

# **Adders (*Vipera berus*) increase movement and shift habitat after translocation**

## **– an example in Bever, Swiss Alps**

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## Abstract

Increasing habitat fragmentation and habitat loss threaten many species by reducing size, connectivity and quality of habitats. A population of adders currently occupies fissured stones on an old dam along the river Inn in Bever (Graubünden, Switzerland). This favourable habitat will be destroyed during a future revitalisation project. From April to July 2016, thirty-five adders were caught, measured, equipped with a transmitter and localised with VHF-Telemetry. Between June and July, seven of them were checked after they were translocated 1 km upstream. Because many adders lost their transmitter, causing limited numbers of localisations, the data of only five translocated and seven resident adders were used to investigate possible differences in microhabitat use, movement and thermoregulation. These parameters were also compared among periods to test for possible confounding effects. Resident adders preferred stones and avoided ground vegetation. In contrast, translocated adders lost their avoidance toward ground vegetation and began to show avoidance toward stones. Home range size averaged at 0.22 ha for resident adders. Movement significantly increased from 7 m/day for resident adders to 17 m/day for translocated adders. Translocation did not affect thermoregulation. Body temperature of the adders approached external temperatures with increasing cloud cover aerial temperatures and toward late afternoon and September. While most adders lost their transmitter, adders

equipped in May lost their transmitter soonest maybe because they move extensively to mate. Adders likely increase movement and shift preferred microhabitat, because at the translocation site they are naive about position and configuration of suitable structures to bask or find shelter and prey. For a complete evaluation of the impacts of the translocation, health and location of the translocated adders has to be determined with recapture or telemetry in the future. To enhance translocation success, adders should be translocated after hibernation to similar microhabitats preferably close or within a 1 km radius of the initial location.

Key Words. — Microhabitat selection; Home range; Movement distance; Thermoregulation; Conservation; Viperidae; Transmitter loss

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## **Dedication**

I dedicate this thesis to my mother, who passed away October 2016 and holds a special place in my heart forever. Despite her fear toward snakes she always supported my research and worried for me till my fieldwork was finished. Without her influence during my childhood I possibly would never have wanted to become a biologist.

## **Introduction**

Habitat fragmentation, habitat loss and habitat degradation reduce size, quality and connectivity of habitat patches with increasing rate and magnitude, hence threaten a broad range of species, such as plants (Tilman and Lehman, 2001), corals (Caley, Buckley and Jones, 2001), insects (Hendrickx et al. 2007; Brown and Paxton, 2009) amphibians (Cushman, 2006), birds (Recher, 1999), and reptiles (Gibbon et al. 2000; Graitson et al. 2008; Todd et al. 2010). Human land-use changes often lead to initial loss and fragmentation (Diaz et al. 2006), because agriculture (Lande, 1998; Seddon et al., 2012), urban areas (Lande, 1998) or roads (Ashley and Robinson, 1996) replace terrestrial habitat (Tilman and Lehman, 2001). In addition, dams, roads, draining for and chemicals from urban areas can change terrestrial (Lande, 1998) and aquatic environments (Sheaves et al. 2014). Possibly global warming magnifies such processes by changing species communities, including the structure of vegetation, because changes in temperature and precipitation patterns alter the distribution of organisms (Tylianakis et al. 2008; Gilman et al. 2010). Such processes are especially worrisome when affecting species-rich systems called biodiversity hotspots.

## **Revitalisation**

The idea of restoring degraded habitat emerged in the last few decades and restoration goals shifted from simply preserving habitat patches to protect their dynamics, integrity and services; by doing so restoration should warrant that such processes contribute to healthy ecosystems in the future (Hobbs and Harris, 2001). In a similar vein, restoration should promote a self-sustainable, resilient system, able to buffer stress-inducing impacts (Palmer et al. 2005). Together with several terrestrial and aquatic systems, river floodplain areas stick out as remarkably species-rich systems (Malanson, 1995). To restore degraded floodplain areas around rivers, revitalisation and restoration projects are integrated into conservation to reestablish accompanying aquatic and terrestrial communities (Panek et al. 2008). Involved revitalisation companies may accomplish this in collaboration with scientists by matching the flow gradient with least degraded reference systems, by increasing the water quality and by reducing extinction rates of freshwater species (Bernhardt et al. 2005). Therefore decision-makers often evaluate revitalisations as beneficial to overall biodiversity. Such evaluations, however, might tempt us to oversee negative consequences on the level of endangered species and populations. Such unintended consequences caused by revitalisation, where some animals may vanish completely locally, rarely emerge in the literature. Especially construction phases within such projects include disruptions and destruction (Muotka and Laasonen, 2002), and thus impact the site of revitalisation, for example by inducing loss of native vegetation. Nevertheless the impact should

be minimised in the long-term (Palmer et al. 2005).

## **Translocation – a brief review**

There are other possibilities to protect species from habitat alteration and resulting declines than restoring one specific site. For instance, conservationists can translocate certain individuals or populations away from threatened areas to other suitable habitats in proximity of their origin to guarantee their conservation. Translocations may help to restore populations, create new populations or move animals away from human disturbances and areas of human-wildlife conflict (Wolf et al. 1996; Bradley et al. 2005).

Humans deliberately moving organisms from one site in the wild or captivity to another site in the wild characterises all translocations (IUCN, 2013).

Implementing translocations includes many obstacles. In the past many translocation programs missed to consider the habitat quality at the new site or moved too few individuals and hence failed (Griffith et al. 1989; Dodd Jr and Seigel, 1991; Germano and Bishop, 2009). Competition at the new site is another factor that can interfere with the success rate of translocations (Germano and Bishop, 2009) and Lande (1998) included species translocation as a cause of species decline. Animals often try to return to initial sites (Reinert and Rupert Jr, 1999), possibly induced by low quality habitat and competition, and as a consequence reproductive success and survival

probabilities are reduced (Roe et al., 2010). Thus changes in animals' movement behaviour can worsen problems of translocation. Different studies assessed translocations of a broad range of predator species (bears, wolves, lions, eagles), because they killed livestock. Huge proportions of these translocated predators showed increased movement distances (Linnell et al. 1997 and references within). A study on badgers, however, revealed that survivorship and home range sizes of translocated badgers is similar to non-translocated badgers (Kinley and Newhouse, 2008), although they missed to give distances of translocations. Applied to reptiles and amphibians translocations predominately fail; only 19 % of herpetofauna translocations were reported to be successful (Dodd and Seigel, 1991), less than half compared to mammals and birds (Griffith et al. 1989). But because different studies reported variable success (Dodd and Seigel, 1991) this success rate could be biased. A later review came to a increased success rate of 41% for herpetofauna translocation (Germano and Bishop, 2009), hence equal to mammals and birds. Generally speaking, translocations are highly problematic because animals interact in a complex way with their environment and the success rate is highly variable (Sullivan, 2015).

## **Herpetofauna – Conservation**



Amphibians and reptiles have a rather low vagility (Colino-Rabanal and Lizana, 2012) and normally, snakes are an exception, occur on narrower geographical ranges than birds and mammals. (Anderson and Marcus, 1992). These factors expose them more to anthropogenic pressures. Moreover overexploitation threats reptiles stronger than amphibians (Gibbon et al. 2000; Ducatez and Shine, 2016). Additionally, global warming will affect populations of ectotherms, like reptiles and amphibians, in a stronger way than mammals or birds because their whole behaviour is tightly connected to thermal conditions within their habitats (Buckeley et al. 2012). Because of such threats conservationist should further improve and increase the knowledge of species richness locally and globally, as well how these species are precisely affected by human disturbances. Such information would be necessary for sustainable protection and proper rescue plans (Seddon, Armstrong and Maloney, 2007).

The conservation status of Swiss amphibians and reptiles is also alarming. For example the European pond turtle (*Emys orbicularis*) was declared extinct in Switzerland (Sommer et al. 2007) while now some small populations persist and the European pond turtle belongs to critically endangered species. It is not clear, however, how much native individuals contribute to these populations (Mosimann and Cadi, 2004). Many other Swiss reptiles face increased extinction risks and all eight species of snakes are considered as

threatened in Switzerland (IUCN 2005).

Conservation biology should reach politicians and the public. Because people care more for cute or known animals, such species are easier to protect and research on these species benefits from more funds for financial aid. Snakes, for example, face more opposition by people than eastern mountain lions and bald eagles (Kellert, 1985). Similarly the intention to support snakes is limited compared to mammals (Knight, 2008). Explanation could include the observation that western myths and religious tales, such as in the bible, often demonise snakes or that fear toward snakes could have evolved in mammals as adaptation (Öhman & Mineka, 2003), thus illustrating that snakes scare and excite humans since ancient times (Kellert and Wilson, 1993; Prokop, Özel and Usak, 2009) and maybe even its precursors.

Notwithstanding snakes, like other predators, may control prey populations (López-del-Toro et al., 2010), but with a reduced food intake rate (Beebee and Griffiths, 2000) that could be compensated by higher population densities (Arnold and Ovenden, 2002; Bonnet et al., 1998). Nonetheless snakes may generally only regulate sparsely distributed prey (Nowak, Theimer and Schuett, 2008) and the occurrence of other predators like birds and foxes increases the complexity of these interactions. Hence, only if snake species disappear locally, we may understand their ecological role within these

complex communities.

## **The problem in Bever**

In Bever (Graubünden) a revitalisation project is carried out focussing on the surroundings of the river Inn. The municipality of Bever decided to remove a portion of the protective bank on one site between Bever and La Punt Chamues-ch to revitalise the river Inn. This revitalisation should help alluvial forests to increase again. One section of the river Inn was already revitalised in Bever and further works affecting the old protective bank are planned for spring 2018 (pers. Comm. Jürg Campensy). Beside its advantages for ecosystem functioning this may be fatal for some adders because it destroys local habitat structures on and around the protective banks used by adders. There a large population of adders (estimations: - 200 adults; pers. comm. Jürg Cambensy) has established. Substitution areas will be built and, for a better knowledge of the adders' habitat requirements, research on adders' habitat use is conducted.

Adders can be rescued from the destruction of their habitat when as many individuals as possible will be translocated, but this strategy actually can bring new problems. Some of these potential problems were already described on a broad scale including mammals and birds earlier. When speaking about the

advantages and disadvantages of translocation it is critical to separate between two kind of translocation; short distance translocation (SDT) to sites near or within an animal's home range and long distance translocation (LDT) to sites well beyond an animal's home range. SDT often induces return behaviour as shown to a large extent by western rattlesnakes (Brown et al. 2009), and to a smaller extent by the aquatic snake *Natrix sipedon sipedon* (Fraker, 1970), but was lacking in the case of Eastern Massaugas (*Sistrurus c. catenatus*) that were translocated the smallest distance though (Harvey et al. 2014).

Thermoregulation did not change significantly after repeated SDT of Northern Pacific rattlesnakes (Holding, Owen and Taylor, 2014). Health status, indicated by body mass, was not decreased in western rattlesnakes after SDT (Brown, Bishop and Brooks, 2009). On the other hand, tigersnakes increased movement after LDT (Butler, Malone and Clemann, 2005 a, b) and had 6-times larger home ranges (Butler et al. 2005 b). LDT also induced increased activity ranges and larger mean daily movement distance in timber rattlesnakes (Reinert and Rupert, 1999) and sometimes homing occurred frequently as in translocated western diamond-backed rattlesnakes (Nowak, Hare and McNally, 2002). Survival duration was three times shorter in translocated hognose snakes during a LDT experiment compared to non-translocated snakes (Plummer and Mills, 2000). Other disadvantages of LDT are diseases transmitted from translocated animals to the population of the same animal residing at the translocation site (Sullivan, Kwiatkowski and

Schuett, 2004), increasing mortality (Cunningham, 1996) or negative genetic effects such as loss of rare alleles found in translocated mosquitofish (Stockwell, Mulvey and Vinyard, 1996). All these problems can be avoided with SDT (Brown, Bishop and Brooks, 2009).

In general most translocation experiments examined non-viperinae snakes and many investigated only the effect of translocation on body mass, on movement and rarely on habitat use (see for example: Reinert and Rupert, 1999; Plummer and Mills, 2000; Nowak, Hare and McNally, 2002), as in a study with tiger snakes that shifted habitats after LTD (Butler, Malone and Clemann, 2005). Movement and habitat use, however, are both central to understand species' basic needs and the function and structure of their interactions (Reinert and Zappalorti, 1988). The revitalisation in Bever offers opportunities to investigate effects of translocation on a population of adders in the Swiss Alps. Furthermore the habitat use of Swiss adders is still poorly known for the summer months, which is also addressed in this research.

