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Migrations and Seasonal Patterns of Habitat Use in the Adder (*Vipera berus*): Implications for the Conservation and Management of Local Populations

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***Abstract*.—Adders (*Vipera berus*), like many other temperate zone snakes, undertake seasonal migrations between wintering areas and feeding grounds. During a mark-recapture study in a large population in northern Belgium, we obtained detailed information on both habitat types and the migrations between them. Wintering areas were located in heathlands on infertile, sandy soils, which offer suitable locations for hibernation and optimal thermal conditions during specific periods in the active season. Foraging grounds were located outside of heathland areas and encompassed a wide variety of habitats that sustained higher prey densities. Adult males remained in the wintering areas in early spring and then in May migrated toward the foraging grounds, where they resided until the end of September. The breeding females resided in the wintering habitats from May through August, and they were observed in the feeding areas only during the short pre- and post-pregnancy periods. Immature Adders spent a large portion of their time in the feeding grounds. During their seasonal migrations, Adders moved 100–500 m. Adders tended to show fidelity to both hibernation sites and feeding areas. Current efforts to safeguard Adder populations focus almost exclusively on wintering areas. The information we present here highlights the importance of feeding areas as a vital component of Adder habitat. We argue that conservation and management actions will benefit from studying and considering the status of both wintering and feeding grounds and the migration routes between them.**

Key Words.—foraging; heathlands; hibernation; philopatry; seasonality; displacements

Introduction

Animals counter seasonal changes in environmental conditions through various behavioral and physiological responses. Most temperate zone reptiles respond to unfavorable weather conditions during fall and winter by seeking refuge underground and entering hibernation. During the active period, some species also show seasonal variation in movement patterns in response to spatio-temporal variation in prey, mates, and other resources (Gibbons and Semlitsch 1987; King and Duvall 1990; Russell et al. 2005). This variation may include temporal changes in the frequency of short-term movements to increase mating opportunities (Madsen et al. 1993; Brito 2003) and seasonal long-distance migrations between winter denning sites and feeding ranges (Larsen 1987; Clark et al. 2010; Tetzlaff et al. 2017; Lomas et al. 2019; Harvey and Larsen 2020).

The Adder (*Vipera berus*) provides a typical illustration of the different behavioral responses and movement patterns to changes in weather conditions, mating opportunities, and food availability. Adders typically gather during the fall in wintering areas where they hibernate. After emergence from hibernation and following their spring molt, adult males undertake short-term displacements in search of receptive females (Viitanen 1967; Prestt 1971; Madsen et al. 1993). After the termination of mating activities, adult males and nonreproductive snakes undertake seasonal migrations to their feeding or summer grounds (Viitanen 1967; Prestt 1971; Madsen et al. 1993). These movements were first documented by Vainio (1931), Viitanen (1967), and Prestt (1971) and were later reported by other authors (Phelps 1978; Neumeyer 1987; Hodges and Seabrook 2019; Otte et al. 2020). Although such seasonal migrations and alternate use of distinct habitat types seem ubiquitous, studies of Adder ecology, behavior, and conservation typically focus on the wintering grounds, where Adders concentrate in the highest densities and are most easily observed (Madsen and Shine 1992, 1993; Forsman 1993a; Gardner et al. 2019; Bauwens and Claus 2021). On the contrary, due to their lower detectability, Adders are seldom studied in their feeding areas (we use the terms feeding areas or foraging grounds instead of the less specific term summer areas). Consequently,

