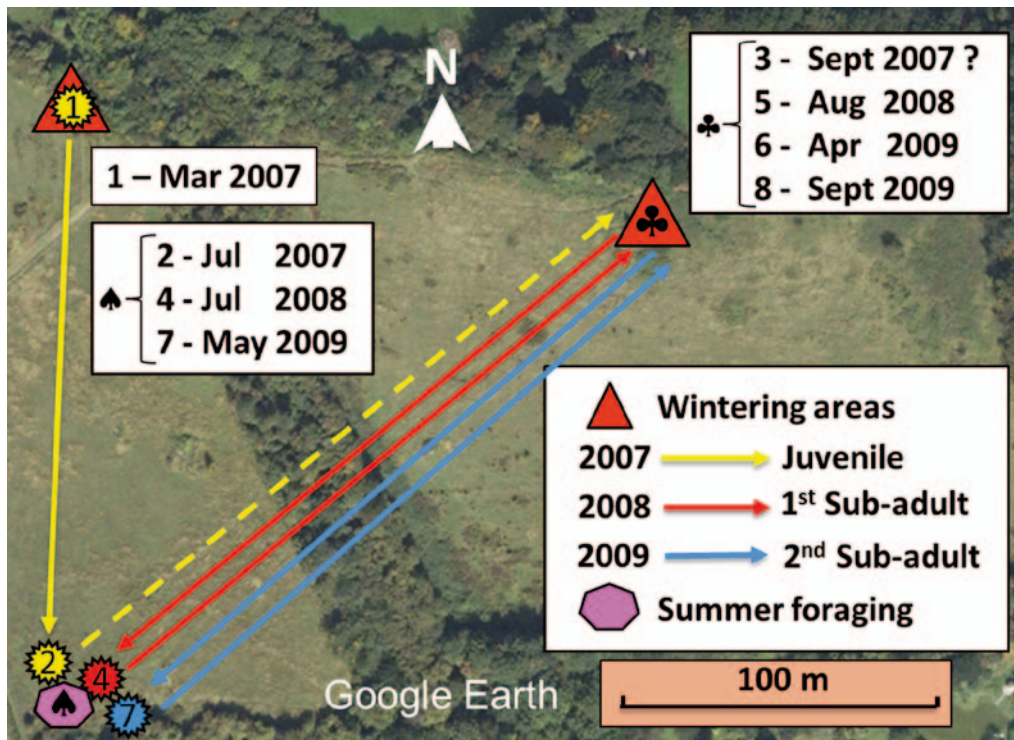

Figure 3. Net displacements of a male *V. berus* (M40) as a juvenile and first and second stage sub-adult
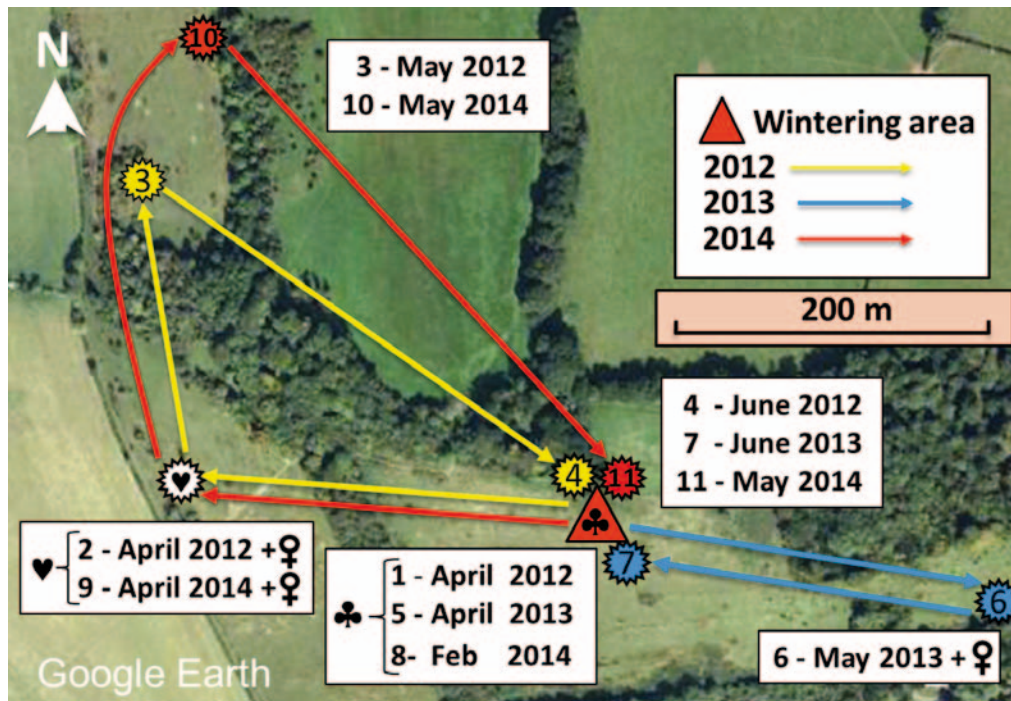
Figure 4. Net displacements of an adult male *V. berus* (M39) in spring and early summer in each of three consecutive years

