



Movements and habitat choice of resident and translocated adult female Grass Snakes (*Natrix natrix*) during the egg-laying period

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We used externally applied transmitters to study movements of female grass snakes (*Natrix natrix*) during the egg-laying period in a near-urban landscape in Sweden. Half of the studied snakes were residents while the other half were translocated individuals with no previous experience of the area. As predicted, resident females moved more goal-oriented and shorter distances than did translocated individuals. Habitat use did not differ between resident and translocated snakes; they were typically found in bushes, reeds, and tall vegetation. Habitat preference (use in relation to availability) showed that bushy habitats, tall grassy vegetation and reedbeds were over-used in proportion to availability, whereas forest and open grass lawns were used less than expected based on availability. Our study highlights the importance of preserving and restoring linear habitat components providing shelter and connectivity in conservation of grass snakes. We suggest that externally applied transmitters are a better option than surgically implanted ones in movement studies of grass snakes, and that translocation as a conservation method for snakes has drawbacks.

Keywords: colubridae; external transmitters; oviposition; radio tracking; telemetry; translocation

INTRODUCTION

Recent global biodiversity trends are of great concern, and arguably seeming especially gloomy for amphibians and reptiles (Gibbons et al., 2000; Wake & Vredenburg, 2008). Recent estimates show that 20 % of reptile species worldwide are threatened by extinction (Böhm et al., 2013). From a European perspective, the situation is hardly any better; several wide-ranging and previously common species are declining for reasons partly unknown (e.g. Reading et al., 2010).

The grass snake (*Natrix natrix*) is one of the most widespread snakes in the northern hemisphere. Several studies indicate that it is declining in parts of Europe, perhaps especially so in the north-western and northern parts of its range (Zuiderwijk et al., 1991; Hagman et al., 2012). There is an urgent need to understand the reasons behind this decline, so that conservation actions can be implemented to reverse the trend. Habitat loss and fragmentation have been suggested to be main drivers behind declines of amphibians and reptiles, not the least in semiaquatic species such as the grass snake (Gibbons et al., 2000). This species is geographically widespread, but at the same time stenotopic. Declines in such species

may be indicative of environmental changes potentially affecting also other species with similar habitat affinities, a fact that may offer valuable insights to conservation biology in general.

The grass snake is the world's northernmost oviparous (egg-laying) snake. In the northerly parts of its range, females are subjected to strong selective pressure to find the most suitable oviposition (nesting) sites. Specifically, finding a nesting site with suitable temperature is a matter of embryo survival, as well as ensuring a normal ontogenetic development versus developing abnormalities at suboptimal temperatures (Löwenborg et al., 2011; Löwenborg & Hagman, 2016; Idrisova & Khairutdinov, 2018). However, over a large swath of its geographical range, ambient heat is not sufficient for successful hatching of grass snake eggs, putting a premium on females finding oviposition sites with elevated temperatures. These sites can be of natural origin (reedbeds, decomposing plant material in littoral drift lines, and wood mould, i.e. loose material of dead wood in hollow trees), but a large proportion of grass snakes in cooler climes instead utilises anthropogenic heat sources such as manure heaps, composts, and sawdust piles for nesting (Nöllert et al.,

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1990; Zuiderwijk et al., 1991; Drews, 2006; Löwenborg et al., 2010; Löwenborg et al., 2012). This association with humans seems to have a long history, as indicated by the presence of grass snake bones and eggs in manure heaps at archaeological sites dating back at least 4000 years (van Wijngaarden-Bakker & Troostheide, 2003; Lenders & Janssen, 2014).

Like many other European reptiles, the grass snake experiences general area loss and fragmentation of its preferred landscapes. In addition, anthropogenic nesting sites have, and are still, declined rapidly due to changes in agricultural practices and environmental legislation pertaining to storage of manure (Hagman et al., 2012). As a consequence, successful conservation of grass snake populations rests on an understanding of preferred habitats, how snakes move in the landscape, and what role nesting sites have for these movements.