## **Study species**

Adders are ovoviviparous snakes with vertical pupils, a triangle shaped head and solenoglyphe dents to inject venom (Valli, 2007). Female adders grow bigger than males (Madsen, 1988) and reach a length of about 45 to 80 cm (Schiemenz 1995) but mostly SVL (snout-vent length; measured from the tip of the snout to the cloaca) is below 50 cm (Lourdais et al. 2013).

Adders feed on different species of small rodents (Luiselli and Anibaldi, 1991; Bea et al. 1992; Dobenkov, 1995; Lourdais et al. 2013;;) when they are adult and on lizards and young amphibians when they are juvenile (Saint-Girons, 1952, 1983; Monney, 1995). Adders populate regions from the Balkan region in the south to the Arctic Circle in northern Scandinavia, and from the longitude of Great Britain to the islands of Sakhalin in the east (Fuhn and Vancea, 1961; Gasc et al. 1997). Adders live in montane regions (above 1000 m altitude), for example in the Swiss Alps. (Gasc et al. 1997). In the Bavarian Alps adders predominantly occupy deforested areas, areas near paths, glades within forests and river floodplains with high radiation (Gruber et al. 2004). When it is cold and windy, especially in early spring and autumn, adders warm themselves in south facing slopes and/or areas where they can avoid wind (Völkl, Hansbauer and Grosch, 2011). McInery (2014) observed that adders are remarkably cold resistant and have a high site fidelity, as they were seen at the same spots for several week. Adders often inhabit fragmented patches of young trees that have open areas and shelter adders against predators and against wind. In spring adders frequently use thickets composed of litter, twigs and dead wood.

Normally adders switch between shaded and neighboring sunny areas during daylight, which involves limited movements (Viitanen, 1967).

The mating period starts shortly after the basking phase and lasts about three weeks. During these three weeks, adders mate near hibernation sites (Andren, 1986; Phelps, 2004) but may sometimes wander 200 m to mate (Viitanen, 1967).

In early summer adders move again farther and can wander from 100 – 400 m up to 1'200 m in special cases (Phelps, 2004).

Although adders occur within a huge extent, many populations are under massive threat on the local scale because suitable habitats lessen as explained above. Their dispersal is restricted to a limited distance (Madsen and Shine, 1992), so adders cannot escape harmful conditions easily. Additionally, human activities further restrict adder movement and population density. Consequently, when adders disperse less among shrinking populations, increased inbreeding (Madsen et al., 1996) may lead to a dangerously reduced evolutionary potential (Frankham, 2005).

## **Aims**

I use VHF-Telemetry to delve into my study's two main aims; First I want to

investigate movement, habitat use and thermoregulation of all non-translocated adders and second I want to compare these elements between translocated and non-translocated adders.

For my first aim I want to check the following three hypotheses; (1) adders avoid ground vegetation because (I) it is less suitable for thermoregulation than stones and (II) offers fewer opportunities for retreat and protection, (2) adders prefer stones, shrubs and trees because (I) stones are needed for thermoregulation mainly in early spring and (II) shrubs and trees offer protection and shades to adjust their core temperatures,(3) temperature differences between the snake and its environment decrease with (I) increasing temperatures because adders, like other reptiles, avoid basking when temperatures are too high, (II) increasing cloud cover because that reduces adders' ability to be warmer or cooler than the environment.

For my second objective I want to check the following three hypotheses: (1) translocated adders increase movement because (I) most studies on translocated animals revealed increased movement and homing activity and because (II) adders have to explore the new, unknown areas to familiarise themselves; (2) translocated adders decrease their preference for shrub, stones and trees and decrease avoidance for ground vegetation because (I) translocated adders are naive about the location and distribution of suitable habitat patches and because (II) translocated adders increase movement and (3) temperature differences



between the translocated snake and its environment are larger, because the snake uses fewer suitable microhabitats.

In summary, I assume that adders profit from the fissured stones, including the vegetation growing on it, and avoid the abundant ground vegetation and grass. Furthermore I predict that after translocation adders not only increase movement, but also shift preference toward less favourable microhabitats with more ground vegetation and less stone cover, fewer shrubs and fewer trees that also affects thermoregulation. In the end, the degree to which my assumptions are supported can be used to assess how much translocations could contribute to the conservation of adders.

## Methods

### Study area

The study took place within an area of approximately 104.5 ha surrounding the river Inn between Bever (46°33'N 9°53'E) and La Punt, situated in the upper Engadin valley, eastern Swiss Alps, at an altitude of 1'700 m. The region is upper montane, has a temperate and continental climate (Bugmann, 2001) and from April to September, the activity period of adders, the mean temperature is 7.5 °C whereas the mean precipitation is 602 mm (<http://de.climate-data.org/location/160315/>).

Along the river, protective banks consist in an old dam on both sides, with fissured stones flanking the river Inn downstream the Isellas bridge, where adders were frequently observed. *Carex* (*Carex spp.*) and willow (*Salix spp.*) species dominate the protective banks within swamp and meadow-adapted communities, although also larch tree (*Larix decidua*) occur. Both sides of the river include pastures, where cows browse in late spring and summer.

### Capture

In April visual search for adders began on both sides of the river Inn downstream the Isellas bridge at a length of about 2 kilometer with slow walking speed ( $\sim 2$  km/h) between 09:00 and 18:30 and continued until August 2016. Adders preferably bask on stones or hide inside shrubs, thus sites with one or preferably both of these habitat features were intensively scanned. Search was only conducted on sunny and moderately cloudy days when temperature was at least positive. Snakes were carefully caught with gloves, protecting against bites, and transported in a dark paper bag in order to reduce stress. Precise georeferenced locations of captured snakes were recorded with a GPS receiver. Time, date of capture (day/month/year) and type of activity (basking, eating, moving) before capture were noted.

Temperature ( $\pm 1$  °C), humidity ( $\pm 5\%$ ) and precipitation were registered from a meteorological database on the internet for each capture (resolution: 15 min) to investigate whether conditions impacted habitat use. Also for each capture cloud cover ( $\pm 5\%$ ) was visually estimated and state of weather was categorised as either sunny, light cloudy or dark cloudy.

## **Measurements and microchips**

All captured snakes were weighted ( $\pm 1$  g), SVL and tail length were measured ( $\pm 0.5$  cm) with a metric tape, sex was determined and blood samples were taken or scale samples were cut with sterilized scissors as fast as possible to minimize stress for future genetic analyses. While measuring, snakes were fixed in a PET tube (when min. 2 examiners were present) or with a foam coated fork (single examiner). To identify recaptured individuals, all adders bigger than 35 cm were equipped with a microchip (Slim microchip T-SL, Datamars) that was subcutaneously implemented beneath lateral scales, toward the posterior end. For visual identification photographs of individual patterns on their head were taken with a camera (Canon Powershot G11) or a mobile phone (Iphone 4, Apple, USA).

## **Telemetry**

In order to daily monitor some individuals, a VHF transmitter was force-fed all caught males more than 37 cm and weighted more than 38 g during spring and several non-gravid females of the same size and weight during summer. Starting in June male adders were scarce and non-gravid females behave similar to males (Viitanen, 1967). Three different types of transmitters (*F1030* – 2.1 g; *F1150* -3.1 g; *F1170* – 4 g; ATStrack, Isanti,

USA) were force-fed so that transmitter weight never surpassed 10% of adder's body weight. Each transmitter has a different frequency between 148 000 Mhz and 148 999 Mhz to distinguish the signal of each different individual. After the implantation adders were released at the capture location except the non-gravid females that were directly translocated. First three days post-capture behaviour was not considered because of possible handling effects.

Each snake with a transmitter was tracked 3 to 5 days per week using a receiver (R-1000 Receiver; Communications Specialists, Orange, USA) and a Yagi antenna (Yagi Three Element Antenna; Titley Scientific, Brendale, Australia) between 09:30 and 18:30. On days with precipitation above 0.1 mm/h snakes were not located because adders were presumably not active. In order to minimise activity biases, individuals were tracked once a day at different times. Each new relocation started near the precedent relocation. The signal was followed until a precise location of the snake could be obtained, but without disturbing the monitored individual. When possible visual observations were included to precisely localize the individual and therefore to obtain the exact location, otherwise two GPS points 4 – 6 m apart each other were taken with angles differing at least 40° (compass) and the direction of signal was noted for both points. Because the strength of signal varied between GPS

points, this information indicated whether the snake was nearer to one GPS point of the two without running a triangulation program and to take habitat parameters nearer to the true location.

### **Microhabitat parameters**

For each location habitat parameters were estimated around the snake's **used localisation** (the exact location determined as mentioned before) and one **available localisation**, defined as one location at 10 m apart in a random direction (N, S, E or W). The habitat measurements conducted on the used localisation allowed to compare with random localisations to investigate preference or avoidance toward different habitat features. The available localisations approximate the overall distribution of habitat features accessible to the snake. The determination of the distance (10 m) was based on a distance that adders can easily travel. Random localisations within the stream or with more than 50% of the area under water were avoided because adders are not aquatic snakes (Filippi et al. 1995). In such cases a other direction was selected. For each used and available localisations, habitat parameters were estimated for a 2 x 2 m area surrounding the spotted snake or based on the localisation deducted from triangulation (see table 1 for the different measured parameters).

## **Thermoregulation**

Thermoregulation is an important physiological process for reptiles, and is potentially affected by translocation. To investigate which environmental factors contribute most to thermoregulation and if translocation, time and date affect their thermoregulation capacity, adders' temperatures were registered during each localisation. The transmitters included a thermal function; indeed, the time between two pulses of the signal was a function of the temperature of the transmitter. Consequently, before field work started, all transmitters were calibrated by submerging them in a water bath that was heated and stored with each temperature, 5°C to 40 °C in intervals of 5°C (Shine et al. 2003), for 2.5 hours to reach a constant temperature in a climate chamber (KBW 400; BINDER GmbH, Tuttlingen, Germany). For that, time needed to count 21 pulses was measured for the eight different temperatures to calibrate each transmitter. A third order polynom ( $y = a_0 + a_1 * x + a_2 * x^2 + a_3 * x^3$ ) was calculated in the software QtiPlot 0.9.8.9 to fit a curve that transforms time for 21 pulses to the snake's temperature for further analysis.

## **Data analysis**

## **Evaluation of causes of transmitter loss**

Almost 60% of equipped snakes lost their transmitter, many within few days to weeks. To test for possible causes of transmitter loss, I fitted a general linearized model in R with days until regurgitation as response variable and date of equipment (April, May, June or July) and weight ratio as predictor variables and SVL, sex, cloud cover and weather as potential covariables. The weight ratio (proportion) was calculated by dividing the transmitter's weight by the snake's weight. When I found a transmitter in the field I could not exactly know how long it has been there, thus I added the number of days until I found the transmitter or the snake was inactive for 21 consecutive days, the longest inactivity of an equipped adder, to the number of days until an adder has been inactive for 10 days, the longest inactivity averaged across all equipped snakes. To proxy the true value I finally divided this sum by two.

## **Habitat use**

As mentioned above a use-available design was conducted to investigate



if adders avoid or prefer certain habitat parameters. In the analysis the used and the available localisations were treated as two different groups. For each location and each habitat parameter only the difference between the used and the available localisation was analysed in order to really evaluate the selection conducted by each individual. So, values below 0 indicate avoidance and values above 0 indicate preference for a habitat parameter. All these differences were averaged for all localisations for each individual in order to avoid pseudo-replication, and then averaged for all resident snakes.

I took the averaged difference (delta) between used and available localisations for each habitat parameter, to avoid comparing all used localisations with all available localisations, and not the mean for each group. To investigate differences between used and available localisations sample size, delta, SD and significance level ( $< 0.05$ ) were used to conduct a t-test with the power t.test function in R.

## **Home range**

The adehabitat package HR was used in R (Version 3.2.2) to calculate home range size [a], core range size [a] and to visualise shape of home

and core ranges for all snakes. Each distance between relocations was split into m/day and then averaged for all movements of a snake. Home range size and core range size can be estimated with different methods.

The Characteristic Hull Method is slightly more robust to biases caused by small sample sizes than Kernel density estimation (Seaman et al. 1996; Downs and Horner, 2009) and deals with concave, disjoint and perforated home ranges (Downs & Horner, 2009), whereas the Minimum Convex Polygon (MCP) method assumes that convex angles confine the home range polygon (Boyle et al. 2009; Xu et al. 2012), without unused space in its interior. Hence, I used the Characteristic Hull method that better fits the observation of adders moving along shelters such as stands of trees or from shrub to shrub leaving a rarely or never used hole in the interior of their home ranges and because the sample size of relocations was small.