Table 1. Springtime migrations following 1st moult of adult male Vipera berus (M39) searching for mates and then returning to the wintering area in time for the 2nd moult. For comparison, data from a telemetry study of an adult male (M235) in England (Hand, 2018; Hand, pers. comm., 2019) is included.

Male	Year	Date of 1st moult	Net displacements (m) from, and back to, wintering area with net directions			Date return recorded	Date of 2nd moult
			Outward	Middle	Return		
M39	2012	<16th April	400 m W	270 m N	367 m SE	20th June	25th June
M39	2013	<30th April	330 m SE	-	330 m NW	29th June	>4th July
M39	2014	30th March	400 m W	329 m N	403 m SE	9th May	13th June
M235	2017	10th April	352 m NW	98 m NE	380 m SE	23rd May	31st May

of that year. By 30th April, M39 had moved 30 m south-east and was recently moulted. Ten days later he was seen 330 m south-east of the wintering area (6, in Fig. 4) and was in the presence of a female and other males. By June, M39 had returned to the wintering area and was found under a refuge tin. His second moult was eventually completed soon after 4th July (Table 1) and there was no evidence of a third moult that year. This unusual easterly displacement in 2013 was also observed in a second adult (M75) which emerged from hibernation within 50 m of M39 and was later detected south-east in the same location (5, in Fig 4), in competition with M39 for a female.

A return to the wintering area in advance of the second moult has not been reported previously but the same phenomenon has been detected in a telemetry study of an adult male (Hand, 2018; Hand, pers. comm.) shown in Table 1. This prompted a wider investigation of the data set of adult male vipers to determine whether this might be a more common behaviour. In the case of 14 individuals there were data on the locations of the first and second moult (9 individuals contributed data for more than one year). The first moult was within the wintering area and for most of these adult males the second moult was in the
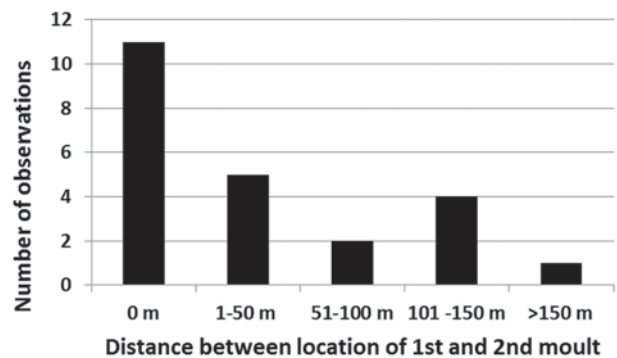

Figure 5. Distance between locations of the 1st moult and 2nd moult of fourteen adult male *V. berus*, some were observed in more than one year (n=23)

same place (Fig. 5). If a distance of less than 51 m between the locations of the two moults is taken as a criterion for remaining within the wintering area then 70 % had either simply remained within this area for both moults or had returned to it (Fig. 5). There was no evidence that these males left the wintering area after the second moult or before hibernation.
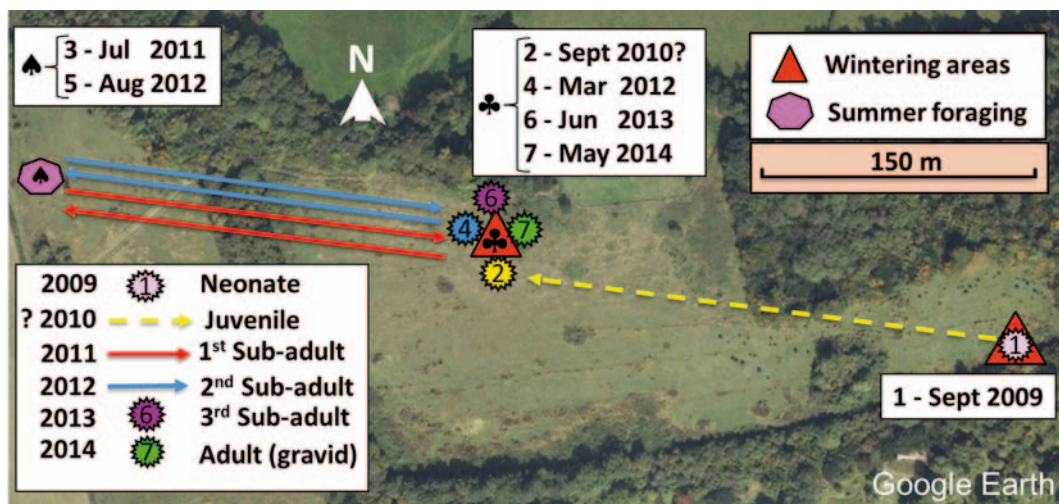
Figure 6. Net displacements of a female *V. berus* (F81) as a neonate, juvenile, in three sub-adult stages, and as an adult