It is inherently hard to study movement patterns of reptiles living in temperate areas. They are secretive to start with; their annual period of activity is short, and they will typically stay hidden even during the active season when weather is unfavourable. All this is true for grass snakes, a species whose populations often comprise rather few individuals. The main objective of the present study was to investigate movement patterns and habitat use in female grass snakes during the egg-laying period in an area close to its northern range limit. A second aim was to evaluate if translocated (non-resident) females have a different movement behaviour compared to resident snakes. The rationale behind the translocation treatment is that natural selection will strongly favour individuals capable of finding high-quality nesting sites, which should be easier for local snakes than for translocated ones released in an area previously unknown to them. Moreover, translocations of snakes are already carried out, either intentionally as part of conservation programs, or unintentionally as long-distance stowaways (Fritts, 1987), or when people move unwanted snakes away from their premises (e.g. Reinert, 1991; Wolfe et al., 2018). Based on previous studies we predicted that: 1) translocated females would be less goal-oriented and move longer distance in search for nesting sites, 2) resident females would move goal-oriented towards nesting sites and then stay in their vicinity.

METHODS

Twelve female grass snakes were caught in April of 2014 (N=6) and 2015 (N=6), and were kept in captivity with one or two males in plastic boxes (matings were observed) with water bowls, heating mats, and offered fresh fish occasionally. All females were assumed to be potentially gravid, ranging in weight from 65 to 396 g (Table 1), which corresponds to a total length of >70 cm (unpublished data), e.g. sexually mature (Madsen, 1983). Six snakes (three per year) were caught within the study area (Stockholm: WGS84 coordinates: 59.365569, 18.077703), and six (three per year) were obtained from two populations located far from the study area (five at Uppsala; >50 km from the study area, WGS84:

59.77769, 17.581558 and one at Huddinge; >20 km from the study area, WGS84 59.229388, 18.009853). After spending time with males, all females were released in the beginning of June the same year they were caught. The study area comprised open lawn fields with groves, surrounded by urban areas, and forests with Norway spruce (*Picea abies*), scots pine (*Pinus sylvestris*), birch (*Betula* sp.) and aspen (*Populus tremula*) (Supplementary material, Fig. S1).

All snakes were equipped with an external radio transmitter (model PIP 3, Biotrack Ltd, Dorset, Wareham, UK), including a thermistor measuring body temperature. The transmitters were attached onto the snakes with cyanoacrylate glue (Tozetti & Martins, 2007; Madrid-Sotelo & García-Aguayo, 2008), thin thread, duct tape and surgical tape, laterally mounted behind the cloaca in order not to obstruct egg-laying and locomotion (Fig. 1). The weight of the transmitter package was approximately 4 g, which is less than 5 % of the body weight of the snakes (Blouin-Demers & Weatherhead, 2001; Tozetti et al., 2009; Conelli et al., 2011). The package's circumference did not exceed the thickest part of the snake.



Figure 1. Position of the attached transmitter, laterally behind the cloaca in order not to obstruct locomotion and egg-laying. Photo by Gustav Pettersson.

After being equipped with a transmitter, snakes were tracked during the egg-laying period from 17th June to 15th July in 2014, and from 16th June to 18th July in 2015 (Table 1). Each tracked position was recorded by a handheld GPS and the type of habitat was noted to validate the satellite data subsequently used for the models (see 'habitat choice model' below). The number of positions differed among individuals for several reasons, for example field work effort, sudden longer movements, detectability (above versus below ground), and technical issues with transmitters (Table 1). Snakes were usually tracked three times per day in 2014 and once a day in 2015, generally between 1000 and 1500 hrs. To be able to pool data from the two years, distance

Table 1. Twelve adult grass snake females ('Ind') were caught and fitted with a transmitter in either 2014 or 2015 ('year'). 'Origin' of individuals is either the study site ('resident') or from a population far away ('translocated'). 'Weight' is body mass in grams, 'Days' is the actual number of days each individual was tracked and 'Positions' is the number of recorded positions.