The Characteristic Hull method connects neighbouring GPS-locations to build triangles of different sizes. Combining these triangles forms the home range and the level of grey visualises the intensity of use. Ninety-five percent of the smallest triangles were defined as total home range area and 50% of the smallest triangles as total core range area if the area did not increase with more localisations included and therefore reached an asymptote. Because the Characteristic Hull method is still rarely used,

I calculated MCPs to compare my results with other related studies that used the MCP method.

## **Thermoregulation**

To analyse thermoregulation behavior of the implemented snakes, the difference between the adders' temperature and aerial temperature was taken for every localisation. Normality of all continuous variables was checked with a D'Agostino skewness test and then a generalised linear model was fitted in R with the temperature difference as the response variable and cloud cover, moisture, temperature, state of weather, date, Snake ID and time as possible predictor variables. A backward model selection was conducted to get the best model.

## **Effects of mating and period**

Shine (1987) found that movement depends on season and individuals likely because weather and habitat availabilities change through the year

and the individual needs could influence movement. For instance, snakes increase movement during mating (Viitanen, 1967) that could lead to larger home ranges. Consequently, seasonality and mating activity could also influence habitat use in this research. Thus, all movement and habitat parameters were grouped into four periods to test for possible seasonal differences in behaviour. Spring was split into mating period (M), from the first date of capture until the last sighted mating (April 12 – May 25) and post-mating period (PM), from May 26. until mid June (June 13). Likewise summer was split into two periods of similar lengths, S1 (June 14 - July 21) and S2 (July 22 - September 1) to reduce number of relocations for each period in order to better compare among the periods. Differences of the habitat parameters between used and available localisations were averaged for each snake per period to avoid pseudoreplication.

## **Translocation**

After each snake was localised at least seven times (the lower limit of relocations for home range estimations), snakes were grouped in two groups (translocated – resident) on June 13. Individuals with different magnitudes of movement were chosen from both sides of the river (see

results) to be translocated. Snakes were translocated about 1 km upstream and switched from the resident group to the translocation group. The other snakes were not moved, and all were localised later on.

To investigate if translocation leads to bigger home ranges, larger mean daily distances and bigger core ranges, a generalised linear model was conducted in R with group (binary; translocated – residents) as the predictor variable and the different periods (categories) and Snake ID as possible covariables. Each movement parameter (continuous) was once the response variable.

Response variables were log-transformed to reach normality of residuals. A backward model selection was conducted in R to choose the best model based on AIC values. If data were overdispersed or underdispersed family was changed to quasipoisson within the reduced model to correct for undesirable effects of biased dispersion.

To investigate if translocated adders use more unfavourable habitats, indicated by a reduced preference for bushes and trees and a reduced avoidance of grass, as response to translocation and not because of the different periods, a generalised linear model was conducted in R. Each habitat parameter (averaged difference as described before) was once the response variable, treatment (binary; translocation, resident) the

predictor variable and period (M, PM, S1 and S2) and snake ID (categories) possible covariables. Again a backward model selection was conducted in R. If data were overdispersed or underdispersed family was changed to quasipoisson within the reduced model to correct for unwanted effects of biased dispersion.

## **Results**

### **Capture and monitoring**

In April and May a total of 25 male adders were equipped with a VHF-Transmitters. Within the first two months 60% of these adders (n = 15) lost their transmitter and approximately 25% of these adders (n = 6) could

not be tracked anymore because signals were lost (e. g. snakes were predated or made large movements) and were consequently undetectable. Thus only four male adders could be localised at their capture sites more than the critical seven times (see Table 2.). Localisations of these four male adders averaged 11 times  $\pm$  3 (SD) until June. In June three of these adders were translocated a distance averaging 1122 m  $\pm$  273 upstream and localised for 28 times  $\pm$  10 until August 2016. Additionally, because the sample size of individual adders was critically low, five non-gravid female adders were equipped with a VHF-Transmitter and translocated immediately in June. Only two of these non-gravid females, translocated on average 964 m  $\pm$  156, kept their transmitter and could be localised for 23 times  $\pm$  8 from June until August. Meanwhile, to further increase the sample size, three additional adders (one male, two females) were equipped with a VHF-Transmitter in July, released at their capture sites and localised for an average of 14 times  $\pm$  1 until August. Between June and September, four adders, approximately 12% of all snakes captured between April and July, lost their transmitter and one adder, approximately 3%, could not be tracked anymore. Thus seven adders could be tracked til September and two adders that lost their transmitters or vanished before still could be used for the analysis.

## Transmitter loss

Weight ratio (Shapiro-Wilk test,  $W = 0.96625$ ,  $p = 0.5523$ ) and snake length (Shapiro-Wilk test,  $W = 0.95009$ ,  $p = 0.2331$ ) were normally distributed, while days until regurgitation had to be log-transformed (Shapiro test,  $W = 0.92048$ ,  $p = 0.04614$ ) and cloud cover had to be arcsinus-square root transformed (Shapiro test,  $W = 0.90799$ ,  $p = 0.02372$ ), to approach normal distribution. Adders equipped in May kept transmitters on average 32.4 days shorter ( $n = 8$ ; mean = 33.8 days  $\pm$  7.5; Fig. 1) than adders equipped in April ( $n = 10$ ; 66.2 days  $\pm$  14.6; GLM, quasipoisson,  $F_{2,19} = 329.6$ ,  $p = 0.039$  \*) while adders equipped in June kept them 25 days shorter ( $n = 5$ , 41.2  $\pm$  5.1;  $p = 0.046$  \*) and adders equipped in July kept them 31.2 days shorter ( $n = 4$ ,  $p = 0.049$  \*). Because not all 35 adders lost the transmitter and vanished adders are not part of the analysis the sample size was smaller than 35. Whereas increasing weight ratio (GLM,  $F_{1,19} = 21.41$ ,  $p = 0.045$  \*), sunny weather ( $F_{2,19} = 184.2$ ,  $p = 0.047$  \*), SVL ( $t = 14.450$ ,  $p = 0.0440$  \*) and light cloudy weather ( $t = 13.51$ ,  $p = 0.047$  \*) affected days until regurgitation, cloud cover only showed a trend ( $F_{1,19} = 5.63$ ,  $p = 0.061$ ). Many interactions of these variables also had significant effects (Table S1).

## Habitat use



If differences of the estimated habitat parameter between used and available localisations converged to zero than the habitat use was stated as random. Resident snakes ( $n = 7$ ; April to September) actually seemed to prefer stones as used sites had on average  $29\% \pm 13$  (SD) more stone cover than available sites (T-test,  $p = 0.02$ ; Table S2). In contrast all resident snakes seemed to avoid grass cover as used sites had on average  $34\% \pm 14$  less grass layer than available sites ( $p = 0.01$ ). Resident adders used sites with  $12\% \pm 12$  more shaded area than available sites, but this preference was not significant ( $p > 0.45$ ). All other habitat parameters were marked by a mean difference below 10% and did not differ significantly between used and available sites (T-test,  $p > 0.45$ ).

### **Movement and home range**

Sample size of the adders was sometimes below two and number of localisations was sometimes below seven for the different periods, hence all periods were combined to get an overall home range. Effects of the different periods on movement are included in the translocation section. Resident snakes covered on average  $7.9$  m/day  $\pm 3.6$  (SD) and had a home range of  $0.22$  ha  $\pm 0.19$  (using the CharHull method) or  $0.26$  ha

(using the MCP method). Resident snakes had a core range of  $0.013 \text{ ha} \pm 0.021$  (CharHull). For instance, Snake 7 had a compact home range where its activity was dense. In contrast home range of Snake 37 included two centres of activity (dark triangles in Figure S3) at either end of the home range and Snake 1 had an elongated area with high activity (dark triangles; Fig. S3).

## **Thermoregulation**

Although different data points of the same individual are not independent, they can be treated as such when varying more within one individual than among different individuals (Shine et al. 2003). Indeed, Snake ID (GLM, quasipoisson,  $t = -1.13$ ,  $p = 0.26$ ) and translocation ( $t = -0.87$ ,  $p = 0.39$ ) had no effect on temperature differences. The D'Agostino skewness test supported a normal distribution for temperature difference between environmental temperature and snake core temperature ( $10.8 \pm 8.17 \text{ }^\circ\text{C}$  (SD),  $z = -0.46$ ,  $p = 0.65$ ), cloud cover ( $z = 0.234$ ,  $p = 0.81$ ), moisture ( $z = 0.23$ ,  $p = 0.82$ ) and environmental temperatures ( $4 - 25 \text{ }^\circ\text{C}$ ,  $z = -1.68$ ,  $p = 0.09$ ). Statistically cloud cover had the most significant effect on thermoregulation (Table 3). Unsurprisingly all adders' body temperatures approached environmental temperature with increasing cloud cover, increasing moisture and increasing environmental temperatures but the

state of weather had no effect ( $p > 0.56$ ). Toward late August snake temperatures approximated environmental temperatures. Temperature differences decreased from the morning (10:00) toward the evening.

## **Translocation**

### **Habitat use**

Average values for the different periods and the different groups were arcsin-square root transformed to better fulfill the assumption of normality and tested for normality with a Shapiro Wilk's test. The model with ground vegetation as response variable had the lowest AIC value when period and group were included as predictor variables (see Table S3). In contrast to resident snakes (ground vegetation difference = -34%),

used ground vegetation according to availability, thus lost avoidance (mean = - 1% ± 6.8 (SE); GLM, quasipoisson,  $F_{1,11} = 9.57$ ,  $p = 0.02^*$ ; Fig. 2. b), which is not explained by the different periods (GLM, quasipoisson,  $F_{3,26} = 1.16$ ,  $p = 0.2$ ; Fig. S1. b). Some translocated snakes even changed it to the opposite and showed a slight preference toward ground vegetation absent in the resident group (Fig. 2. b). Translocated adders not just lost preference for stones seen in resident snakes, they exhibited avoidance toward stones (-10% ± 5, GLM, quasipoisson,  $F_{1,11} = 5.86$ ,  $p = 0.023^*$ ; Fig. 2. a) not explained by the different periods (GLM, quasipoisson,  $F_{3,26} = 1.19$ ,  $p > 0.3$ ; Fig. S1. a). Even though translocated adders seemed to prefer trees slightly more (10% ± 1.4) than resident adders (7% ± 2), the pattern was not significant ( $p > 0.45$ ) and also did not differ among periods ( $p = 0.15$ ). Also translocated adders had a higher but not significantly different preference for shaded area (17%) than resident adders (12%, GLM, quasipoisson,  $p = 0.3$ ) that was reduced in S2 for the resident snakes (6% ± 11%, GLM, quasipoisson,  $p = 0.09$ ).

## **Home range**

Home range size, mean daily distances and core range size were normally distributed when log-transformed (Shapiro-Wilk test:  $p > 0.50$ ). Core range could not be compared among periods, because too few points could

be included per period and was not different between translocated (sample size, mean  $\pm$  SE, range; 5,  $0.020 \pm 0.007$ , 0.005 – 0.041) and resident snakes (GLM, quasipoisson,  $F_{1,11} = 2.11$ ,  $t = 1.2$ ,  $p = 0.26$ ). Models had the lowest AIC value when both period and group were included as predictor variables for either home range size or mean daily distances as response variable (see Table S3).

Translocated snakes ( $n = 5, 18 \pm 2.8$  m/day; Fig. 4) covered on average more than two times the mean daily distance of resident snakes ( $n = 7, 7.50$  m/day  $\pm 1.69$ ; GLM, quasipoisson,  $F_{1,11} = 0.15$ ,  $t = 2.43$ ,  $p = 0.04$ ), while there was no significant difference among periods M (4,  $15.2$  m/day  $\pm 9.54$ ; Fig. S2), PM (4,  $8.65$  m/day  $\pm 2.34$ ; GLM,  $F_{3,10} = 0.24$ ,  $p = 0.87$ ), S1 (1,  $17.4$  m/day; GLM,  $p = 0.50$ ) and S2 (3,  $9.44$  m/day  $\pm 1.42$ ; GLM,  $p = 0.92$ ). Similarly home range size, obtained through the Characteristic Hull method was on average more than two times bigger in translocated snakes (5,  $0.56$  ha  $\pm 0.24$ ; Fig. 3. a) compared to resident snakes (7,  $0.22$  ha  $\pm 0.07$ ) but the effect of translocation was not significant (GLM, quasipoisson,  $F_{1,11} = 0.97$ ,  $p = 0.21$ ). While the effect of period S1, that included only Snake 37, was significant ( $0.53$  ha; GLM,  $F_{3,10} = 6.86$ ,  $p = 0.02$ ; Fig. 3. b), the effects of period M (4,  $0.013$  ha  $\pm 0.003$ ) and period PM (4,  $0.010$  ha  $\pm 0.005$ ; GLM,  $t = -1.01$ ,  $p = 0.35$ ) were not significant and the effect of period S2 showed a trend (3,  $0.14$  ha

$\pm 0.07$ ; GLM,  $t = 2.18$ ,  $p = 0.07$ ). Because some individuals switched from the resident group to the translocation group, possible effects of translocation on movement can be illustrated with individual cases. For example, after translocation Snake 7 had a 3-fold larger home range (after translocation = 0.51 ha; before translocation = 0.16; Fig. S4) than before the translocation and had a less condensed home range with two centres of activity. One of its centres was near a municipal building. This snake crossed a tarred road to access this location and returned again near the place to where this individual was translocated in the first place. On the opposite, snake 16 halved its home range (after translocation = 0.08 ha, before translocation = 0.16 ha) and exhibited an extremely narrow home range.

