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Research paper

Between housing and deep forest: Long-term population biology and dispersal of suburban Smooth snakes (*Coronella austriaca*)

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ABSTRACT

We investigated the characteristics of a small smooth snake population in central Germany after it experienced a rapid loss of habitat between 1955 and 1990. We hypothesised that local smooth snakes might demonstrate abnormalities in population characteristics such as age of maturity, growth rates, sex-ratio, reproduction, movement behaviour or in population density, indicating degradation. To address this issue, we analysed data of a 17-year visual encounter survey (VES) accompanied by mark-recapture methods and complemented by a short-term radiotelemetry study of nine adult snakes. We then compared the population and behavioural characteristics with those from other European smooth snake populations. Our results indicated a healthy population despite the severe habitat loss. The population was characterised by a balanced sex-ratio and large litter sizes. Gender specific differences in migration behaviour and home ranges were typical for this species. However, the home ranges were unusually small which agrees with the noticeably high population density and the short time periods tracked. Although adult migration to adjacent habitats was never detected, some migration to and from other suburban sites likely occurred, evidenced annually by the high rate of first-captures of previously unregistered adults. Our results suggested that even a very small area could be sufficient for the survival and maintenance of a viable population of smooth snakes if the habitat provides a high abundance of essential microhabitats. Comparing our population variables with those from other studies help (1) to reduce potential threats at a regional level and (2) to define specific conservation actions for the population.

1. Introduction

Today, the cultural landscape of Europe is characterised by a high degree of fragmentation and degradation. Originally, Europe provided heterogeneous habitats for many species, but has suffered by the historical transformation of traditional land use practices to intensive farming and expansion of anthropogenic infrastructure (Meyer, 2004; Didham et al., 2012; Fischer et al., 2012). This, in turn, threatens many species that inhabit traditional cultural landscapes and increases their risk of local extinction, as has been found for birds (Isenmann and Debout, 2000), small mammals (Andrén, 1994), and amphibians and reptiles (Hels and Nachman, 2002; Moreira and Russo, 2007; Pernetta et al., 2011; Spellerberg and Phelps, 1977). Whereas habitat loss results in direct local extinction, fragmentation leads to reduced gene flow of previously connected populations (e.g., Cheptou et al., 2017; Shine et al., 2012; Stelkens et al., 2012), whereupon marginalised or isolated populations survive under suboptimal conditions. This may cause the degeneration of the remaining populations, recognised by diverging traits in morphology (e.g., increased abnormalities, e.g., Mebert, 2011) and genetics (reduced molecular diversity, e.g., Gautschi et al., 2002), but also in population variables, such as a skewed sex-ratio, reduced reproduction rates, small individual density, small and overlapping home ranges (Banks et al., 2007; Cheptou et al., 2017), and slow growth rate (Filippakopoulou et al., 2015). Such population abnormalities may correlate with a decrease or even failure of reproduction, and ultimately will end also in local extinction (e.g., Cheptou et al., 2017; Didham et al., 2012). Hence, understanding population demography helps to identify isolation (Galarza et al., 2014; Walkup et al., 2017), and comparing its population variables with other studies might indicate a response of a population to a heavily altered habitat.

The smooth snake (*Coronella austriaca* Laurenti, 1768) is a typical element in the cultural landscape of Europe (Pernetta et al., 2011; Reading, 2012; Vacher, 2010). It is restricted to open areas that receive plenty of solar radiation and suitable microhabitats

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(e.g., Engelmann, 1993; Käsewieter and Völkl, 2003). Habitat loss and degradation by intensive agriculture, settlement and roads, has caused a wide-spread decline of smooth snakes in the highly modified European landscape, and many populations are threatened today (Jost and Müller, 1977; Luiselli and Capizzi, 1997; Malkmus, 1973; Pernetta et al., 2011; Santos et al., 2008). Hence, the smooth snake is classified as Vulnerable (category 3 in the Red List) in Germany and (Alfermann et al., 2013; Kühnel et al., 2009). Furthermore, the once cultivated open habitats (e.g., heath, pasture) are often left alone and exposed to succession of rapid bush and forest growth, which results in a shading and cooling effect, and thus exerts suboptimal conditions for local populations in temperate central Germany.

Population characteristics in snakes likely correlate with variations in habitat conditions, such as prey and predator densities, thermoregulation capacities, shelter quality and abundance, and the availability of oviposition and hibernation sites. Unfortunately, ecological studies and observations at population level are particularly challenging in smooth snakes due to their general secretive behaviour (Engelmann, 1993; Hartel et al., 2009; Spellerberg and Phelps, 1977). Yet, geographic variations in population characteristics are known from this species at a large and a fine spatial scale (e.g., Engelmann, 1993; Völkl and Käsewieter, 2003). Smooth snake populations are known to vary in growth rates, maximal body lengths, and habitat use (Engelmann, 1993; Goddard, 1984; Günther and Völkl, 1996; Spellerberg and Phelps, 1977).