Ind	Year	Origin	Weight	Start	End	Days	Position
1	2014	resident	396	17 June 2014	11 July 2014	24	24
2	2014	resident	126	17 June 2014	11 July 2014	24	24
3	2014	translocated	150	17 June 2014	11 July 2014	24	24
4	2014	translocated	121	17 June 2014	15 July 2014	28	23
5	2014	resident	152	17 June 2014	6 July 2014	19	8
6	2014	translocated	390	17 June 2014	3 July 2014	16	16
7	2015	translocated	160	17 June 2015	6 July 2015	19	15
8	2015	translocated	75	16 June 2015	9 July 2015	23	18
9	2015	resident	200	16 June 2015	9 July 2015	23	16
10	2015	resident	65	16 June 2015	9 July 2015	23	16
11	2015	translocated	165	21 June 2015	18 July 2015	27	14
12	2015	resident	230	19 June 2015	18 July 2015	29	17

sums of multiple daily positions in 2014 were used in the movement distance analyses, resulting in 215 positions used in the movement model. However, in the habitat model all positions were used ($N = 258$). There was no difference in mean body mass, neither between years (t-test: $t = 1.21$, $p = 0.264$, $N = 12$) nor between resident and translocated individuals (t-test: $t = 9.98$, $p = 0.786$; $N = 12$).

Statistical Analyses

For analyses of movement and habitat choice (see below), mixed models were used to control for non-independence of data points, with individual as a random effect to obtain the correct level of replication for the fixed effects. Linear mixed models (LMM) were used for movement analyses and generalised mixed models (GLMM) were used for habitat analyses. In addition, for movement analyses we added body mass nested with individual to increase the fit, a recommended procedure for e.g. repeated measures (Schielzeth & Forstmeier, 2008), and year was included as a fixed factor in all models to control for inter-annual variations. To separate movement variations between years we included an interaction between year and origin (translocated versus resident snakes). Prior to movement analyses, all continuous variables were standardised to a mean of zero. All environmental variables in the habitat model were extracted from satellite data (raster; 2×2 m pixel size), and processed in ArcMap 10.4 (ArcGIS, ESRI, Redlands, CA, USA).

Movement Model

Data concerning moved distance (mid-June to mid-July) and turning angle (the relative movement angle measured by the change of direction between two subsequent relocations), were processed and analysed with the package *adehabitatLT* (Calenge, 2011) in R (R Core Team, 2018). A greater turning angle was assumed to indicate a less goal-oriented movement. Body temperature, body mass, air pressure, sampling day (day of the year) and origin (resident versus translocated) were included as explanatory variables in the models. The response

variable movement distance was set to $\log + 1$ to obtain normal distributions of the models. All twelve snakes were used for each sampling date with missing data (NA) included if no signal was recorded, resulting in regular trajectories. Data handling and statistical analyses were conducted in packages *adehabitatLT* (Calenge, 2011) and *lme4* (Bates, 2010) in R.

Habitat Choice Model

The study area was delineated by a minimum convex polygon (overall home range) enclosing the relocations of all individuals with a 100 m buffer zone added. This area was subsequently divided into 58,702 pixels (2×2 m resolution) corresponding to ca. 63 hectares. Habitats were extracted from rasterized land cover data (Swedish environmental protection agency; www.naturvardsverket.se). The habitat variables initially used in the study were bushes, forest, open areas (grass lawn), tall grass, reedbed, and water, which together covered all pixels. However, water was later excluded, as few individuals were found or located in this habitat. Binary variables were used in this model, i.e. presence or absence of snakes (response variable) and habitat presence (explanatory variables). In addition, individual was included as a random factor and year as a fixed factor to control for these variations.

RESULTS

Field Data

Cumulative movement distances of female in grass snakes varied substantially among individuals. Resident females moved between 174 m and 1578 m, whereas translocated moved 233 to 1985 m (Fig. 2). One resident female (#12) travelled 650 m (Euclidian distance) from the release point to a manure heap, probably to lay her eggs, and one translocated female (#4) travelled 540 m (Euclidian distance) from the release point, reaching the waterfront of the inner archipelago of the Baltic Sea (Fig. S1). Average daily movements of resident females were 26 m, in comparison to translocated that moved 33 m per day. However, most of the translocated grass snakes

Table 2. Output from a linear mixed model showing variables associated with distance moved (dependent variable) by female grass snakes. Individual was set as a random effect and body mass was also nested within the random factor. Sampling days is the number of days with relocation data. Bold *p*-values indicate significant results ($p < 0.05$) and italics denote marginal significance ($p < 0.10$).

