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Where do snakes cross roads? Habitat associated road crossings and mortalities in a fragmented landscape in western France

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Reptiles are commonly impacted by roads. Mortalities from road traffic are best documented in snakes, but information on roadside habitat features where snakes cross or attempt to cross roads are less frequently reported. If roadside habitat is important, then snakes should be selective of where they make a crossing. To test this hypothesis, roadside habitats where snakes crossed or attempted to cross roads were compared with roadside habitat availability in a study site in western France. *Vipera aspis*, *Hierophis viridiflavus*, *Natrix natrix* and *N. maura* crossed roads more often than expected next to woodland and low density urban areas. Road crossing locations were also compared with snake abundance in roadside habitat. Frequencies of crossings were higher than expected in woodland and high-density urban areas in relation to their abundance in these habitats. However, abundance related road crossings were less frequent than expected near hedgerows. This suggests that snakes were reluctant to emerge from a habitat pathway that connects prime habitat patches in a fragmented landscape.

Key words: mortalities, road crossings, roadside habitat, roadside snake abundance, snakes, western France

INTRODUCTION

The effects of roads on wildlife include habitat fragmentation as well as direct mortalities from road traffic, but impact on different species in different ways (Fahrig, 2007). For instance, many snakes employ a wide foraging lifestyle that, in landscapes with dense road networks, may necessitate frequent road crossings. Sentinel snake predators, in contrast, have smaller home ranges, cross roads less frequently and usually suffer fewer casualties (e.g., Bonnet et al., 1999, Roe et al., 2006; Meek, 2009). Road mortalities are often spatially distributed due to a suite of factors that include traffic volume on different roads, road width, roadside habitat, road configuration and abundance of snakes in roadside habitats. However, some species avoid roads altogether, for example due to predation risk (Lima & Dill, 1990; Fitch, 1999; Denno et al., 2005; Fahrig, 2007; Shepard et al., 2008b). If snake road crossing locations are indeed primarily determined by predation risk, it might be expected that road crossings are not made at random points but at locations where risk is minimised. Testing these predictions requires null models designed to produce patterns of expected probabilities (Gotelli & McGill, 2006).

A previous study of snake road mortalities in western France found temporal and size class differences that were associated mainly with traffic volume (Meek, 2009). This study adds to these findings by employing new data collected over a nine-year period at the same study locality, and by examining whether snake mortalities and crossings were randomly distributed or clustered using null models (Gotelli & McGill, 2006). Evidence for habitat-associated road crossings is so far limited (reptiles and amphibians: Shepard et al., 2008a; Langen et al., 2009; Meek, 2012; mammals: Clevenger et al., 2003; Clevenger & Waltho, 2005; Dickson et al., 2005), however elucidation of patterns of habitat or abundance-related road crossings could form the foundation of future conservation planning.

METHODS

The data are derived from two sources; snake road mortalities from road vehicles (attempted crossings) and observations of live road-crossings. Four species were observed: *Vipera aspis*, *Hierophis viridiflavus*, *Natrix natrix* and *N. maura*. Surveying was carried out throughout the snake activity period (April–November) between April 2005 and April 2014 in Vendée, western France (46°27'N). Repeated field trips of between 4 and 6 surveys per month at around 4-day intervals during all weather conditions were carried out by a single observer usually between 1000–1700 hours on a bicycle

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at a maximum speed of around 5–10 km/hour. Use of a bicycle has advantages for detection, since slow speeds are more effective in detecting small snakes on roads, which are often overlooked when using a car or other motor vehicle When a live or road-killed snake was encountered, its total length (TL), location and proximate roadside habitat were recorded. Measurements of road-killed snake TL had an estimated error of 10–30 mm depending on body condition and body size. To determine relative abundance in roadside habitat, searches were made for live snakes along road edges. When capture was not possible, snakes were photographed to minimise double counts. Live snake data up to 2008 were already reported in Meek (2009).

The six roads surveyed connect the town of Lucon with the villages of Chasnais, St Denis-Du-Payre, Lairoux and La Brettoniere-La-Clay. They were 5 to 7 metres wide, with one lane in each direction; distances surveyed ranged between 1 km and 6 km (16 km in total). Additional details, including a map of the study locality, road traffic volumes and mortalities on each road can be found in Meek (2009). Major habitats were measured as linear distances on roadsides and classified as follows: monocultures or pastureland with hedgerow borders adjacent to the road (33.6%), monocultures without hedgerows (18.2%), woodland edge (16.5%), high-density urban areas (25.0%) and low-density urban areas (6.7%).