Case study 4 - Emigration and seasonal migration of a female viper (F81) when immature and when adult

Female F81 was oberved for five years, from new born to adulthood but with direct observations on the juvenile stage lacking. From the observed positions of the neonate and first sub-adult stage, it may be inferred that after juvenile emergence from hibernation (1, in Fig. 6) F81 achieved a displacement of 280 m north-west where she probably selected her wintering area in September 2010 (2, in Fig. 6). The first sub-adult stage was detected a further 243 m north-west in a foraging area in July 2011 (3, in Fig. 6) but then returned south-east to the same wintering proposed for the juvenile, where in March 2012 F81 emerged as a second stage sub-adult (4, Fig. 6). This viper then dispersed again to the north-west and was detected in precisely the same foraging area (5, in Fig. 6). Thereafter, the third stage sub-adult (seen x3 in 2013) and the adult itself (seen x16 in 2014) showed no evidence of any movement away from the wintering area (6 & 7, in Fig. 6). F81 bred in 2014 and was observed basking in the open or present under either the felt or tin refuge.

It seems likely that juvenile emigration established the wintering area (♣, in Fig. 6) and then the first and second stage sub-adults established a routine foraging migration to a specific feeding area to the north-east (♠, in Fig. 6) with accurate return to the wintering area. Subsequently, there was a switch in behaviour with both the last sub-adult and adult viper apparently remaining in the wintering area throughout the year.

Emigration revealed by analysis of the distances between wintering areas

To give an indication of the extent of emigration by the immature stages, observations were made of the wintering areas selected by 20 male and 22 female vipers as neonates and then by the same individuals when they had reached the last sub-adult stage. Detection was in autumn, just prior to hibernation or in early spring at the time of emergence. Further observations were made on the wintering area selected by the same, albeit somewhat fewer, vipers as first year and second year adults to give an indication of adult emigration.

Emigration by immature vipers

The distances between the neonate wintering areas and those chosen by their corresponding last sub-adult stages (immature emigration) were highly variable (Table 2, Fig. 7 a & b). Given the criterion that emigration is recognised when the wintering area of last stage sub-adult is more than 150 m from that of their neonate, it would appear that 45 % of males have emigrated compared with only 23 % of females. When the distances between the wintering areas of neonate and last sub-adult stage males and females were compared, the male distances were significantly greater (Mann Whitney 2-tailed test, z = -2.2281, p = 0.025).

Emigration by adults

The distances between the wintering areas of the last sub-adult stage and those selected by the same vipers as first or second year adults (adult emigration) were relatively short (Table 2, Fig. 7 a & b,). When compared, there was no statistically significant difference between the first and second year adults for males (U = 53.5, p >0.05) or for females (U = 25, p >0.05). Consequently, for further testing the data for year one and two adults were combined. When these combined emigration data for adult males were compared with that for adult females, there was no significant difference between them (Mann Whitney 2-tailed test, z= 1.395, p> 0.164), indicating that there was no difference between adult males and adult females in the probability that they would return to the wintering area of the last sub-adult stage.