Variables	Estimate	SE	t-value	<i>p</i> -value
Body temperatures	0.027	0.092	0.289	0.773
Body mass	0.446	0.246	1.814	<i>0.070</i>
Air pressure	0.125	0.097	1.285	0.199
Sampling days	-0.107	0.112	-0.951	0.342
Origin	-0.969	0.316	-3.069	0.002
Year	-0.652	0.299	-2.182	0.029
Origin*Year	1.031	0.477	2.163	0.031

Table 4. Output from a generalised linear mixed model of habitat utilisation (presence/absence) by female grass snakes and its association with different habitats. Individual was set as a random effect. Bold *p*-values indicate significant results ($p < 0.05$) and italics denote marginal significance ($p < 0.10$). Local and translocated females did not differ in habitat use ('origin' term non-significant in the model).

Variables	Estimate	SE	t-value	<i>p</i> -values
Bushes	2.379	0.386	6.164	<0.001
Forest	-0.530	0.341	-1.557	0.120
Grass lawns	-0.525	0.277	-1.895	<i>0.058</i>
Tall grass	1.530	0.237	6.447	<0.001
Reedbed	2.072	0.231	8.989	<0.001
Origin	0.270	0.485	0.557	0.578
Year	-0.690	0.489	-1.410	0.159

moved > 30 m per day on average (Fig. S2). Number of registered positions did not differ between resident (mean = 17.5) and translocated (mean = 18.3) individuals (t-test: $t = -0.278$, $p = 0.787$).

As is evident from the relocation positions, grass snakes were typically found in open habitats with some kind of cover, often hiding in bushes, reeds, and tall vegetation (Supplementary material, Fig. S1). Habitat preference (use in relation to availability) showed a somewhat different pattern; grass snakes used more bushes, tall grassy vegetation and reedbeds in proportion to availability (Fig. 3) whereas forest and open short-grass habitat were used less than expected based on availability.

Movement Model

In our modelling analysis, origin was the only variable significantly associated with distance moved and turning angle; in other words, translocated females moved longer distances than resident (Table 2) and were less goal orientated (Table 3). The difference in movement between snakes of different origin was most pronounced in the first study year (2014; see interaction term in Table 2). Neither body temperature nor air pressure was significantly associated with distance moved, but body mass came close to contributing significantly to the

Table 3. Model outputs (LMM) of variables associated with turning angle by female grass snakes (the relative movement angle, measured by the change of direction between two steps). Individual was set as a random factor and body mass was also nested within the random factor. Bold *p*-values indicate significant results ($p < 0.05$).

Variables	Estimate	SE	t-value	<i>p</i> -values
Body temperature	0.136	0.222	0.612	0.540
Body mass	0.175	0.286	0.613	0.540
Air pressure	0.194	0.237	0.821	0.412
Sampling days	-0.076	0.292	-0.259	0.796
Origin	-1.670	0.786	-2.125	0.034
Year	-0.329	0.823	-0.399	0.690
Origin*Year	1.424	1.069	1.332	0.183

model (Table 2). Also, sampling days was not significantly associated with distance moved, showing that there was not a bias from individuals tracked for a longer time.

Habitat Choice Model

The habitat model shows that bushes, tall grass and reedbeds were the most important variables significantly associated with presence of female grass snakes (Table 4 and Fig. 3). Open grass lawns were marginally negatively associated with habitat choice. Habitat choice was not associated with the individual snakes' origin (resident versus translocated) and did not differ between the years.

DISCUSSION

Movement patterns

Our initial predictions were supported by field data, that is, translocated snakes moved longer distances and were less goal-oriented (based on turning angle data) than resident snakes. It seems plausible that this is because translocated snakes were searching for familiar habitats, including new locations of oviposition sites, or exploring and becoming familiar with their new environment (Reinert & Rupert, 1999; Nowak et al., 2002). The fact that translocated snakes travelled greater distances concurs with studies of other snake species, including tiger snakes *Notechis scutatus* (Butler et al., 2005), rattlesnakes *Crotalus* spp. (Nowak et al., 1998; Brown et al., 2008; Reinert & Rupert, 1999), the hognose snake *Heterodon platirhino* (Plummer & Mills, 2000), and the dugite *Pseudonaja affinis* (Wolfie et al., 2018), for all of which resident individuals were more confined to home ranges compared to translocated individuals. The same pattern has been found in the common adder *Vipera berus* (largely sympatric with the grass snake), where translocated individuals undertook long-distance and more erratic movements, compared to resident individuals (Nash & Griffiths, 2018). Translocation of snakes is generally perceived as a humane conservation strategy (Reinert, 1991). Nonetheless, this study together with others suggest that such actions are negative, as longer and erratic movements of translocated snakes may result in higher mortality rates compared to