The studied snake species comprise both habitat generalists and specialists (Wisler et al., 2008; Scali et al., 2008). The whip snake (*H. viridiflavus*) is a mainly saurophagus long-range forager (Ciofi & Chelazzi, 1991; Fornasiero et al., 2007), and in the study locality also feeds on other snakes, small mammals and nestling birds (unpublished observations). The grass snake (*N. natrix*) is sedentary when prey is abundant, shifting to foraging when prey is scarce. It feeds mainly on amphibians and sometimes fish (Nagy & Korsos, 1998; Wisler et al., 2008; Reading & Jofré, 2009); regurgitated stomach contents of 17 *N. natrix* in the study area almost entirely contained common toads (*Bufo bufo*, Meek & Jolley, 2006; unpublished data). The viperine snake (*N. maura*) is semi-aquatic, ambushing fish and amphibians from the bottom of ponds or foraging slowly alongside waterways when prey is scarce (Hailey & Davies, 1986). The aspic viper (*V. aspis*) is a sentinel predator preying mainly on small mammals (Canova & Gentilli, 2008).

A Null Model of habitat availability

To structure a null model of expected proportions it was assumed that the locations of dead snakes on roads and where live snakes crossed roads would be randomly distributed if they were found in proportion to the availability of roadside habitat. Whenever a road-kill or road crossing was recorded, a score of 1 was applied when habitats at the point of observation were identical on each side; when habitats differed between sides they were scored as 0.5:0.5. Available roadside habitat was measured by recording approximate linear distances (estimated error ±2m) of habitat on both sides of the road using survey points (e.g., buildings, bridges) and by

employing the distance-calculating tool on Google Earth. Roadside habitat was considered up to 50 m away from the road. The availability of different roadside habitat was converted to decimal fractions and compared with the frequencies of habitat associations of road crossings or mortalities using a one dimensional χ^2 goodness-of-fit test. Selection of roadside habitat is represented by habitat frequencies next to snake crossing points deviating from the null model.

Testing for crossings in relation to roadside abundance

If road crossings or mortalities distributions are a function of roadside abundance, then snake presence in roadside habitat should have a distribution in agreement with corresponding locations of road crossings and mortalities. To construct the null model, VEF (Visual Encounter Frequency; Blomberg & Shine, 1996) was used to estimate snake numbers and the proportions of live snakes caught or observed in different roadside habitat was employed as expected values. Snake road crossing and mortalities in agreement with numbers of snakes in roadside habitat indicates random crossings.
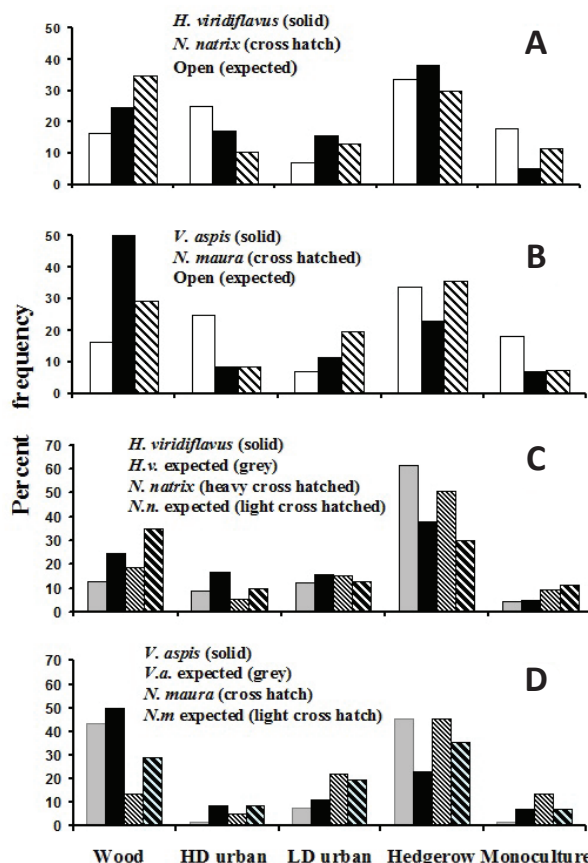

Fig. 1. Graphical summary of frequency (expressed as percentages) of habitat associated road crossings in relation to expected frequency based on habitat availability (A & B) and expected frequency based on snake abundance in roadside habitat (C & D). Definitions of habitat types and data sources are given in Table 1. Grey histograms in C and D are expected frequencies for *H. viridiflavus* and *V. aspis* respectively; light cross-hatched in C and D are expected frequencies for *N. natrix* and *N. maura* respectively.