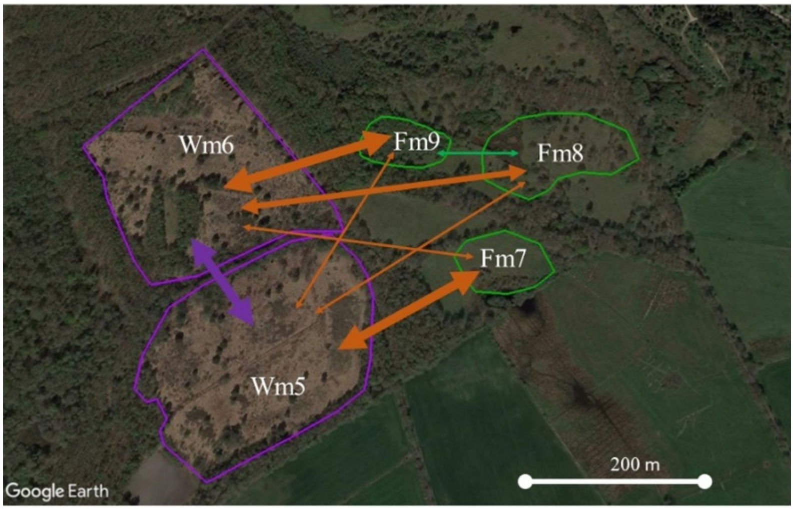

Figure 1. Map of the study plots showing locations of the two wintering (Wm5, Wm6) and three foraging areas (Fm7, Fm8, and Fm9). Arrows depict the observed movements by individual Adders (*Vipera berus*) among the distinct plots; the width of the arrows is proportional to the number of observed movements (narrow: < 10 displacements; intermediate: 15 displacements; wide: 25–30 displacements).

detailed information on the characteristics of the feeding grounds and of the migratory movements towards them is often fragmentary and rarely based on individual data (but see Hodges and Seabrook 2019). The scarcity of studies in the feeding grounds results in incomplete and biased information on the annual activity cycle and the life history of the Adder.

Here we report on a long-term and intensive mark-recapture study of a large Adder population in northern Belgium (Bauwens and Claus 2018, 2019a,b), during which we collected extensive data on habitat use and movements of individual snakes. Because the wintering and feeding habitats have visibly different characteristics, we could classify displacements of individual Adders *a priori* as either seasonal migrations, as dispersal movements, or as wandering movements within the home range. Here, we only consider the seasonal migrations.

Our objectives are two-fold. First, we provide detailed information on the seasonal variation in the use of wintering and feeding grounds by different age and sex groups. We also present detailed information on seasonal migrations between habitat types by individual snakes. Second, we assess the importance of feeding grounds for the conservation and management of local Adder populations. Adder conservation projects typically focus on wintering habitats, while feeding grounds are often unexplored and therefore rarely considered in population studies and management plans. We argue that by considering the importance of both wintering and feeding grounds, conservation actions can become more effective, and potentially reverse declines in Adder populations.

Materials and Methods

Study species and study area.—The Adder is a small, stout-bodied venomous snake with a vast distribution area that encompasses large parts of Europe and Asia (Otte et al. 2020). Adders are live-bearing, and females typically reproduce bi- or triennially. The young are born from August to September. Adders exhibit delayed maturity, with males first engaging in reproductive activities during their fourth active season, and females typically during their fifth active season. Detailed information on the life history, demography, and annual activity cycle of the species can be found in Prestt (1971), Madsen and Shine (1993), Madsen et al. (1993), Bauwens and Claus (2018, 2019), and Otte et al. (2020).

Our global study area is the Groot Schietveld, a military exercise zone (area = 1,570 ha, 51°21’N, 4°35’E, province of Antwerp, Belgium). The central part of this lowland area (elevations range 18–25 m above sea level) is a mosaic of various types of Atlantic Heathland, moors, and fens. Along the borders, there are Oak (*Quercus* spp.)-Birch (*Betula* spp.) Forests, Scots Pine (*Pinus sylvestris*) Plantations, and Alder (*Alnus* spp.) Swamp Forests. The area is surrounded by cultivated grasslands and residential areas.

In this paper, we present data collected between 2011 and 2020 in five study plots (Fig. 1) located in the northernmost part of the global study area, where we obtained the most detailed information on seasonal migrations and use of habitat types. We classified the plots as wintering (Wm5 and Wm6, area size: 4.5 and 6.1 ha) or foraging areas (Fm7, Fm8 and Fm9, area size: 0.7, 1.2 and 0.6 ha) according to their vegetation characteristics. The two neighboring wintering sites are typical Atlantic Heathlands covered by diverse and dense vegetation, dominated by dwarf shrubs of Common Heather (*Calluna vulgaris*), Cross-leaved Heath (*Erica tetralix*) and Bog-myrtle (*Myrica gale*), tussocks of Purple Moor Grass (*Molinia caerulea*), patches of mosses (including *Sphagnum* spp.), and some localized groups of scattered Birch (*Betula pubescens*; Supplemental Information Fig. S1). They are separated from each other by a narrow (10–30 m) stretch of Alder Swamp Wood along a temporary brook (Fig. 1).