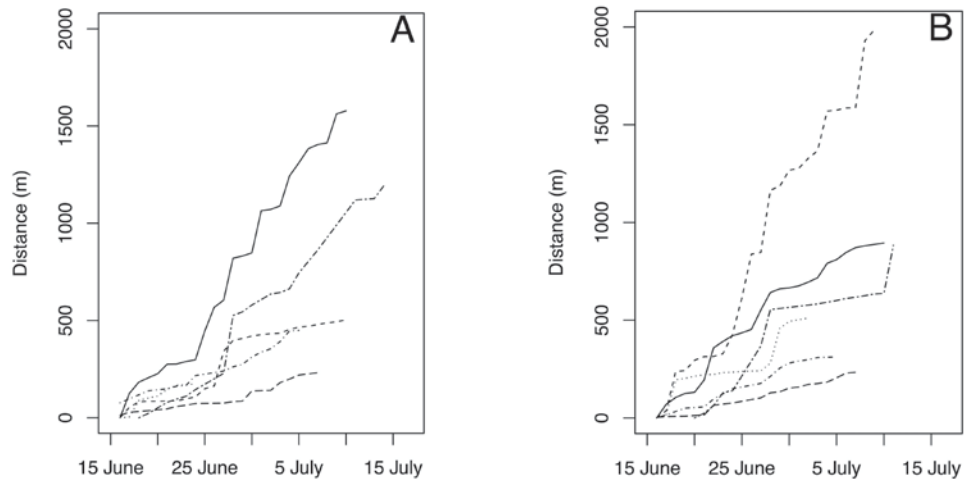


Figure 2. Cumulative moved distances of (A) resident and (B) translocated Grass Snakes (N=6 in both groups) during the egg-laying period (June and July). Different line types represent different individuals.

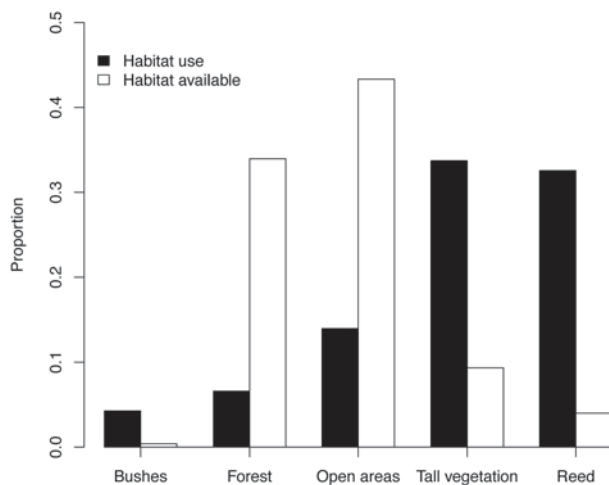


Figure 3. Proportion of used habitat (Habitat use) including 2 x 2-m pixels of bushes; 11 out of 258 pixels, forest; 17/258, open (lawn) areas; 36/258, tall vegetation; 87/258 and reed; 84/258 by all female grass snakes included in the study and proportion of the habitat available in the study area.

resident snakes (e.g. Reinert & Rupert, 1999; Plummer & Mills, 2000; Sullivan et al., 2015; see Implications). In our study, movement differences between resident and translocated females were more pronounced in the first study year, which may be due to greater fieldwork effort in this year. Sampling day had no significant effect on movement patterns among individuals, which may be related to the short study period.