Comparison between immature and adult emigration

The distances recorded between the wintering areas of the neonates and those of the last sub-adult stages were longer than those between last sub-adult and adults (Table 2) and this difference was statistically significant for both males (Mann Whitney 2-tailed test, z = -3.1168, p = 0.0018) and females (Mann Whitney 2-tailed test, z = -2.587, p = 0.0096). This confirms the immature stages as the most active source of emigration.
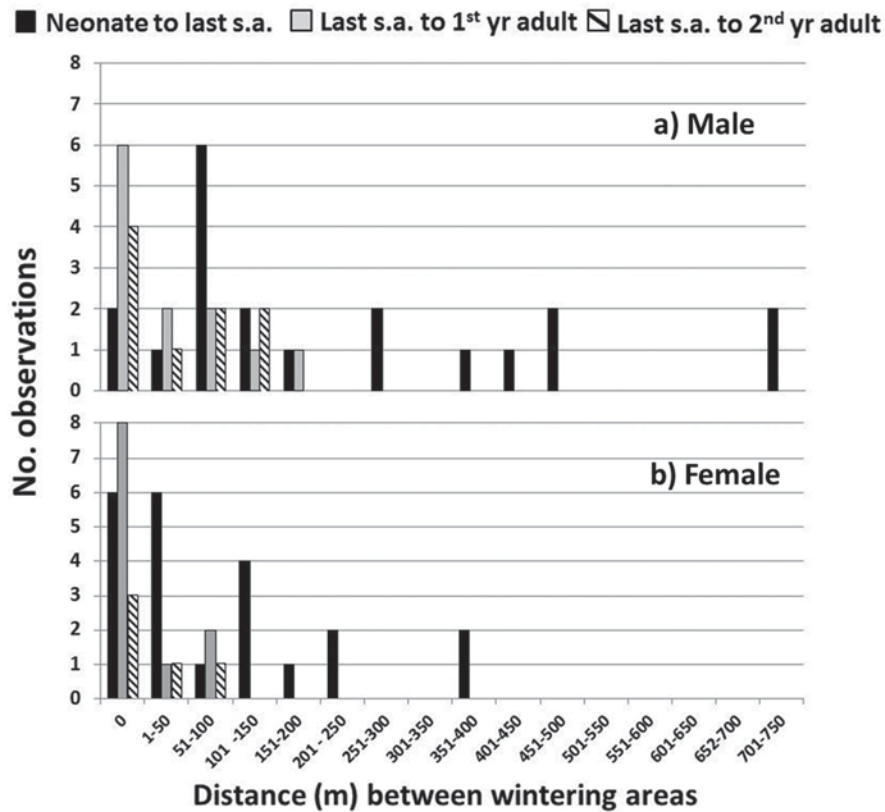
Figure 7. Distances (m) between the wintering areas of neonates and their corresponding last sub-adult stage (s.a.), and between those wintering areas selected by last sub-adult and the corresponding first and second year adults for a) Males and b) Females

Table 2. Summary of distances between the wintering areas of male and female *V. berus* as neonates and in the last sub-adult stage, and distances between the areas selected by same individuals as last sub-adult stage and as first and second year adults

Gender	Stages compared	n	Distance between wintering areas		
			Median (m)	Range (m)	Cases > 150 m
Male	Neonate to last sub-adult	20	131	0 - 738	45 %
	Last sub-adult to adult	21	20	0 - 200	5 %
Female	Neonate to last sub-adult	22	43.5	0 - 434	23 %
	Last sub-adult to adult	16	0	0 - 84	0 %

DISCUSSION

Emigration

For this study, emigration has been defined as the selection of a new wintering area at least 150 m from that used previously. Assessment of the movements of 20 male and 22 female vipers according to this criterion, combined with detailed observation on individuals, reveals that emigration is undertaken mostly by immature stages, in particular neonates and juveniles. There were no observations of juveniles leaving wintering areas and then returning to them; those that had clearly departed selected new wintering areas. By the time vipers had developed to the sub-adult stages, wintering areas appeared to have become more or less fixed. Almost no adult males or adult females adopted wintering areas further than 150 m away from that used by their last sub-adult stage.

Previous accounts of landscape movements by neonates and juveniles are sparse. Emigration by neonates was investigated in an experimental study by Saint Girons (1981) who found that those released early (August) would cover considerable distances (up to 90 m in little over one day) before hibernation but those released later (September) would instead hibernate close to the release site. Similarly, neonate M100 (Case study 1) moved to a wintering area 200 m north-west of where it was first observed in a warm autumn when the vipers were still active even in October. It seems probable that warm autumns and/or favourable summers that result in earlier births will increase the likelihood of neonate emigration. In the case of juveniles, Viitanen (1967) mentions that they "… spend their first summer in the immediate vicinity of the wintering area. In spite of this, only a small number of them find their way back to the common wintering dens", and concludes that "…this age group is especially apt to winter outside the wintering area proper. As they grow older the tenacity to the wintering