The foraging sites designated as Fm8 and Fm9 are made up of small patches of abandoned pastures and arable fields, which are mixed with rugged edges of hay fields that have thickets of blackberries (*Rubus* spp.; Supplemental Information Fig. S2). Additionally, the edges of Oak-Birch Forests and Alder Swamp Forests also make up these plots. The Fm7 study plot is a hayfield with a rugged edge that has blackberry thickets and Soft Rush (*Juncus effusus*) bordering an intermittent pond (Supplemental Information Fig. S2). Wintering and foraging areas are separated by Oak-Birch and Alder Swamp forests (Fig. 1).

Field sampling.—We collected data during a citizen science project led by the authors and trained volunteers. Our methodology followed the classic capture-mark-release-recapture approach, adhering to a strict field protocol. We visually located Adders while walking slowly and erratically through a study plot. We captured them by hand, using leather gloves for protection, and released them immediately after handling. Individual identification of Adders was facilitated by taking a digital photograph of the upper side of the head (Bauwens et al. 2018). At each encounter, we recorded the date, time, exact location (GPS coordinates), sex, snout-vent length (SVL, to the nearest 5 mm), body mass (to the nearest 1 g), shedding status, and breeding status of females. Determining the breeding status of adult females involved palpating the abdomen to detect oviductal eggs or developing embryos from May to August, as well as observing signs of postpartum body condition, such as the presence of a flaccid abdomen and extensive skin folds in August to October. Additionally, we identified instances of recent food consumption by the presence of a visible swelling of the mid-body (a stomach bolus), palpable remnants of prey (bones) in the digestive tract, and/or voiding of solid feces. We classified adders into one of three age classes: (1) newborns, which were in their first active season (August to October); (2) young/immature animals in their second, third (both male and female), or fourth (female) active years; and (3) adult animals in at least their fourth (male) or fifth (female) active years. The assignment of age class was based on previous capture history and/or SVL criteria inferred from the growth trajectories of known-aged Adders as outlined in previous work (Bauwens and Claus 2018).

We visited all plots several times per year during favorable weather and throughout the active season of the Adders (late February to late October). For every visit to a study plot, we documented the date, start and end times, and the number of trained field workers involved. This information allowed us to calculate the total number of search hours (i.e., sampling effort) per study site and specific time intervals (e.g., half-month, year). The data presented in this study were collected over 1,102 search hours.

Data handling and statistical analyses.—We quantified seasonal variation in general activity levels of the distinct age/sex classes in the two habitat types by estimating encounter rate, i.e., the number of captures per search hour. The high frequency of visits to study sites throughout the active season of the Adders allowed us to estimate the encounter rate per half-month, providing a rather fine-grained time-dependent index. We examined the movements of Adders using the location data from two successive captures of an individual snake. We classified a movement as migratory when the displacement was between a wintering and foraging study site (WF) or the other way around (FW), or as nonmigratory when the snake had moved within or between wintering (WW) or foraging (FF) habitats. Hereafter, we focus on migratory movements (i.e., seasonal migrations). We calculated movement distance as the straight-line distance between the two successive capture locations. We estimated the duration of the displacement by the number of days between the capture dates; when the capture dates were in different years, we discounted 150 d per yearly interval to account for inactivity during hibernation. We estimated body length (SVL) as the average of the values recorded at the beginning and end of the recapture event.