There is little previous research on grass snake movements based on telemetry (but see Madsen, 1984; Nagy & Korsós, 1999; Wisler et al., 2008; Reading & Jofré, 2009). By and large, movements in gravid female grass snakes appear to be rather limited, except during the egg-laying period proper, when they have been reported to increase to 100 m/day on average (Madsen, 1984) and even 26-46 m per hour (Wisler et al., 2007). Although we do not know exactly where the resident snakes laid their eggs, there was at least one example of a female (#12; Supplementary material S1a) moving determinedly

to a manure heap where several other gravid females (without transmitters) most likely also came to lay their eggs. Other females in this study may potentially have found oviposition sites during days of missing tracks, or if they occasionally were out of the tracking range. The maximum Euclidian distance covered by female #12 (650 m) compares well to those documented for egg-laying grass snakes in Switzerland (e.g., ca 500 m from release site to oviposition site in Wisler et al., 2008). Daily movements of resident females in the present study are similar to those published by Madsen (1984), that is, 9-65 m versus 10-50 m.

Habitat choice

By and large, habitat use patterns in the present study fall well in line with previous research (Madsen, 1984; Nagy & Korsós, 1999; Wisler et al., 2007; Reading & Jofré 2009). Specifically, we found that bushes and reedbeds were important habitats for female grass snakes. Both offer thermal benefits and some protection against predators – avian as well as terrestrial – and both have a largely linear configuration in the landscape. A preference for linear habitats offering protection as seen in our study fits very well with results in Madsen (1984), Nagy & Korsós (1999), Wisler et al. (2007), and Reading & Jofré (2009), in which stone walls, embankments, bushes and ‘habitat interfaces’ were preferred.

The frequent use of reedbeds by females in our study may be explained by this habitat offering good opportunities for feeding as well as for thermoregulation. Reedbeds are typically a mix of dense stands and open patches. By moving between these microhabitats, it is easier for snakes to thermoregulate, which is important for gravid females (Madsen, 1987). Possibly for the same reason, cornfields and cereals can provide good habitat for grass snakes at this time of year (cf. Wisler et al., 2008). In comparison to previous studies, which generally tracked grass snakes over several months, the present study was conducted during a relatively short time period (a few weeks). Still, we found strong associations with similar habitat preferences, such as tall vegetation, reedbeds in riparian zones and bushes. This

indicates that grass snakes are strongly associated with these habitats during their active season, and that they may be particularly important for females during the egg-laying period (Wisler et al., 2007).

Implications

Human-mediated translocations of nuisance snakes from urban areas occur globally, including of non-venomous species (Shine & Koenig, 2001). The grass snake is frequently removed from private properties in Sweden and at the same rate as the common adder (T. Thunmark; Snake removal company, pers. comm). The present study identifies potential risks with translocations of female grass snakes, in the form of more erratic movements and longer moved distances post-release compared to resident snakes. Such behaviour may increase energy expenditure (Secor et al., 1992), the cost of reproduction (Devan-Song et al., 2016), and exposure to predators and motor vehicles (Shine & Koenig, 2001; Shine & Mason, 2004). Accordingly, translocated reptiles are commonly reported to have decreased survival rates (e.g. Nowak et al., 2002; Reinert & Rupert, 1999; Sullivan et al., 2015). Therefore, we suggest that long-distance translocations of female grass snakes should be avoided.

The present study also offers implications for habitat conservation. When preserving or restoring environments for grass snakes, it is important to secure linear structures and habitats that provide opportunities for shelter and thermoregulation (cf. Nagy & Korsós, 1999). Doing so will also facilitate dispersal and connectivity between other key habitats, such as foraging and oviposition sites. The crucial role of anthropogenic heat sources for egg-laying grass snakes has been highlighted in previous studies (Hagman et al., 2012; Löwenborg et al., 2010; Löwenborg et al., 2011; Löwenborg et al., 2012), a point further illustrated by a female in the present study that travelled more than one kilometre to a manure heap (cf. Wisler et al., 2007).

ACKNOWLEDGMENTS

Purchase of telemetry equipment was supported by funding from Kristianstad University to Johan Elmberg, by the Swedish University of Agricultural Sciences, and by Helge Ax:son Johnsons Foundation. The study was conducted with permits from Uppsala ethical committee for animal experiments (N77/14), the county administrative boards of Stockholm and Uppsala. We sincerely thank Marcus Hedblom for valuable assistance in methodological matters. We thank Ulrich Hofer and Rachael Antwis for constructive criticism on the original manuscript.

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Accepted: 12 June 2019

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