## **Discussion**

The majority of adders lost their transmitter after a limited number of days so that most equipped adders were localised insufficient times to provide enough information for statistical analyses. Similarly in a study on Smooth Snakes (*Coronella austriaca*) in Bavaria (Käsewieter, 2002) a huge proportion (ca. 70%) lost their transmitters. In another research all Arafura filesnakes force-fed with a transmitter lost the transmitter within 23 days and sometimes even after 2 days (Shine and Lambeck, 1985).

Losing signals for many adders also decreased the sample size for further analyses. Scientists may lose telemetry signals because of fast dispersal outside the range of the antenna or the signal may become faint because of wet conditions or the occurrence of too many obstacles (Sawyer and Baccus, 1996; Käsewieter, 2002). Hence, the results presented in the project have to be discussed with caution considering the small sample size (respectively 5 and 7 individuals per group). Nevertheless the results presented here can be seen as guidelines or start point for further research with bigger sample sizes.

In this study, adders equipped in May kept their transmitter for the shortest time, potentially coinciding with increased activity during the mating period, where they extensively searched for mates including combats with other males. On the other hand, Krupitz (2009) noted that during the mating period adders should least likely lose the transmitter. Although adders equipped in June and July also lost their transmitter much sooner than in April this could be because all adders equipped in June were translocated directly after they got a transmitter and all adders in July kept their transmitter until the field work was done and potentially still had it longer than I tracked them. The high ratio reduced durability of transmitters within the stomach of adders likely because the ratio was often nearer to 10% than 5%, while in most other studies transmitters did

not cross an upper threshold of 5%. Therefore the ratio could have been sort of a general problem possibly explaining the short durability. During sunny weather adders may move more after equipment and also may resist stronger as transmitters were force-fed because adders were likely more active on days with few or no clouds. Thus, the transmitter could be in a less comfortable position within the adder caused by the stronger resistance or the transmitter could interfere stronger with their active behaviour shortly after equipment causing increased disturbance during the critical phase of customization. Therefore adders may regurgitate transmitters sooner. Transmitters should weight around 5% of the snake's weight and adders should be equipped preferably before the mating period to avoid fast regurgitation.

## **Habitat use**

Resident adders preferred stones, sand and grit, but avoided ground vegetation. Sun exposed stones, which warm up fast, provide heat for thermoregulation and also offer quickly reachable shelter in the form of fissures. Even during summer days with elevated temperatures adders preferred stones. In Italy adders used stonepiles within grasslands mostly during August but not in spring and autumn (Luiselli et al. 1994), maybe also because stonepile habitats were mostly within shaded areas.



Although adders caught in similar altitudes in Slovenia and Italy, also used stonepiles and rocks, used habitat patches had only around 10% stone cover while having more than 80% grass cover with herbs and short scrubs (Mebert et al. 2015). The smaller proportion of stone cover used by these adders could be related to the fact that the Slovenian and Italian Prealps are nearer to the Mediterranean Sea, thus have a slightly milder climate and because the study included habitat on south exposed slopes including warmer microclimatic conditions. At the opposite of their distribution areas, adders above the Arctic Circle in Sweden also used stony substrate mainly during basking at moraine ridges and south facing slopes shortly after hibernation (Andersson, 2003) but the preference for stones was not revealed by other studies that essentially did not include bare soil or stony substrates in their habitat use analysis in Latvia (Čeirâns, 2007) and the UK (Palmer, 2011). Possibly because stony substrates or bare soils are rare or associated with unsuitable habitat in Latvia or are simply not used by adders in the UK as the oceanic climate leads to more narrow temperature ranges through the year coupled with fewer events of freezing compared to areas in the Alps. In Bever adders avoided ground vegetation, maybe because it warms up slowly and offers less shelter to protect against the cold and predators. When temperatures rise toward summer and grass grows larger it is easier for the adders to reach preferred temperatures in grass and the ground vegetation offers

more hiding places than in spring. Possibly these two aspects explain the slight decreased avoidance toward ground vegetation in the summer months. In contrast to my findings, Italian adders used open, grassy patches in spring and autumn but not in summer (Luiselli et al. 1994), potentially because prey species are more frequently encountered in the structurally richer habitats at the border of forests or adders evade the higher predation risk of open areas. A survey conducted in the UK revealed that adders prefer ground and understorey vegetation (Palmer, 2011), while the former was avoided and the latter was not different between used and available locations in my study. In the same survey litter was not different between used and available locations, also supported by my study. The lack of avoidance or preference toward trees, shrubs and shaded area could be caused by the scale of my study or because a relatively small coverage of shrubs and trees is enough to provide protection.

Strong differences among these studies and my study could be because other studies defined the habitat parameters differently, had another scale or included other habitat parameters. Furthermore different local populations/subspecies may have different adaptations caused by warmer, cooler and either more or less stable climatic and microclimatic conditions and may inhabit areas with either a different set of structures

or with similar but differently arranged structures. Therefore the results of this study should primarily contribute to translocation efforts in similar environments.

## **Home range**

Knowledge of the area requirements of adders is essential to choose potential translocation sites that provide enough space. Preferably places that not are currently occupied by another population of adders because the existence of other adders may increase area requirements. Adders are known to have a remarkably high site fidelity (Viitanen, 1967), hence their small home range size averaging around 0.22 ha and their mean daily distances averaging around 7.5 m/day are no surprise. Activity ranges and mean daily movement distances varied much among different populations of adders (see Table 4). In Sweden adders had activity ranges much smaller than in Switzerland, but activity ranges were not calculated with the Minimum Convex Polygon method and localisations were obtained with mark-recapture. A population of adders in Davos,

Switzerland had much larger activity ranges around 7.6 ha potentially because summer habitats were situated 800 m away from hibernation sites and activity ranges were calculated by summing all quadrants used by the adders. In contrast, hibernation sites in Bever were directly at the river with ideal habitat to feed nearby. Thus, the proximity of habitats preferred at different stages of the annual cycle of adders in Bever may explain partly the smaller home range compared to previous studies. Species like the congeneric *V. latastei* and *the V. aspis* but also the crotalinae *Gloydius shedaoensis* had almost same-sized home ranges while moving up to 5 times less. Other viperidae like *Crotalus cerastes* or *Sistrurus c. catenatus* had much larger home ranges around 22 ha but are much larger and have a decreased site fidelity compared to *Vipera berus*. Movement of *Vipera berus* (7.2 m/day) was close to movements of the distantly related *Lampropeltis calligaster* (7 m/day) and *Agkistrodon contortrix* (7.5 m/day) in North America (Fitch and Shirer, 1971). My study contributes evidence that it is difficult to compare among studies focusing on different or even on the same species, because methods vary, geographical regions differ and seasons affect results of the research (Shine, 1987; Maccartney et al. 1988). Because of this variation scientists proposed that snakes might not have species-specific home range sizes (Shine, 1987). Snakes have to access resources to fulfill their needs like other species and because resources are unevenly distributed in space and

time there is a high variation among individuals of the same species (Plummer and Congdon, 1994; Shine and Fitzgerald, 1996; Plummer and Mills, 2000). Therefore the spatial distribution of resources could determine the size of home ranges and the minimum area providing all habitats for different phases during a snake's life cycle according to the size and density of a population. Moreover places, where resources for different needs during the activity period like basking and feeding occur on a relatively small area similar to Bever are desirable sites for translocation programs.

### **Thermoregulation**

Snakes need to thermoregulate and hence their body temperature is linked tightly to environmental conditions (Bouazza et al. 2016). Besides characteristics of the habitat, like structural properties of biota or occurrence of stones, abiotic factors, such as exposure to sun, moisture or cloud cover, may dictate their capacity to change internal temperatures against the temperature from the environment. . On rainy days both moisture and cloud cover are high, hence adders likely search shelter and reduce thermoregulation. When external temperatures increase toward summer the external temperatures reach the preferred temperature for adders resulting in smaller differences. In accordance with these gradients

I assumed that when one or multiple of these abiotic factors increase internal temperature become more similar to external temperatures. Adders, indeed, approached environmental temperatures with increasing cloud cover, increasing moisture and increasing external temperatures. The small differences during days with high cloud cover and high moisture could further be explained by the observation that some species of reptiles stay inactive when they cannot reach their preferred body temperatures (Tosini et al. 2001; Seebacher and Franklin, 2005). Moreover snakes can elevate body temperatures only slightly above aerial temperatures when cloudy circumstances lead to a temperature that is homogenous across most microhabitats (Hammerson, 1989). Like other reptiles adders hide inside refugia during too hot days (Beebee and Griffiths, 2000), what is supported by the small difference between internal and external temperatures with increasing aerial temperature. Such small differences were also observed in the colubrid snake *Coluber flagellum*, where mean temperature differences dropped from 10.5 °C at 21.7 °C to 6.6 ° at 25.6 °C and 4.8 °C at 27 °C in California, though temperatures were measured directly above the shaded soil (Hammerson, 1989). Astonishingly increased movement and shift in microhabitat used by the translocated adders did not impair their thermoregulation. This indicates that thermoregulation is only negligibly affected by the translocation and that adders still thermoregulate like usual despite

moving farther and more frequently with possible direct and indirect effects on health and survival. The increase in movement, on the other hand, may assure that adders can regulate their temperature adequately in the unknown area.

## **Translocation**

### **Habitat use**

Changes in habitat choice after translocation point to problems mainly during the first months at the new site. Although adders spend more time in ground vegetation during summer, when diverse herbs offer shadow and shelter, avoidance was still maintained in summer while lacking in the translocation group. Therefore period alone did not strongly reduce avoidance toward ground vegetation. Adders may lose avoidance toward ground vegetation after translocation because they increasingly move through abundant grass, while exploring new features within the new habitat (Plummer and Mills, 2000), thus may use less favourable habitats while travelling. Moving snakes are also supposed to be exposed to a greater risk of predation (Madsen and Shine, 1993; Shine and Fitzgerald, 1996), a problem that should be considered. After translocation adders

started to avoid stones, sand and grit. In contrast resident adders preferred stones in all periods, so it is likely a favourable habitat element even during hotter conditions. Stones in the translocation area were often smaller or looser, with less grass and fewer bushes in between, than in initial areas, hence possibly less suitable. Translocated tigersnakes (*Notechis scutatus*) also shifted habitat by using previously avoided floodplain riparian woodland according to its availability (Butler, Malone and Clemann, 2005), just like translocated adders did with grass dominated habitat in Bever. Nevertheless adders shifting toward different microhabitats could be less problematic than suspected because they can live within different habitats (McInerny, 2014). There are no other publications about habitat use shifts induced by translocation, at least for reptiles, to my knowledge. Adders in Bever shifted use of two important habitat parameters after translocation perhaps caused by lack of knowledge at the new site or because these habitat parameters occurred in a different context. Effects on survival or health through physiological and ecological processes are still unknown.

## **Home range**

I translocated adders out of their natural home range and thus I consider it long distance translocation. Indeed adders did not return to original home



ranges within four months after the release but slightly increased home range size similar to other long distance snake translocations (Reinert and Rupert, 1999; Plummer and Mills, 2000; Nowak, Hare and McNally, 2002). Activity consumes energy in reptiles and snakes (Walton, Jayne and Bennett, 1990; Plummer and Congdon, 1994). Therefore a more than 2-fold increase of movement (7 m/day to 17 m/day) likely reduces body mass because more energy is depleted. Normally snakes stick to the same home range for more than one year because snakes can orientate themselves better within known areas (Madsen, 1984). When snakes are translocated they lose this familiarity and need time to memorise the new site, thus increasing their movement. In my study adders increased mean daily movement and decreased avoidance for ground vegetation, hence indicating that they spend more time traversing thorough exposed areas, while exploring the unknown landscape. Maybe suitable features and prey species were scarcer in the translocation area or competition for available resources increases as translocated adders augment the original population density. . During the summer months more people used the places inhabited by adders for recreation and sports leading to higher chances of disturbance and cattle browsed mainly in June and July. Both disturbances could have increased movement more in translocated adders than in resident adders. Normally snakes do not move through open areas and often travel parallel to roads to circumvent open area (Fitch and

Shirer, 1971). While only anecdotal and maybe because of chance the resident Snake 37 behaved similarly, whereas the translocated Snake 7 crossed a tarred road two times. Such aberrant behaviour could be detrimental for translocated adders but is not a major problem when only occurring in one of five adders.