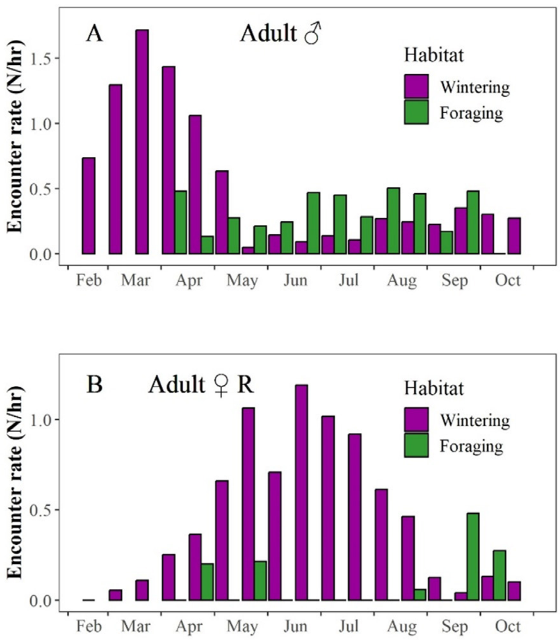

Figure 2. Seasonal variation of detectability (number of adders encountered/field hour) in adult male (top panel) and reproductive adult female (bottom panel) Adders (*Vipera berus*) per half-month in wintering and foraging habitats in Belgium. Based on 654 and 407 observations of males and reproductive females, respectively.

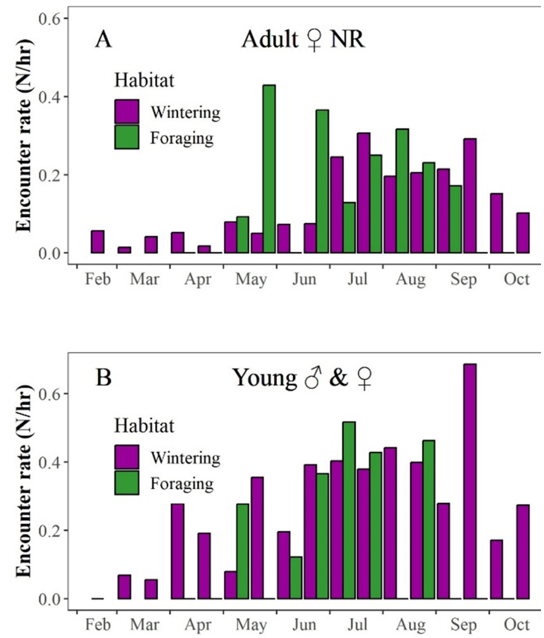

Figure 3. Seasonal variation of detectability (number of adders encountered/field hour) in non-reproductive adult female (top panel) and immature (bottom panel) Adders (*Vipera berus*) per half-month in wintering and foraging habitats in Belgium. Based on 152 and 302 observations of non-reproductive females and immature adders, respectively.

We analyzed the variation in movement distance (log10-transformed) of seasonal migrations as a function of sex, SVL, and duration of displacement using general mixed effects modeling methods. Because we recorded several individual Adders to have undertaken multiple movements, we included the code of the individual as a random effect. We used the lme4 package (Bates et al. 2015) in R v4.0.2 (R Core Team 2023) to fit the fully additive global model and various constrained versions of it, including a null model (intercept and random effect only).

We restricted the analysis of recent food intake occurrences to the period May to October when the vast majority (95%) of 336 incidences occurred. We excluded breeding females as they feed only occasionally (Bauwens and Claus 2019c). We analyzed the incidence of recent feeding as a function of habitat type and age-sex class using Logistic Regression, exploring the fully interactive model and various constrained versions of it. To find the most parsimonious model within a set, we used an information theoretic approach and ranked the models according to the sample-size-adjusted Akaike's Information Criterion (AICc; Anderson 2008) using the AICCmodavg package (Mazerolle 2015) in R v4.0.2 (R Core Team 2023).

Results

The seasonal pattern of encounter rates differed significantly between wintering and foraging grounds across all age and sex classes. Newborns were exclusively observed at wintering sites and will not be discussed in more detail. Adult males were predominantly sighted at wintering sites from mid-February to mid-May, but thereafter, from mid-May to the end of September, their encounter rates were highest in the foraging grounds (Fig. 2). In contrast, breeding females exhibited an inverse pattern: during the period from May to August, their encounter rates were highest in wintering habitats, while observations in the foraging grounds were limited to the pre- and post-breeding periods (Fig. 2). The seasonal patterns of habitat use were similar between nonbreeding females and immature adders (Fig. 3). During March-April and September-October, they were exclusively observed in the wintering sites, while from May to August they were encountered at roughly equal rates

Table 1. Observed number of displacements and number of individual Adders (*Vipera berus*) involved (in parentheses) for movements between a wintering and a foraging study site (WF and FW) and between two different feeding (FF) or two distinct wintering (WW) sites in males and females from Belgium.