area grows stronger." These observations are confirmed by the present study. It would appear that neonates and juveniles have little or no homing instinct (Cases Studies 1, 2 and 4). This may be why many (or most) neonates and juveniles do not venture far from their natal wintering areas. Nevertheless, some juveniles make a springtime dispersal that results in emigration since lacking the homing ability to return to their previous wintering area they are obliged to select a new one. The sub-adults developing from them have sufficient homing abilities to return to the juvenile-selected wintering areas (Cases Studies 1, 2 and 4). Whether or not each year a sub-adult occupies exactly the same hibernaculum in the wintering area was beyond the scope of this study but Viitanen (1967) suggests they do not. There is little evidence that adult vipers contribute to emigration although perhaps occasionally there are adults with poor homing abilities, due perhaps to disease or injury, or as Viitanen (1967) suggests the rapid and early onset of cold weather may occasionally compel individuals to seek a hibernaculum before they have had an opportunity to return to their wintering area.

It is not known why some juveniles disperse over relatively long distances in springtime while most others appear restricted to small areas. An understanding of this difference in behaviour is the key to understanding what drives emigration in *V. berus*. However, it would seem that not all emigrating vipers behave in the same way. A greater number of immature males emigrated than immature females (45 % v. 23 %) and the displacements of males were significantly longer than those of females with the longest for females being about 400 m and for males about 700 m. In the case of the males this may be an underestimate of their emigration potential since the dimensions of the study site preclude recording much greater displacements; if there were greater displacements then the vipers would have moved off site into unsuitable habitat; presumably vipers turn away from this or perish. Such differences are not well known in other snakes but in the case of the slatey-grey snakes (*Stegonotus cucullatus*) hatchling males dispersed away from their release points whereas hatchling females did not, and adult males moved further than adult females (Dubey et al., 2008). It would seem that adult male *V. berus* are naturally more active than females as shown by two recent telemetry studies (Hand 2018; Nash & Griffiths, 2018) where adult males were recorded moving considerably greater distances. Male investment in more active and exploratory behaviour would have selective benefits as there is strong sexual competition between males and Madsen et al. (1993) have noted that the number of matings obtained by male northern vipers is enhanced by the distance travelled during the breeding season. However, this does not explain why pre-reproductive males should also be more active than females. It could perhaps indicate gender differences in foraging strategy which is the case in certain rattlesnakes (Duvall et al., 1990). Further research into this may give deeper insights into the life history strategy of *V. berus*. Viewed from the perspective of the female, there may be strong selective advantages in being more sedentary, perhaps avoiding predation and helping to accumulate the body weight required for successful reproduction.

The observation that emigration is a behaviour of the neonates and juveniles may have some bearing on approaches to conservation. Since these life stages establish the behaviours that become routines in the sub-adults and adults, it would be expected that they are probably more robust colonisers. In this case reintroduction programmes based on young immatures may be particularly successful as they may be more tolerant of being displaced than older individuals. It might be thought that reliance on young immature vipers in a reintroduction programme would risk higher mortality than the use of more mature specimens but recent long-term studies on the mortality rates of *V. berus* on heathland in Belgium suggests that mortality among this group is not especially high (Bauwens & Claus, 2018).

Seasonal migration
Previous accounts of northern viper behaviour suggest that after the adult males have completed their search for mates they move to cooler, moister 'summer areas' to forage and do not return to the wintering area until autumn (Viitanen, 1967; Prestt, 1971; Neumeyer, 1987). An interesting behaviour shown by M39 as an adult was always to return to the wintering area prior to the second moult of the year (34 days earlier in 2014) which usually happens about mid-June. This return happened in three consecutive years suggesting an entrenched pattern of behaviour. Such behaviour has not been reported previously, but in a telemetry study of *V. berus* (Hand, 2018; Hand N., pers. comm.) an adult male made a typical seasonal migration and was back in its wintering area for the second moult (Table 1). Failure to document this behaviour in earlier studies may be due to the fact that moulting snakes are secretive and therefore often remain unseen. In the case of M39 there was a refuge positioned close to the hibernaculum, under which it remained when moulting, so recording this behaviour was easy and in the study by Hand (2018) telemetry facilitated the observation. It seems possible that a return to the wintering area for the second moult is not uncommon; indeed in our study there was evidence that this may be the case in at least 70 % of adult males. Such males may remain unnoticed because they are hidden in deep cover at this time of year (Hand, 2018) and perhaps remain so until there is a need to bask when cooler weather arrives in September. This would give the impression that males have only returned to their wintering areas at this time of year when in fact they were already close by. The early return to the wintering area, typically a warm sunny location, may be connected with reproductive performance. The second moult is believed to coincide with a critical stage in germ cell development; the formation of primary spermatocytes (Volsøe, 1944). The successful proliferation of these cells is essential for the repopulation of the testes prior to hibernation. This will enable spermiogenesis to proceed without delay next spring. However, in some individuals, spermatids may already be present by October (Marshall & Woolf, 1957) and it is tempting to suggest that such males may be those that undergo a third moult, which was the case with M39 in this study. Early advancement in germ