Mean daily distances increased on average by 11 m/day after translocation, therefore indicate that adders move more frequently and farther apart because of a translocation. In contrast, translocated Timber Rattlesnakes increased mean daily distances on average 4 times and home range size up to 10 times (Reinert and Rupert, 1999). But their translocation distance was highly variable (8 – 108 km) and possibly involves different macrohabitats making it difficult to compare their results with my smaller scale study. Furthermore resident rattlesnakes had almost a 300-fold bigger home range (59.9 ha) than resident adders (0.224 ha). Still mean daily distances were only 3-fold different between residents of the two species (rattlesnake = 36.9 m/day; adder = 12 m/day). Western Diamond-Backed Rattlesnakes translocated 2 km away from origin increased activity ranges almost twice while their residents having approximately 100-fold bigger home ranges (24.3 ha) than resident adders. Besides their movements were only 3-fold larger (rattlesnake = 35 m/day; adder = 12 m/day) but did not increase after translocation

(Nowak, Hare and McNally, 2002). Concordant with these studies translocated adders may have to explore the new habitat to find suitable habitat structures. Translocated adders also need to find prey species, seek shelter to avoid predators and need features to bask, hide or cool down when the weather is hot. Such behavioural responses could explain why they increase their average moves. On the other hand, home range did not significantly differ between translocated and resident adders. Two points could explain it. First, while adders do not expand their home ranges, they may move more often within their home ranges because they are not comfortable with the unknown landscape. In a previous study translocated timber rattlesnakes left the release site soon and returned later to that same site. Many translocated snakes repeated this movement (Reinert and Rupert, 1999). I also saw such movements of translocated adders, what could explain that they increase mean daily distance stronger than their home range size. Second, a bigger sample size could show a significant increase of home range sizes still less affected by translocation than overall movements but also may give further evidence for no increase.

While adders shifted use of important habitat features such as stones, sand, grit and ground vegetation after translocation and increased their daily movement distances they required almost the same amount of area,

regulate their body temperatures normally and stay at the translocation site at least till hibernation. Fortunately at least some problems of previous translocation efforts did not occur in Bever. Further research could investigate the effect of translocation on resident adders at the translocation site or how translocation differs when subsets of adders are translocated to structurally dissimilar habitats with different degrees of fragmentation. The composition of vegetation or soil properties may also have an impact on microhabitat use.

Adult adders strongly stick to their respective groups (Phelps, 2004) and translocations interrupt this relationship. A possibility would be to translocate groups of adders together. Whereas increase of movement after translocation seems less severe than leave them at the origin to be killed, a crucial next step in evaluating translocations is to assess if translocated snakes go to places where hibernation is possible. Changes in hibernating behaviour would severely harm and ultimately kill snakes. If this is the case this strategy clearly does not serve its conservation purpose most notably in cases where the threat is less lethal than in Bever. For a sound implication in conservation plans the study on adders in Bever should continue this spring. The fate of translocated adders should be assessed by recapture or observations to find out if these adders are still alive, healthy and at their new locations or if they have returned

to their original hibernation sites. Only if this is proven translocations can be continued on a solid scientific basis without negative consequences that question its benefit.

### **Conservation implications**

Adders should be translocated in great numbers and early in the year so they can familiarise themselves with the new location and should be monitored after the translocation, so in case of homing behaviour they can be translocated again. A suitable translocation site should have stones with access to below ground, f.e through fissures in stones, for hibernation and some shrubs and few trees in vicinity. Furthermore this site should be as near as possible to the sites where adders originate. Preferably they should be translocated in a similar configuration and to microhabitats that are structurally similar to microhabitats at the capture location.

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## Tables

**TABLE 1.** Habitat parameters measured for each used and available localisations with the included features and their definitions. Features were not exclusive (e.g litter on stones, shadow area), thus total percentage could be > 100%.

<b>Habitat parameter</b>	<b>Included features</b>	<b>Definition (% of 2x2 m)</b>
Stones, sand, grit ->SSG	Stones, sand, mud, bare soil, grit	% substrate stones, sand, mud, bare soil, grit
Ground vegetation -> GL	grass, mosses, herbs, ferns	% area covered with non woody, herbaceous plants
Shrub layer -> SL	Woody vegetation up to 100 cm	% area stems and branches (< 4 cm) because both are obstacles
Tree layer -> TL	Woody vegetation from 100 cm	% area stems and branches (< 4 cm) because both are obstacles
Litter -> L	shed leaves, shed needles, debris	% soil covered with litter
Dead wood -> DW	dead wood	% soil covered with dead wood
Water bodies -> WB	flooded areas, ponds, small streams	% area covered with water
Shaded area -> SA	Shades of grass, trees, shrubs, canopy	% permanently shaded

**TABLE 2.** Week (21. – 40.) when each monitored snake was localised (in dark grey) and when signals could not be heard and the status was unknown (in light grey). Status is denoted by v (vanished) and l (transmitter lost). For translocated adders weeks are in light and dark blue.

ID	April		May		June				July				August							
	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
1																v				
6							l													
7																			l	
9	v																			
10							l													
11								l												
12								l												
14						l														
15								l												
16																				l
17					v															
18							l													
19							l													
23																				l
30										l										
32							l													
33								l												
34					v															
35							l													
37															l					
40								l												
45				v																
46							l													
47					v															
49					l															
50												l								
52												l								
55													l							
56															l					
58																				
67																				
68																				
70																				

**TABLE 3.** GLM, quasipoisson statistics showing significant effects of the different variables on temperature differences between aerial and snake core temperature.

<b>Variable in GLM</b>	<b>F - value</b>	<b>p - value</b>
Cloud cover	$F_{1,211} = 14.52$	$p = 0.002$
Moisture	$F_{1,211} = 10.51$	$p = 0.006$
Temperature	$F_{1,211} = 6.53$	$p = 0.010$
Time	$F_{1,211} = 2.88$	$p = 0.005$
Date	$F_{1,211} = 14.14$	$p = 0.006$

**TABLE 4.** Summary statistics of activity ranges and movement distances of other closely and distantly related snake species obtained by different methods spanning almost four decades and three different continents.

<b>Snake species</b>	<b>Year</b>	<b>Activity ranges (ha)</b>	<b>Country</b>	<b>Movement (mday<sup>-1</sup>)</b>	<b>Method</b>	<b>Author(s)</b>
<i>Vipera berus</i>	1967	0.002	Sweden	3	-	Viitanen
	1987	1.06	Switzerland	-	Convex Polygon	Neumayer
	1988	7.9	Switzerland	-	used quadrants area	Moser
	2016	0.24	Switzerland	7.4	Minimum Convex Polygon	
<i>Vipera latastei</i>	2003	0.24	Portugal	5.4	Harmonic Mean	Brito
<i>Vipera aspis</i>	1968	0.3	-	-	-	Naulleau
<i>Gloydius shedaoensis</i>	2003	0.29	China	1.7	Minimum Convex Polygon	Shine et al.
<i>Crotalus cerastes</i>	1994	21	USA	-	Minimum Convex Polygon	Secor
<i>Sistrurus c. catenatus</i>	1992	25	Canada	-	Complex Polygons	Weatherhead and Prior
<i>Lampropeltis calligaster</i>	1971	-	USA	7	-	Fitch and Shirer
<i>Agkistrodon contortrix</i>	1971	-	USA	7.5	-	Fitch and Shirer



# Figures

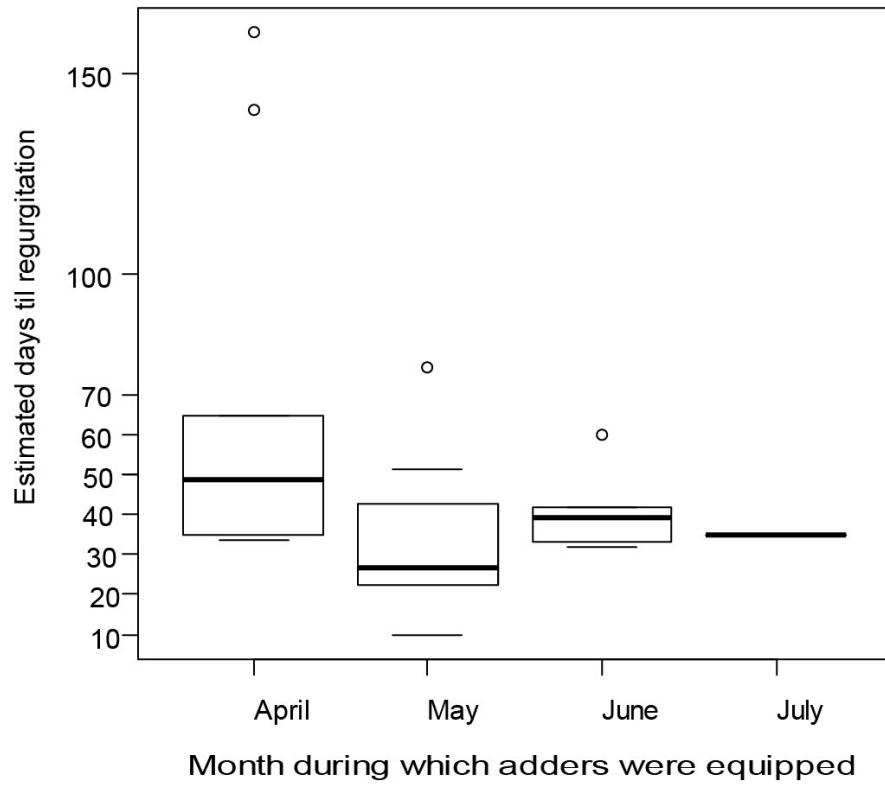


Fig. 1.

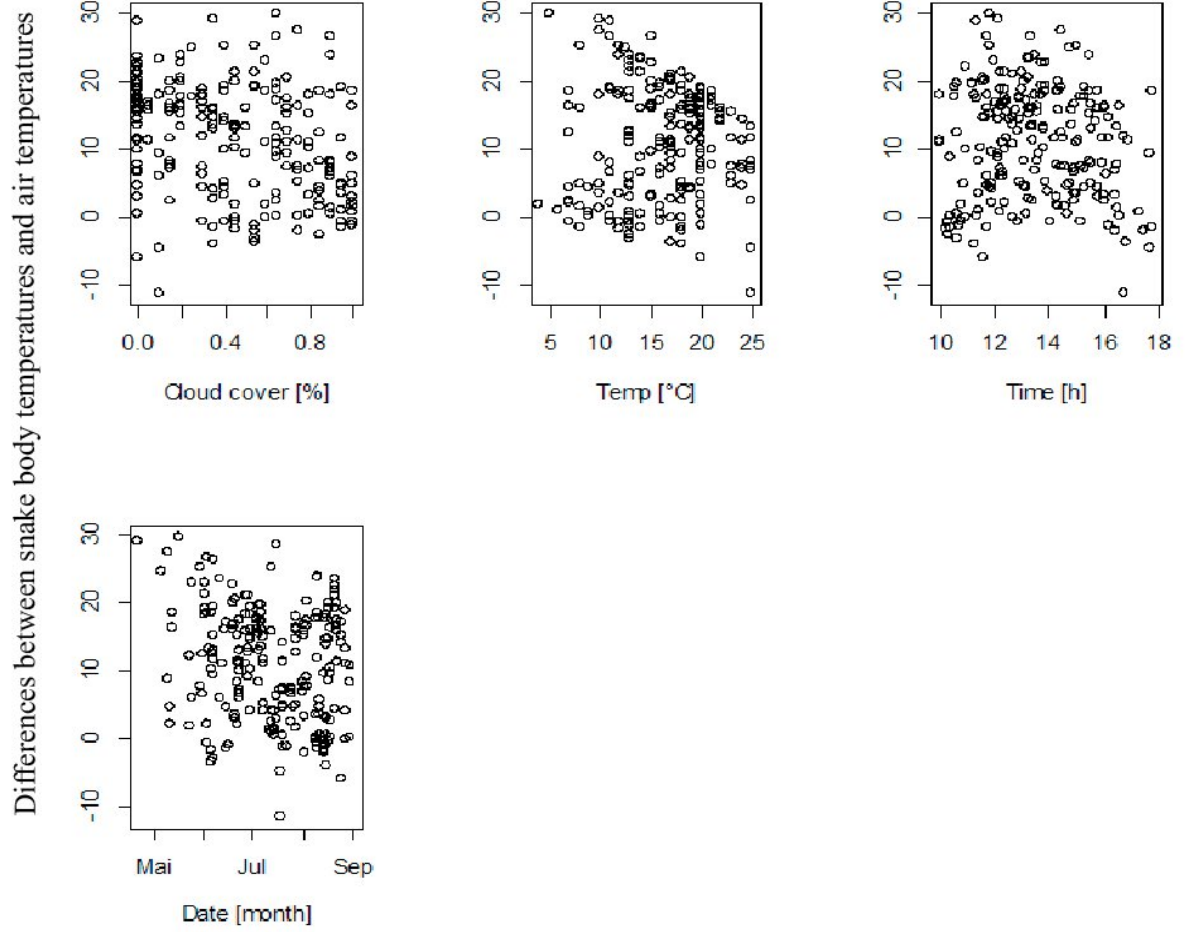


Fig. 2.