Sex	WF	FW	FF	WW	Total
Males	28 (24)	32 (26)	3 (3)	21 (18)	84 (49)
Females	15 (11)	18 (14)	0 (0)	8 (7)	41 (23)

in both feeding and wintering grounds (Fig. 3). It is worth noting that their encounter rates were generally lower than those of adult males and reproductive females (Figs. 2 and 3).

We observed 125 displacements between the distinct study plots, involving 72 individual Adders (Table 1). The number of observed movements and the number of individuals involved was higher for males (Table 1). There was a clear tendency for snakes wintering in area Wm6 to migrate to study plot Fm9 (or Fm8), while adders hibernating in plot Wm5 migrated predominantly to site Fm7 (Fig. 1).

We identified 48 individual Adders that were observed to undertake one to eight seasonal migrations over time intervals ranging from one to six active seasons. Among Adders that were observed to undertake multiple seasonal migrations, 22 of 28 (79%) individuals moved between the same pair of wintering and feeding habitats; the number of repeated seasonal movements in these individuals was 61 of 68 displacements (90%). In addition, nine of 12 (75%) individual Adders that made displacements in foraging areas always did so within the same study plot; in these individuals, the number of displacements within the same feeding site was 24 of 27 (90%). We compared the distribution of the SVL of Adders that undertook seasonal migrations to that of individuals that had moved between the two wintering plots (Fig. 4). This explorative graphical examination indicated that individuals of all sizes were documented to undertake seasonal migrations.

Virtually all recorded seasonal migrations covered distances between 100 and 500 m (median = 269 m; Fig. 5). The model that included only the intercept and the random effect (i.e., individual) was strongly favored relative to the other models (Supplemental Information Table S1), indicating that Adders of both sexes and all body sizes moved similar distances during their seasonal migrations. The most parsimonious model of feeding incidence included the effects of habitat type and age-sex class, but without an interaction between the main effects (Supplemental Information Table S2). In all age-sex classes, the relative number of recently fed snakes was higher in the foraging habitats (Fig. 6). The Logistic Regression coefficient for habitat type was 0.47 (95% confidence interval = 0.01–0.95), indicating that the odds of finding a recently fed Adder were 160 % higher in feeding than in wintering habitats.

Discussion

Our findings confirm that Adders split their annual active cycle over two spatially separate and ecologically distinct habitat types and undertake seasonal migrations between them. Unlike several other studies in which inference is based on the temporary absence of Adders in one habitat type, our conclusions are based on concurrent, full active

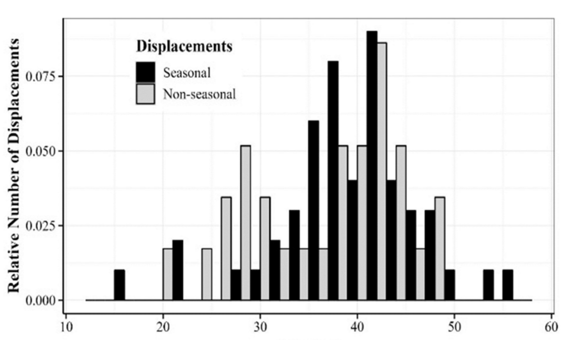

Figure 4. Distribution of snout-vent-lengths (SVL) of Adders (*Vipera berus*) in Belgium observed to undertake seasonal and non-seasonal displacements. As several individual snakes were recorded to have undertaken multiple movements, and thereby possibly introduced pseudoreplication bias, we used only the data for the first observed displacement per individual.