In this study, we hypothesised that a population of smooth snakes from a very small site at the periphery of the village Bad Orb in central Germany shows signs of abnormal population characteristics due to survival in a severely altered habitat. The original habitat of the local smooth snakes was a large vineyard that has been reduced in size by 98% between 1955 and 1990. Thereafter, a 17-years long-term monitoring was conducted by a third person and provided to our study, while the data sampling was expanded and a short-term telemetric study of nine snakes added in a follow-up year by the first author. Our objectives were to investigate population characteristics of the smooth snakes from that small site and compare them to other studied populations in Europe. Our null hypothesis designates abnormal characteristics that might indicate altered population conditions, including i) reproduction: fewer offspring, or a later age of maturity; ii) age structure and sex-ratio: unbalanced due emigration of fertile males, lack of immigrant males, age-related mortality; iii) growth rates: lower; iv) population density: lower; v) home ranges: larger; and vi) microhabitat: indication of unusual structure use? In return, these analyses may contribute to deduce relevant factors impacting the study site and to formulate potential conservation actions for the local population of smooth snakes in the future.

2. Material and methods

2.1. Study site

The study site is located between the eastern peripheral houses of the village Bad Orb and the adjacent Mount Wintersberg (440 m a.s.l.), part of the forest of the Natural Park "Hessischer Spessart" of the Spessart Mountains, Hessen, Germany. Historically, about 65 ha of the western and southwestern slopes of Mount Wintersberg consisted of a traditionally-used wine-growing area. In 1955, the reptile-friendly vineyards were increasingly changed through reforestation and the former open area was reduced to 10 ha. Since then, further housing and road development restricted the habitat suitable for smooth snakes to approximately 2% of its original size until 1990 when the data collection for this study started (Sauer, 1997a,b). Today, the study site is characterised by a south-westerly exposed slope along the foot of Mount Wintersberg, at ca. 25 m a.s.l., with a mosaic of open meadows, hedges, forest edge, and open gardens providing plenty microhabitats suitable for reptiles. In particular, more than 70 m of elongated stone piles with deep rocky structures of several meters width, ca. 120 m of traditionally-built, not-sealed dry walls, and stacks of wood along the foot of the slope provided an optimal microniche-rich habitat for the snakes (Fig. 1). The core area of the study site, in which monitoring and radiotelemetry were conducted, is approximately 1 ha in size (45 × 235 m). However, the entire study site with favourable microhabitat conditions (structures and exposition) increased to 2 ha (70 × 300 m), considering adjacent open edge ecotones along the forest and gardens that was used by some smooth snakes, but not monitored due to time constraints. Suitable habitats in the greater surrounding of our study site (up to 2 km, see also Fig. A1 in the Supplementary Material) were inspected for the occurrence of smooth snakes in the proximity, with visits intensified to every second week in the last year of the survey in 2007 (Sauer, 1994, 1997a,b; Dick, 2008).

2.2. Field work and data sampling

Data acquisition on smooth snakes from our study site was partitioned into two sets. A first data set was collected by A. and H. Sauer and provided to us to evaluate population characteristics, such as size and ages of the snakes, sex-ratio, reproduction rates, and population density. They conducted a capture-mark-recapture survey with frequent visits (mean 142 ± 28 visits on 104 ± 25 days per year) of the study site over the period of 17 years from March to November 1990–2006, accumulating data on >200 individuals. A Visual Encounter Survey (VES) was conducted to search and capture snakes by walking on a given path along suitable structures through the study site (see Sauer, 1994, 1997a,b). To facilitate capture of snakes and census a high percentage of the local population, black foils and snake-boards were distributed across the study area with a density of approximately one cover object per 200 m^2 according to Reading (1997) and Mutz and Glandt (2004). Each captured snake was measured on site and photographed for individual re-identification (Fig. A2 in the Supplementary Material). The following variables were measured: body mass (g), number of embryos in gravid females, total length (TOL), snout-vent length (SVL), and tail length (TL) with an accuracy of ±1 cm. Sex was estimated by TL to SVL or TOL ratios. All snakes were released afterwards at the point of their capture.

In 2007, the survey was complemented by a radiotelemetric study on six adult males and three females from the same population to investigate daily migration distances, habitat use, and estimate short-term home ranges. For radiotracking, single-stage transmitters (SOPI 2070, *Wildlife Materials Int.*) were implanted subcutaneously in the stomach region and removed after a period of 24–46 days to minimise the physical stress for the snakes. The mass of the transmitter was ≤4.2% of body mass, which was within the recommended range (Kenward, 2001; Újvári and Korós, 2000). Tracking was executed by direct-positioning with a MVT 7100 (*Yupiteru*) receiver, reaching 150 m in open areas. The individuals were located daily every two hours from 8:00 am to 8:00 pm (European summer time), which corresponds to their activity phase (Engelmann, 1993). Identified point-localities were marked in a detailed map of the area to calculate distances moved and areas covered. Microhabitat data were recorded for each new location (see below).

2.3. Measurements and analysis of population variables

The analysis of population variables was conducted in two ways. Each individual smooth snake contributed only one data point for