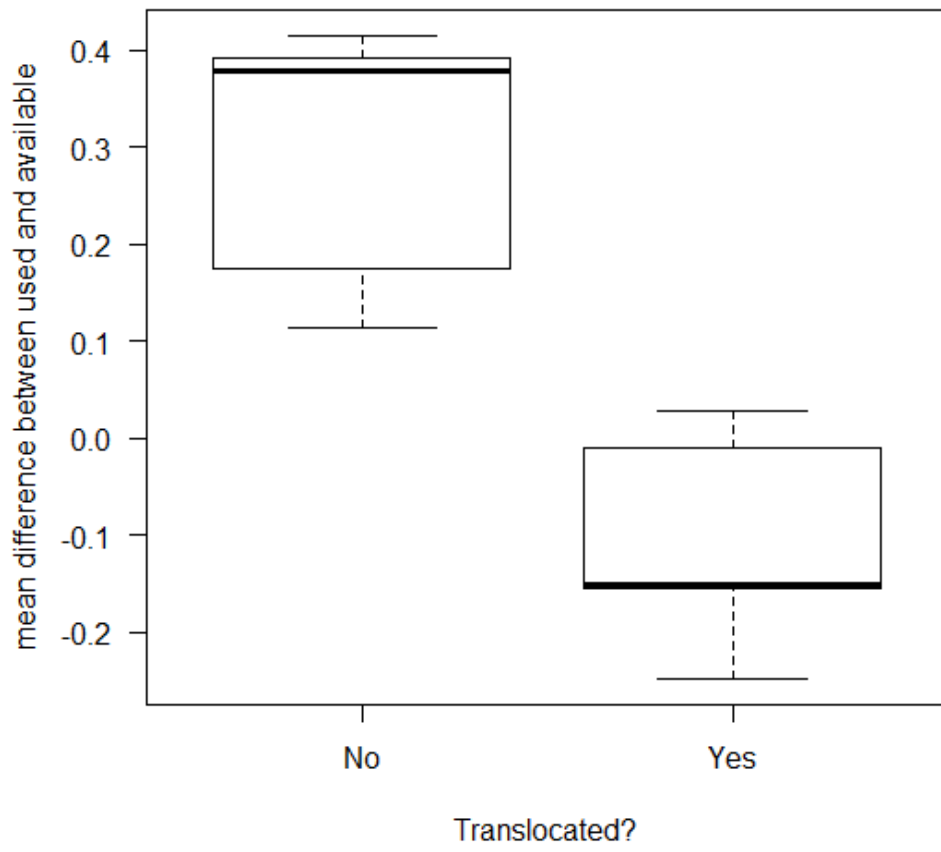


Fig. 3. a.

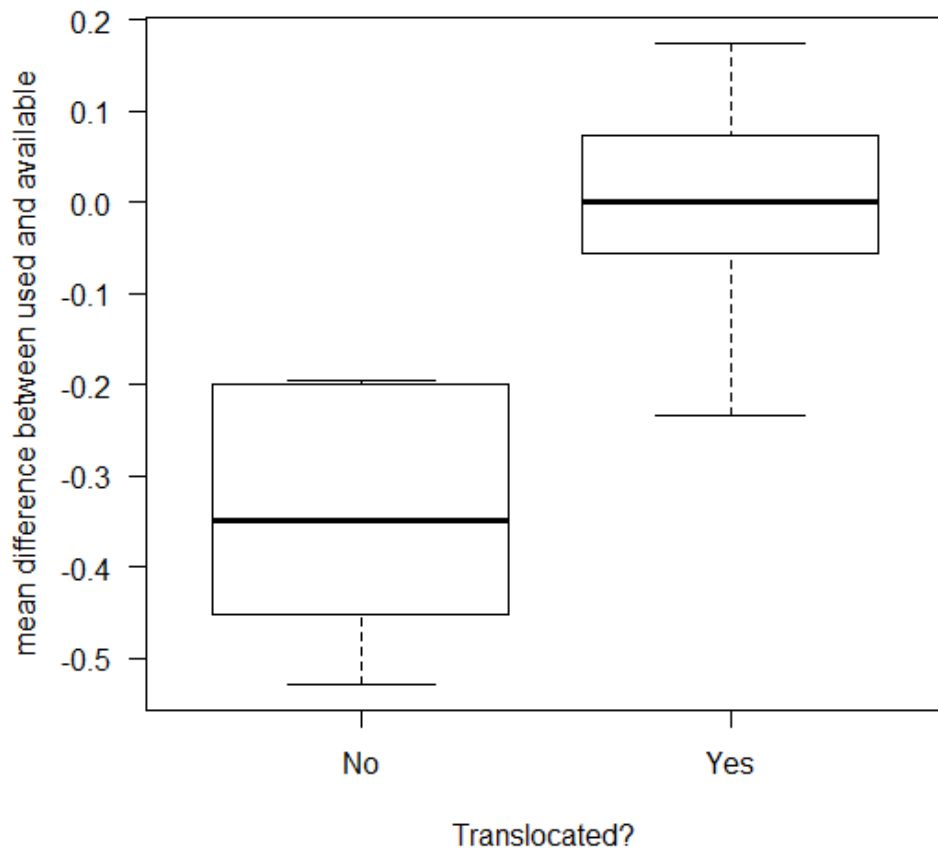


Fig. 3. b.

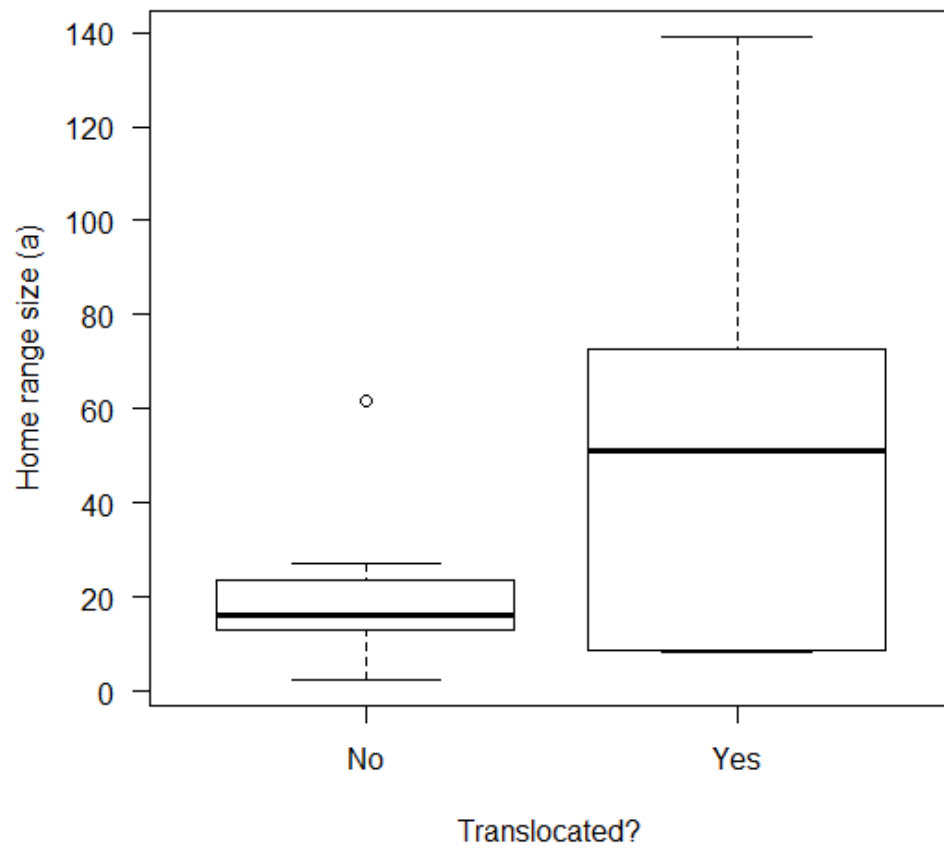


Fig. 4 a.

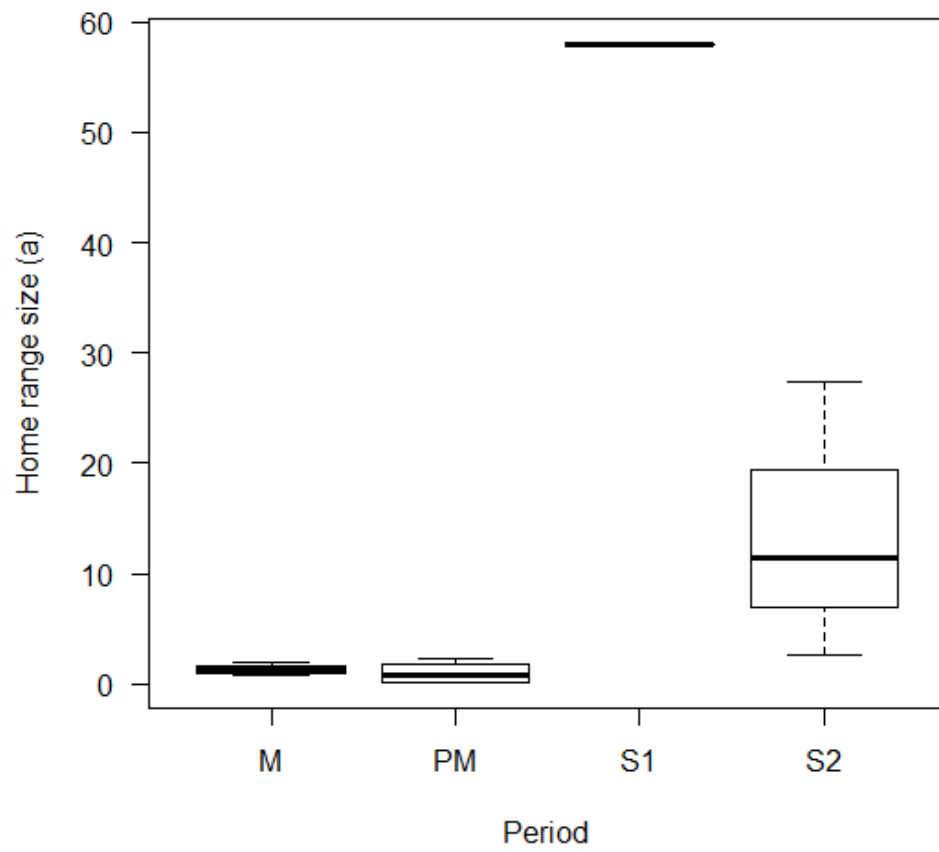


Fig. 4. b.