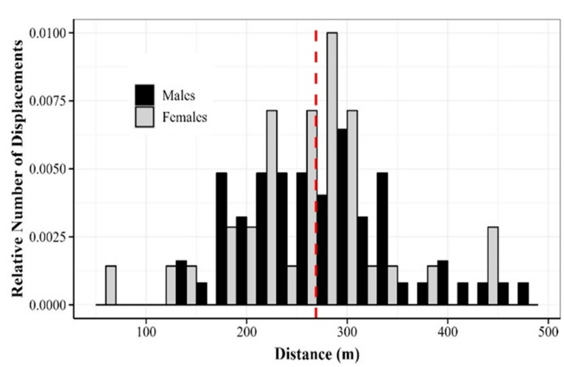

Figure 5. Distribution of distances (m) covered by male and female Adders (*Vipera berus*) in Belgium during seasonal migrations. The vertical red dashed line indicates the median distance (= 269 m).

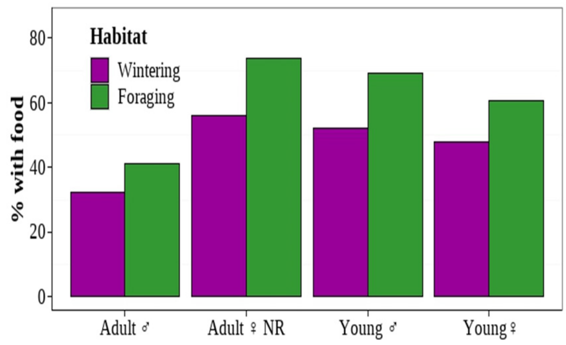

Figure 6. Relative frequency of Adders (*Vipera berus*) of distinct age/sex classes with visible signs of recent feeding in wintering and foraging habitats in Belgium.

season observations of Adders in both wintering and foraging sites. Recaptures of individual snakes confirmed their migratory movements between the two habitat types and, in addition, demonstrated that these movements were repeated over multiple years. The quantitative information presented here highlights the importance of feeding areas as a vital component of Adder habitat, an aspect that has been too often underrated.

Characteristics of the wintering and feeding areas.—In our study area, and many other parts of northwestern Europe, the wintering sites of the Adders are predominantly located in various types of Atlantic Heathland. These areas are generally characterized as low-productive ecosystems in dry, sandy, and nutrient-poor soils (Loidi et al. 2010; Løvschal and Damgaard 2022). Within these areas, Adders have a clumped distribution, being confined to spatially concentrated locations with specific microclimatic characteristics. These locations offer adequate conditions during two important episodes of the annual cycle.

The first episode is the hibernation period, which lasts 5–6 mo in our population. Suitable hibernacula must buffer the Adders against subzero temperatures and flooding (Viitanen 1967; Prestt 1971; Andersson 2003). Such locations are seemingly locally scarce, as deduced from them being used year after year and sometimes by large numbers of Adders (Viitanen 1967; Andersson 2003; Lenders 2003).

The second episode concerns periods within the active season when Adders have special demands to maintain body temperatures at near-optimal performance levels. This is particularly relevant for adult males following emergence from hibernation when precise thermoregulation at high body temperatures stimulates the production of sperm (Nilson 1980). Thus, during early spring, male Adders are typically found at distinctive locations near the winter shelters (Viitanen 1967; Prestt 1971; Madsen et al. 1993), where they bask overtly, sometimes forming small aggregations of piled up and loosely intertwined snakes (Bauwens and Claus 2021). Comparable behaviors are also observed in gravid adult females, which typically reside in wintering habitats during the summer months. They bask openly in characteristic microhabitats, especially on cloudy days, when maintaining body temperatures above ambient levels is essential to accelerate the development of the embryos (Lourdais et al. 2013). In short, wintering areas provide suitable locations for hibernation and, during the active season, thermally favorable microclimates when demands for adequate thermoregulation are high.