cell production would contribute to male competitiveness per se. It would also have the advantage of apportioning some of the energy costs of sperm production, which are a significant drain on resources in springtime (Olsson et al., 1997), to the prior year at a time when the males are still feeding and now in a warmer zone where physiological process such as digestion and shedding are more rapid. If this is the case then such confinement of adult males to the wintering areas appears equivalent to the confinement of gravid females to the same areas until after parturition. In contrast, it would seem that sub-adult vipers make a slower return to the wintering areas (e.g. Case study 2) and those that have dispersed widely may not return until the autumn.

Direction of movement and homing

The case studies have allowed an assessment of the extent to which the directions taken by emigrating or migrating vipers follow those predicted by the position of the sun as explained by Viitanen (1967), south-west in spring and the north-east in autumn. In the springtime, vipers on the south facing slope (Area 3 in Fig. 1) showed strong westerly (NW, W or SW) displacements as immatures and adults. The behaviour of M39 in 2013 was the 'exception that proves the rule'. In that year the spring weather was cold and damp and the first moult delayed until around 30th April so that migration was late. By this time temperatures had risen steeply so that snake activity could probably be initiated earlier in the day. It would appear that adult males instead of being most active in the afternoon would instead become active earlier in the morning. At this time of day the sun would be in the east and south-east and this would explain the unusual direction of travel. Thus it would appear that the timing of warm weather in springtime can have a distinct effect on the direction of travel of adult male vipers. There were however exceptions to the westward movement. The wintering area of the adult M100 was established on level ground below a south-west facing slope and in receipt of somewhat later sunshine than on the south facing slope. In this situation it dispersed northwards up the valley two years in a row (5 & 7, Fig. 2), presumably following the sun but constrained by the need to keep in the cover of the hedgerows which happen to run in a north-south direction; the importance of such linear features for viper migration has been emphasised by Prestt (1971). Similarly, the migration of adult M39 involved first a typical westward displacement but once this male had moved across the south facing slope to the south-west facing slope the direction of travel was changed and this male also headed northwards up the valley (3 & 10, Fig. 4). Other observations (not detailed here) on males and females at the northern end of valley on a west facing slope were different. The area is backed by shaded woodland and the vipers receive their first direct sunshine from the south, the net directions of their movements were south-west or west. It would seem that at least in springtime, the position of the sun combined with weather conditions, topography, barriers to movement, and corridors of cover have profound influences on the direction of viper movement.

In the autumn (or before in the case of many adult males) migrating vipers return to their wintering areas. The expectation is that their homing behaviour is again mediate by the sun which at this time elicits the opposite reaction to that in the springtime and so results in a reversal of movement back to the wintering areas (Viitanen, 1967). In the case of M100, the return to the adult wintering area involved movement south (Fig. 2), M40 moved north-east (Fig. 3), F81 moved back east (Fig. 6) and in the case M39 there were two returns to the east and one return to the north-west (Fig. 4). It seems that from whatever compass direction vipers left their wintering areas they could make an accurate return journey. This suggests that the simple negative photo-response suggested by Viitanen (1967) is unlikely. For those making the return journey, the actual route used was not clear from the current study. It would have been of interest to know if the vipers had retraced their tracks or used a completely new route. Telemetry studies on at least one case in *V. berus* (Hand N., pers comm.) and in *Natrix natrix* (Madsen, 1984) suggest that return movements do not involve backtracking and investigation of the seasonal migration of rattlesnakes to and from their hibernacula has shown that the movements are directed by orientation to the sun (Landreth, 1973). The ability of sub-adult and adult *V. berus* to return to their wintering areas is impressive and navigation by this species is worthy of closer study especially now that path integration has successfully explained considerable feats of navigation in species of both invertebrates and vertebrates (Biegler, 2000).

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