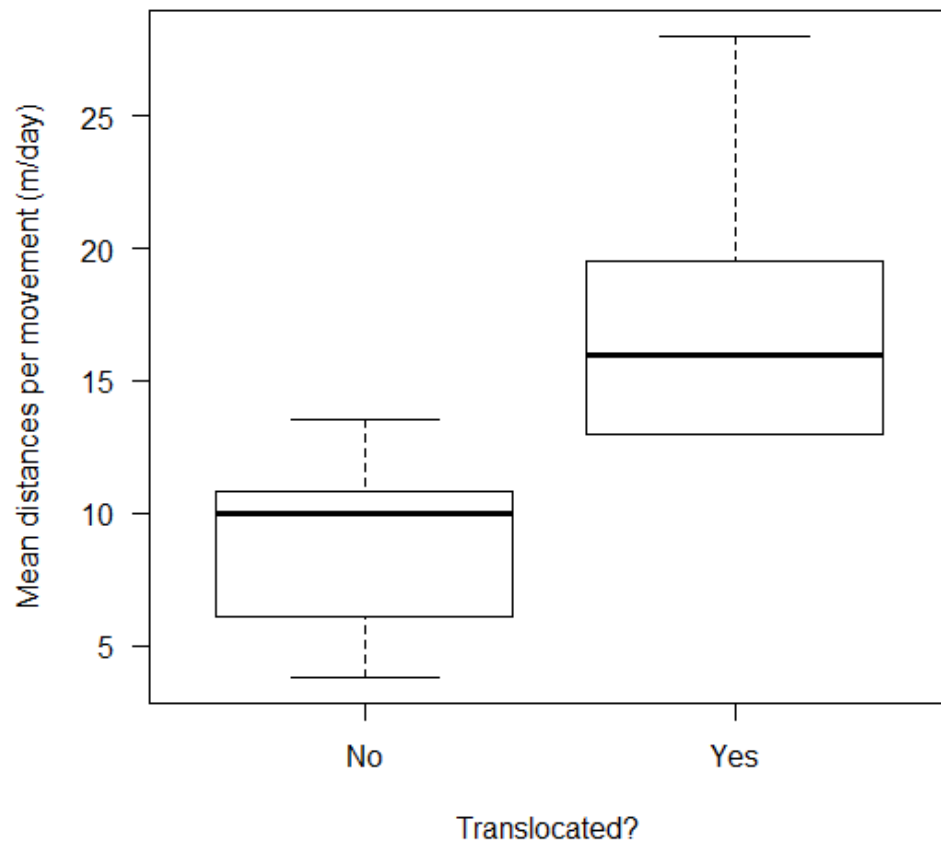


Fig. 5.

## Figures Text

**Fig. 1.** The effect of different months when adders were equipped on days until regurgitation (median  $\pm$  1.5 IQR).

**Fig. 2.** The effect of cloud cover, air temperature, time and date on thermoregulation of adders.

**Fig. 3. b.** The effect of translocation on the difference between proportions of ground vegetation layer on used locations and on available locations (median  $\pm$  1.5 IQR) comparing translocated adders (n = 5) and resident adders (n = 7).

**Fig. 3. a.** The effect of translocation on the difference between proportions of stone, sand, grit layer on used locations and on available locations (median  $\pm$  1.5 IQR) comparing translocated adders (n = 5) and resident adders (n = 7).

**Fig. 4. a.** The effect of translocation on adders' home range size (median  $\pm$  1.5 IQR) comparing translocated adders (n = 5) and resident adders (n = 7).



**Fig. 4. b.** The effect of periods on the home range size (median  $\pm$  1.5 IQR) of resident adders (n = 7).

**Fig. 5.** The effect of translocation on adders' daily movement distances (median  $\pm$  1.5 IQR) comparing translocated adders (n = 5) and resident adders (n = 7).

## **Supplementary information**

Distance does not depend on weight (GLM,  $t = 3.34$ ,  $p = 0.185$ ), length (GLM,  $t = -1.28$ ,  $p = 0.422$ ), side (T-test,  $t = 0.33$ ,  $p = 0.78$ ) and sex (T-test,  $t = 0.4$ ,  $p = 0.71$ ). Area does not depend on weight (GLM,  $t = -0.074$ ,  $p = 0.953$ ), length (GLM,  $t = 0.762$ ,  $p = 0.585$ ), side (T-test,  $t = 1$ ,  $p = 0.48$ ) and sex (T-test,  $t = -0.64$ ,  $p = 0.58$ ). Core area does not depend on weight (GLM,  $t = -6.807$ ,  $p = 0.0929$ ), length (GLM,  $t = 1.421$ ,  $p = 0.3904$ ), side (T-test,  $t = 0.79$ ,  $p = 0.57$ ) and sex (T-test,  $t = -1.56$ ,  $p = 0.19$ ).

# Supplemental Tables

**Supplemental TABLE S1.** Summary of interaction analyses in GLM to investigate why some adders kept their transmitters shorter than others.

<b>Interaction in GLM</b>	<b>Number of days adders kept their transmitter (log-transformed)</b>	<b>p-value</b>
Ratio:equipped in July	$F_{2,19} = 1.28$	$p = 0.045$
Ratio:equipped in May	$F_{2,19} = 1.28$	$p = 0.069$
Ratio:SVL	$F_{1,19} = 101.4$	$p = 0.042$
SVL:equipped in July	$F_{2,19} = 203.6$	$p = 0.048$
SVL:equipped in June	$F_{2,19} = 203.6$	$p = 0.078$
SVL:equipped in May	$F_{2,19} = 203.6$	$p = 0.041$
Ratio:cloud cover	$F_{1,19} = 70.14$	$p = 0.05$
Cloud cover:equipped in June	$F_{1,19} = 88.69$	$p = 0.048$
Cloud cover:equipped in May	$F_{1,19} = 88.69$	$p = 0.076$
Ratio:WeatherLightCloudy	$F_{2,19} = 64.48$	$p = 0.047$
Ratio:WeatherSunny	$F_{2,19} = 64.48$	$p = 0.048$

**Supplemental TABLE S2.** Difference (percentage) of the habitat parameters; ground vegetation layer (GL), shrub layer (SL), tree layer (TL), sand stone grit layer (SSG), water bodies (WB), shaded area (SA) and litter (L), between available and used localisations and number of localisations is given for each individual and averaged for all resident snakes for each period and each group (resident - translocated). T-tests with p-values is only given for resident snakes combining all periods.

Group	Period	ID	Localisations(n)	GL	SL	TL	SSG	WB	SA	L
<b>Resident</b>										
M	1	1		1	0	30	10	0	15	5
	7	2		-38	0	13	40	0	33	53
	16	6		-13	5	3	44	-33	6	28
	37	4		-10	1	-5	16	0	-10	-6
	mean	3.3		-15	2	10	28	-8	11	20
PM	1	6		-62	2	13	43	5	20	9
	7	11		-45	0	8	40	-3	26	14
	16	6		-28	-1	5	32	-3	-10	10
	37	7		-11	1	3	0	0	25	3
	mean	7.5		-37	1	7	29	0	15	9
S1	37	18		-26	7	-1	19	6	7	-13
S2	37	2		-20	0	3	0	18	-3	-21
	67	14		-47	2	4	41	0	21	7
	68	15		-35	0	13	22	0	-3	-13
	70	14		-20	3	6	11	-1	9	-6
	mean	11.3		-30	2	5	19	5	6	-9
all	1	7		-53	1	15	38	4	19	9
	7	13		-44	0	8	40	-3	27	20
	16	12		-20	2	4	38	-18	-3	20
	37	11		-20	4	0	13	45	9	-9
	67	14		-47	2	4	41	0	21	7
	68	15		-35	0	13	22	0	-3	-13
	70	14		-20	3	6	11	-1	9	-6
	mean	12.3		-34	2	7	29	4	11	4
	t-test			p = 0.01	p = 0.34	p = 0.26	p = 0.02	p = 1	p = 0.57	p = 1
<b>Translocated</b>										
all	1	18		-23	-1	13	3	2	14	16
	7	37		-5	0	5	-1	3	10	-1
	16	31		7	-2	12	-15	0	28	1
	56	18		17	0	10	-25	-1	16	-4
	58	29		0	2	11	-15	3	0	-56
	mean	26.6		-1	0	10	-11	1	14	-9

**Supplement TABLE S3.** Model selection (backward) for all the generalised linear models and the corresponding AIC values. Adders are either belonging to the translocation or resident group if group is noted. Predictor and co-variables are either categorical (group, period, month, Snake ID, state of weather), numeric (Temperature), time variables (Time, date) or proportional (Cloud cover, all habitat parameters, Moisture, ratio).

<b>Response variable</b>	<b>Predictor -and covariables</b>	<b>AIC</b>
<b>Habitat parameters<sup>2</sup></b>	<b>Model = GLM</b>	<b>AIC</b>
GL	Period + Group	-13.2
	Group	-14.6
SSG	Period + Group	-13.9
	Group	-17.7
SL	Period + Group	-107.1
	Group	-107.2
TL	Period + Group	-45.1
	Group	-48.9
	1	-49.6
L	Period + Group	-2.0
	Period	-4.0
SA	Period + Group	-21.2
	Group	-25.4
	1	-26.1
WB	Period + Group	-44.6
	Period	-46.0
<b>Movement<sup>1</sup> analyses</b>		
Mean daily distances	Period + Group	46.2
	Group	41.9
	Period + Group + Snake ID)	82.8
	Period + Snake ID	80.8
	Period	80.0
Residents	Period + Snake ID	29.4
	Period + Snake ID	22
	Snake ID)	20.2
	Group + Snake ID)	28.1
	Group + Snake ID)	10.6
<b>Thermoregulation</b>		
Temperature differences	Group + Snake ID + Time + Date + Temp + State of Weather + Cloud cover + Moisture)	1402.3

Snake ID + Time + Date + Temp + State of Weather + Cloud cover + Moisture)	1401.7
Time + Date + Temp + State of Weather + Cloud cover + Moisture)	1400.97
Group * Time * Date * Temp * State of Weather * Cloud cover * Moisture	1369.97

**Transmitter Loss**

Days til regurgitation <sup>1</sup>	Month equipped + ratio + weight + SVL + Cloud cover <sup>2</sup> + Weather + sex	53.0
	Month equipped + ratio + SVL + Weather + Cloud cover <sup>2</sup> + ratio: month equipped + ratio:SVL + month equipped:SVL + ratio:Cloud.cover <sup>2</sup> + month equipped:Cloud.cover <sup>2</sup> + SVL:Cloud.cover <sup>2</sup> + ratio:Weather + month equipped:Weather	-93.0

## Supplemental Figures

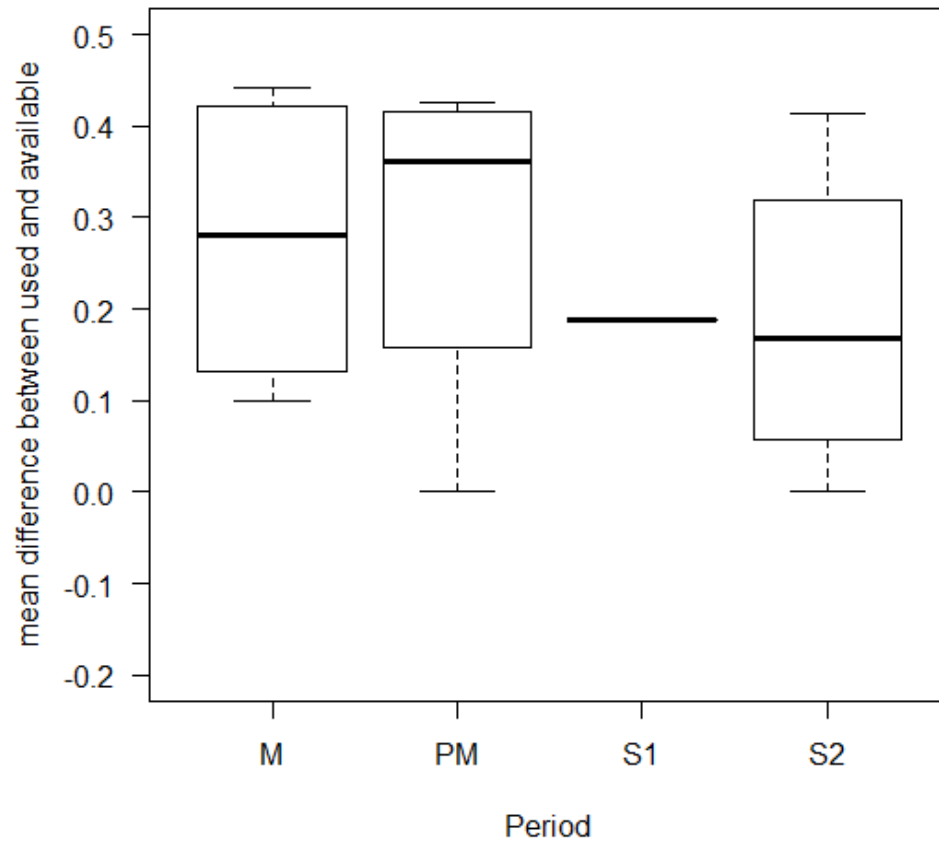


Fig. S1. a.