The foraging grounds are quite different from the wintering habitats in our study area and elsewhere. They are located near, but outside of, heathland areas and encompass a wide variety of habitat types (Viitanen 1967; Prestt 1971; Völkl and Thiesmeier 2002; Hodges and Seabrook 2019; Otte et al. 2020). An essential and common characteristic of feeding habitats is that they have relatively high levels of soil fertility, either naturally or because of past or current fertilization. Consequently, they sustain higher levels of primary productivity than the nutrient-poor heathlands and support high densities of mice and voles, which are the main food types of Adders (Viitanen 1967; Prestt 1971; Luiselli et al. 1994; Völkl and Thiesmeier 2002). Consequently, the proportion of Adders with food in their stomachs, an index that addresses their rate of food consumption, was considerably higher in the feeding areas than in the wintering habitats. The importance of foraging areas for food acquisition is further accentuated by adult males and reproductive females refraining from eating while they reside in the wintering areas (Viitanen 1967; Prestt 1971; Bauwens and Claus 2019c; Otte et al. 2020).

In general, the encounter rates of the Adders were lower in the feeding sites than in the wintering areas. Several factors contribute to this difference. First, Adders are less spatially concentrated within the foraging grounds compared to wintering habitats. That is, they are less restricted to specific and easily recognizable microhabitats. Second, the relatively high operative temperatures during the summer months reduce the need for Adders to bask extensively, reducing their detectability. Furthermore, during sunny days, the operative temperatures often exceed the critical thermal maximum temperature of Adders (Worthington-Hill and Gill 2019). This may deter Adders from being active in open areas and may prompt them to seek refuge within dense and cool vegetation or even underground (Hand 2018). Third, the limitations of available time and field searchers hindered our ability to survey the feeding areas more intensively. Therefore, it is highly likely that we detected only a limited fraction of Adders in the foraging grounds. This is supported by the sightings of Adders by occasional observers at locations that we did not or only sporadically visit (Supplemental Information Fig. S3). The scattered distribution of the foraging grounds across a wide expanse is likely the main reason they remain undetected in many areas. Locating them is facilitated by examining areal maps of the surroundings of wintering habitats. Candidate sites can then be explored at favorable times, or with the aid of artificial refuges (Hodges and Seabrook 2019). For a more comprehensive and detailed understanding, telemetry studies offer valuable insights (Hand 2018).

Temporal patterns of habitat use.—Our results confirm the patterns of seasonal habitat use by adult males and females as reported by other studies (Viitanen 1967; Prestt 1971; Bauwens and Claus 2019b; Hodges and Seabrook 2019; Otte et al. 2020). Importantly, our observations also shed light on the habitat use patterns of immature Adders, a group that is often overlooked due to its elusive nature and low capture probabilities (Bauwens and Claus 2018, 2019b). Neonates were exclusively observed in wintering areas from their birth in August until the onset of their first hibernation period. During their second active season, however, we observed their presence from May onwards in the same feeding areas as the adult snakes. This suggests that they migrate to feeding grounds shortly after emerging from their first hibernation and subsequently spend a significant portion of the ensuing active seasons in these areas. Adult vipers also stay there for almost half of each active season (males) or during one in two active seasons (females). This suggests that Adders may spend more time during their life in foraging habitats than in heathland wintering areas. This underscores the importance of paying more attention to the feeding grounds in studies of Adder ecology and conservation efforts.

Seasonal migrations.—We observed Adders migrating 100–500 m between their wintering and feeding areas. These values are consistent with those reported in other studies (Viitanen 1967; Hodges and Seabrook 2019), although distances of up to 1,200 m have been documented (Viitanen 1967). It is important to note that logistical constraints imposed limits on the areas covered by our searches, which in turn may have restricted the displacement distances that we could detect.

Most of the Adders that undertook consecutive seasonal migrations did so between the same pair of wintering and foraging sites, consistently returning to the same locations year after year. These observations not only confirm that Adders are philopatric to their wintering grounds (Viitanen 1967; Prestt 1971; Völkl and Thiesmeier 2002; Otte et al. 2020) but also demonstrate fidelity to their feeding areas. The method by which Adders navigate between distinct habitats remains unknown; however, in situations where visual information channels are obstructed, such as in densely vegetated habitats, chemical cues probably become particularly relevant. Other species of snakes use scent trails to navigate to suitable habitats (Russell et al 2005). The mechanism of following the pheromone trails deposited by conspecifics, such as demonstrated in juvenile rattlesnakes (Graves et al 1986), is particularly relevant for immature snakes while undertaking their first seasonal migration.