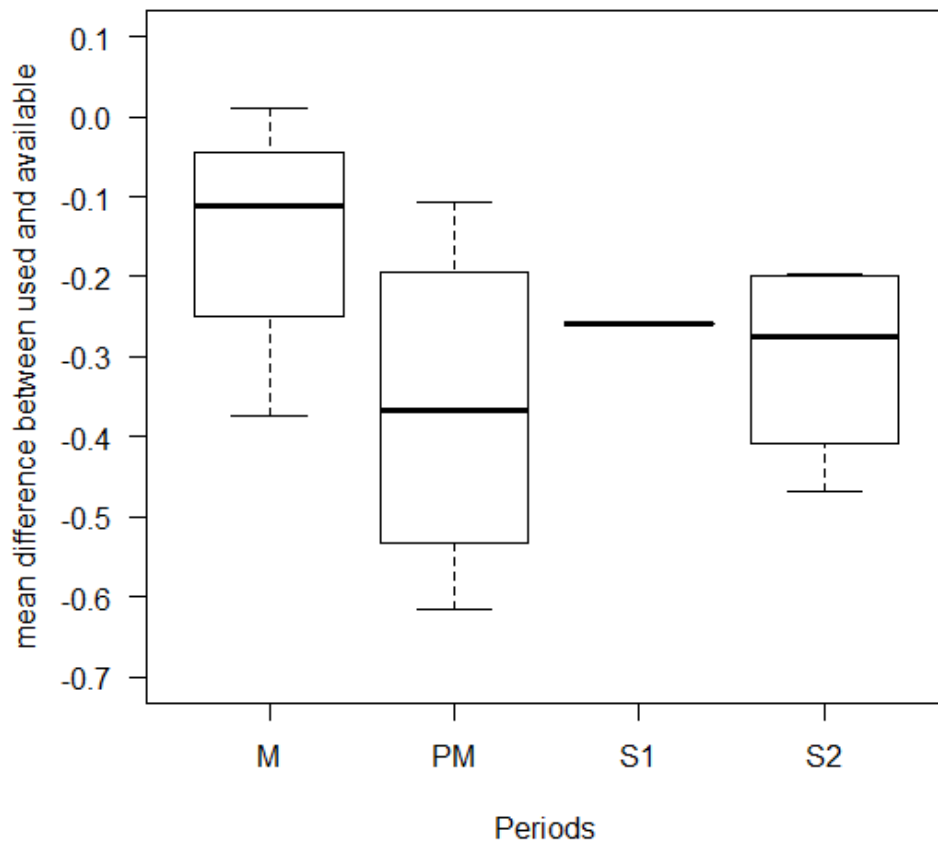


Fig. S1. b.



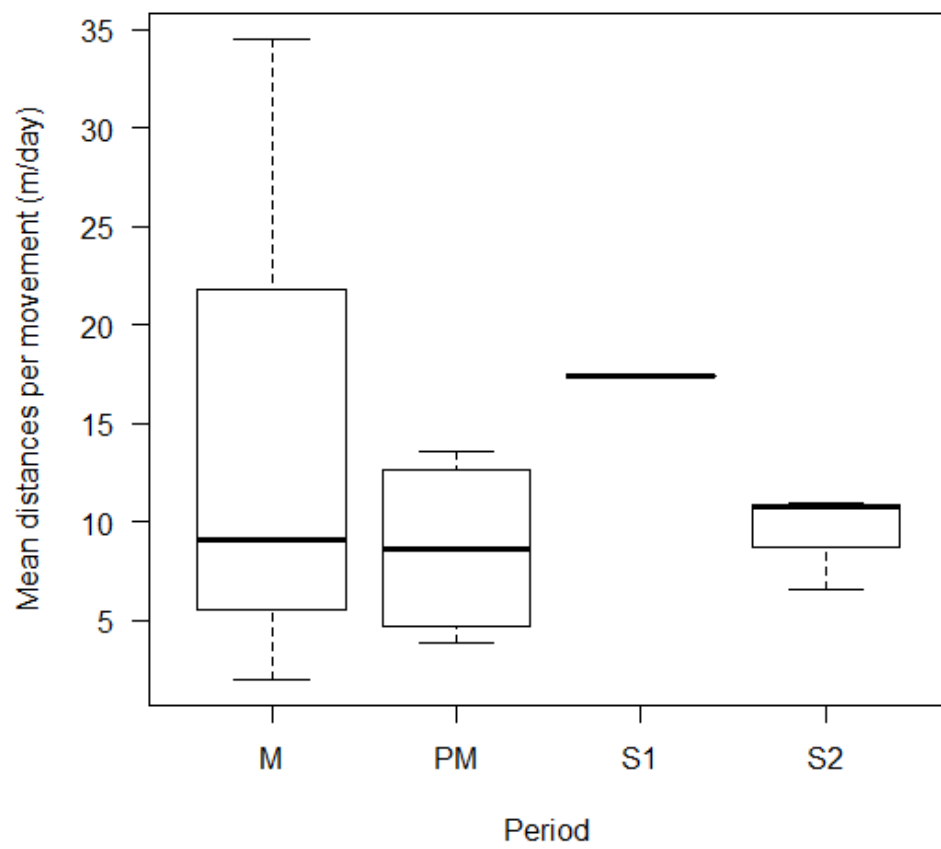


Fig. S2.

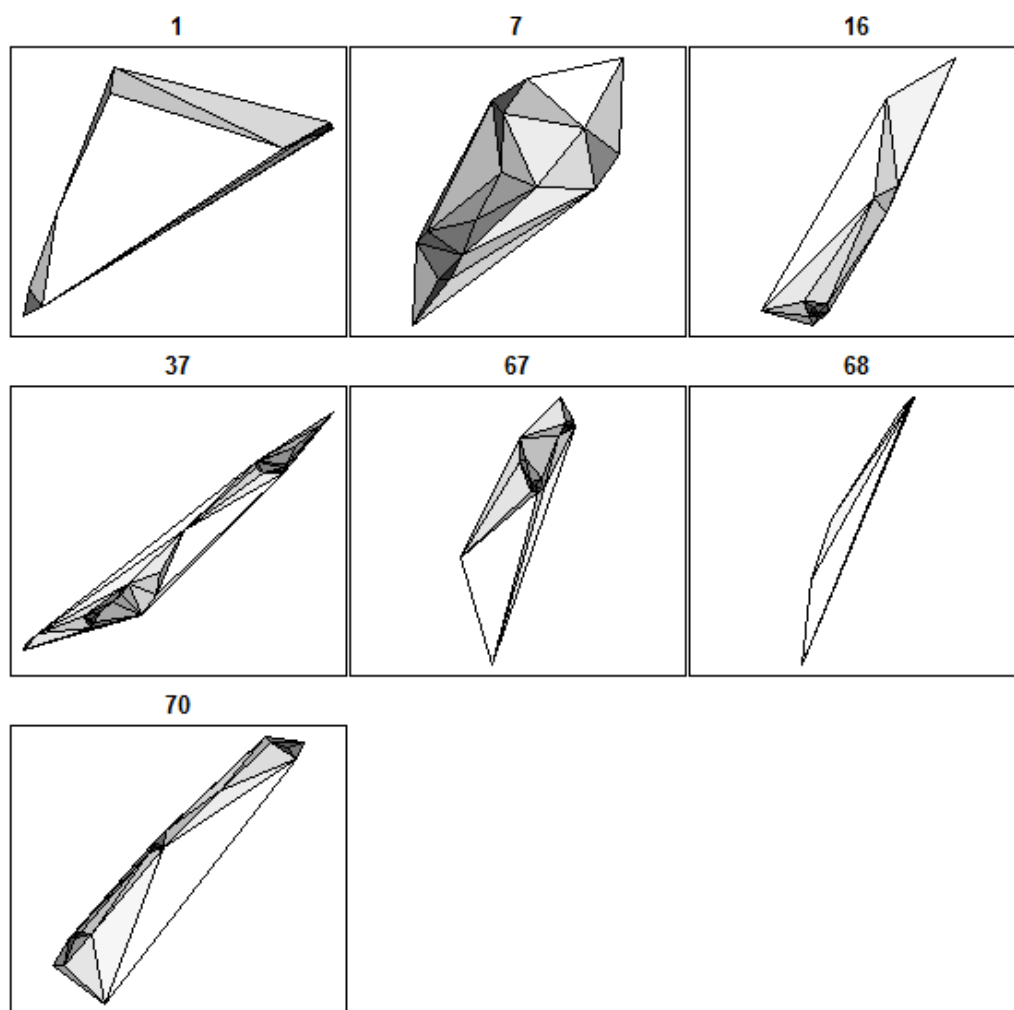


Fig. S3.

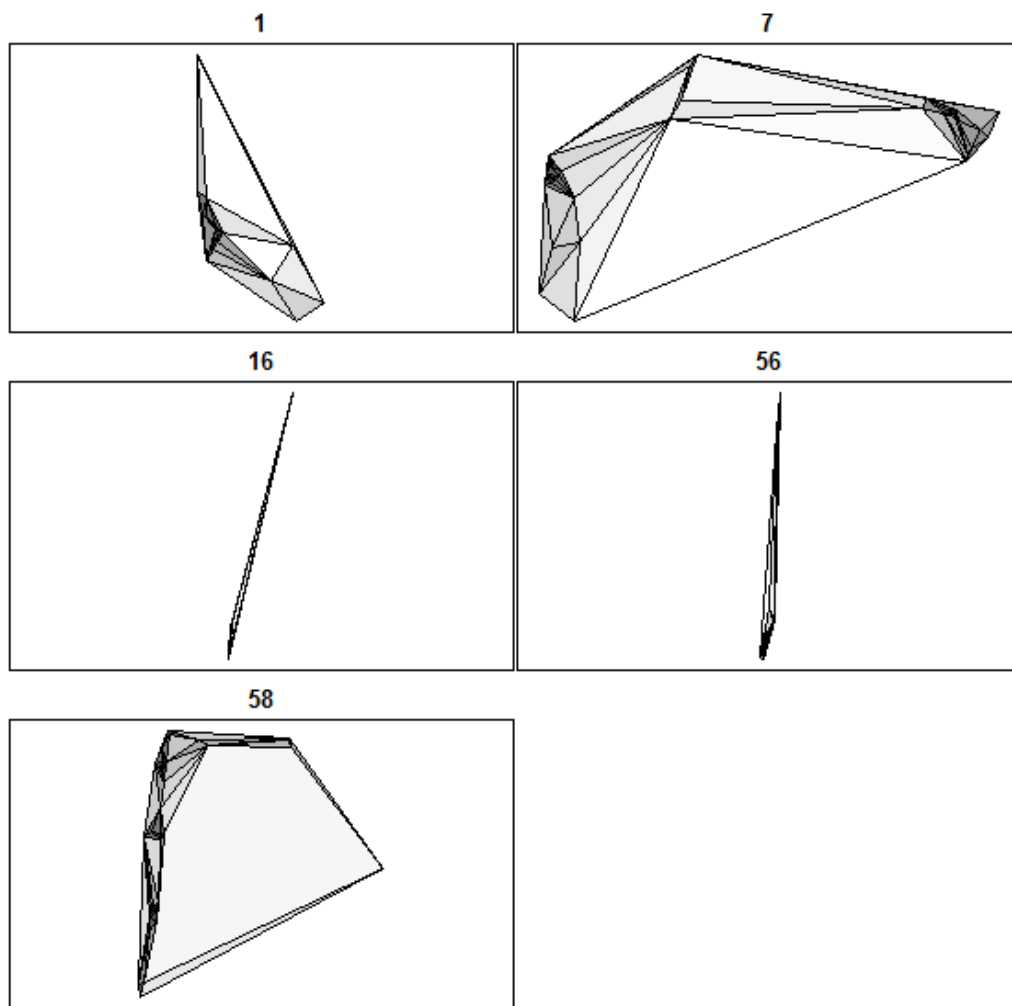


Fig. S4.

## Supplemental Figures Text

**Fig. S1. a.** The effect of periods on the difference between proportions of stone, sand, grit layer on used locations and on available locations (median  $\pm$  1.5 IQR) comparing all resident adders (n = 7).

**Fig. S1. b.** The effect of periods on the difference between proportions of ground layer on used locations and on available locations (median  $\pm$  1.5 IQR) comparing all resident adders (n = 7).

**Fig. S2.** The effect of periods on daily movement distances (median  $\pm$  1.5 IQR) of resident adders (n = 7).

**Fig. S3.** Characteristic Hulls showing home range shape and density of activity for resident adders. Snake ID is given above each home range.

**Fig. S4.** Characteristic Hulls showing home range shape and activity of translocated adders. Snake ID is given above each home range.