Implications for conservation and population management.—The increasing concern for the conservation and management of declining Adder populations, as highlighted in recent literature (Edgar et al. 2010; Stumpel and van der Werf 2012; Whiting and Booth 2012; Gardner et al. 2019; Worthington-Hill and Gill 2019), is an important acknowledgement of the vulnerability of the species. Current conservation efforts predominantly target wintering habitats, including the maintenance and creation of hibernacula. This emphasis is understandable given that the availability of suitable hibernacula is crucial for winter survival. In addition, key reproductive activities (mating, pregnancy, and parturition) occur in wintering areas. Moreover, the conspicuous basking of adult male Adders during early spring makes them more visible to human observers. This increased visibility also heightens the risk of persecution by malicious individuals, which has been identified as a significant factor contributing to the decline of Adder populations in Britain (Gardner et al.

2019). In broader terms, it is assumed or suggested that high detectability by humans is associated with increased susceptibility to visually hunting predators, potentially leading to higher mortality rates in wintering areas (Andrén 1985; Bonnet et al. 2002; Sperry and Weatherhead 2009; Lourdais et al. 2015). This idea is not supported, however, by an extensive analysis of our long-term mark-recapture data, which did not provide evidence for seasonal differences in mortality rates in either male or female Adders (Bauwens and Claus 2019b). Hence, demographic data do not indicate that mortality risks in Adders is more elevated in wintering areas.

The findings reported here, building upon the work of Viitanen (1967) and Prestt (1971), emphasize that a singular focus on one habitat type oversimplifies the life cycle of Adders. The observed migratory movements have significant implications for population dynamics and influence conservation and management strategies. Several key aspects deserve consideration in this regard. First, it is crucial to recognize that Adders spend significant portions of their annual cycle and lifespan in the foraging grounds. This alone merits increased attention to these habitats. Any degradation or loss of these sites is likely to have far-reaching impacts on Adder population dynamics. Without adequate information on the location and condition of these foraging habitats, changes can go unnoticed. Overlooking the status of these areas could lead to population declines being erroneously attributed to perceived negative processes in wintering areas. Consequently, conservation and management efforts can be misdirected, failing to address the actual causes of population decline and resulting in ineffective outcomes.

Second, it is important to note that Adders primarily feed in the foraging habitats. Fluctuations in the abundance of voles, a key prey species for Adders, have been demonstrated to impact survival rates and population numbers (Andrén 1982; Forsman 1993b; Lindell and Forsman 1996). It is crucial to understand that fluctuations in food availability in foraging habitats can lead to year-to-year variations in Adder abundance at their wintering grounds, where they are typically surveyed. Third, in our study area, the feeding grounds are spread over a wide range. Even partial destruction or deterioration of these habitats could have adverse effects on demography. We observed individual snakes that showed site fidelity, returning to the same feeding locations in different years. Therefore, alterations to these sites, even during periods when Adders are absent (e.g., during hibernation), could negatively affect the behavior of Adders. Consequently, changes in the conditions of the feeding grounds are likely to influence population parameters as much as deterioration in the wintering habitats. Additionally, obstruction of migration routes between wintering and feeding grounds may lead to severe population declines (Madsen and Ujvari 2011).

In short, threats to Adders may not be as seasonal or location-specific as often assumed. We hence argue to consider a broader range of factors and threats across the habitats and life cycle of Adders. By acknowledging the importance of both wintering and feeding grounds, as well as the routes that connect them, conservation strategies can become more effective and potentially reverse declines in Adder populations. These considerations apply particularly to projects of trans- or relocation, which often fail to achieve their goals (Nash et al. 2020).

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Katja Claus obtained her M.S. in Biology (1986) at the University of Antwerp, Belgium, and had a keen interest in reptiles, particularly snakes. She works for the Flemish government on defragmentation measures of transport infrastructure. In 2000, Katja initiated a volunteer program to study a large population of Adders in northern Belgium. Over the years she trained and coordinated several co-volunteers who participated in the field and office work. (Photographed by Dirk Bauwens).