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Table 1. Observed versus expected frequencies of habitat-associated crossings (A) and road crossings in relation to roadside snake abundance (B). Columns indicate multiples of greater or less (negative values) than expected crossings in relation to habitat availability or species abundance (a value of 1 indicates observed=expected). Urban HD represents high-density urban areas; Urban LD represents low-density urban areas. Values of *p* specify levels of significance in χ^2 tests at df=4 in all tests. The *p*-values for Monte Carlo randomisation tests represent outcomes of probability that χ^2 statistics were equalled or exceeded after 5000 randomisations. Sample sizes (*n*) in A are derived from snakes observed crossing roads or were killed during road crossings; in B they represent live snake numbers used to calculate null models for tests of crossings against snake presence in roadside habitats. See text for further details.

A	Wood	Urban HD	Urban LD	M/culture with hedgerow	M/culture with no hedgerow	χ^2	*p*	Monte Carlo	*n*
H. viridiflavus	1.5	-1.5	2.4	1.1	-3.7	71.2	<0.0001	<0.0001	259
N. natrix	2.1	-2.5	1.9	-1.1	-1.6	48.1	<0.0001	< 0.0001	140
N. maura	1.9	-3.1	2.9	1.0	-2.5	26.4	<0.0001	<0.0001	48
V. aspis	3.0	-2.9	1.7	-1.5	-2.5	32.4	<0.0001	<0.0001	35
B									
H. viridiflavus	1.9	2.0	1.3	-1.6	1.0	72.3	<0.0001	<0.0001	63
N. natrix	1.9	1.9	-1.1	-1.7	1.2	37.1	<0.0001	<0.0001	55
N. maura	2.3	1.5	-1.1	-1.3	-1.9	14.1	0.007	0.009	22
V. aspis	1.2	4.9	-1.1	-2.1	- 2.5	19.7	0.001	0.005	57

Sampling effort for live snakes was approximately proportional to habitat availability. Occasional forays up to 100 m into habitat at roadsides to search for snakes, mostly to confirm identification of a snake seen along the roadside were limited to around 5 minutes. All surveying was carried out across edge habitat, including off road searches. Live snake counts in roadside habitat were of snakes basking (74%) and snakes in movement (26%). The observed live frequencies (percent of total/sample size) in each habitat category were as follows: wood (12.7/8), urban HD (9.5/6), urban LD (11.1/7), hedge (61.9/39), and mono (4.7/3) for *H. viridiflavus*; wood (18.1/10), urban HD (5.4/3), urban LD (14.5/8), hedge (52.7/29), and mono (9.1/5) for *N. natrix;* wood (13.6/3), urban HD (5.4/1), urban LD (22.0/5), hedge (45.4/10), and mono (13.6/3) for *N. maura*; and wood (43.4/23), urban HD (1.9/1), urban LD (6.8/4), hedge (45.3/24), and mono (1.9/1) for *V. aspis*. Percentages were converted to decimal fractions to represent null models for each species, again employing χ^2 goodness-of-fit tests. In Table 1, a value of 1 indicates that observed habitat use equals habitat availability.

The χ^2 statistics in both tests were further evaluated using Monte Carlo analysis (Gotelli & Ellison, 2004) where categorical frequencies were randomised 5000 times to generate simulated χ^2 values. The proportion of simulated χ^2 values that equalled or were greater than the true χ^2 statistics was used to determine significance. The null hypothesis was rejected when this occurred less than 5 percent of the time. The Monte Carlo randomisation test is especially robust when the expected values in the categorical frequencies are low (McDonald, 2009).

Testing for road crossings

An implicit assumption of this study is that, due to the expectation of rapid movement through habitat with increased predation risk (Fahrig, 2007), snake road mortalities were consequences of attempted road crossings. If snakes used roads for basking (Rosen & Lowe 1994), then most carcasses should be situated close to the road edge. Partial support for the road-crossing hypothesis was derived from the observation that all live snakes observed on roads were actively moving approximately perpendicular to the road edge (*n*=35). The position of carcasses was further quantified by dividing them into three categories of 1, 1–2 and 2–3 m away from the road edge, respectively, for *H. viridiflavus* (*n*=206) and *N. natrix* (*n*=108). The data were compared with carcass distribution data for the green lizard *Lacerta bilineata* (*n*=123), a road-basker with a carcass distribution skewed towards the road edge (Meek, 2014), using a Kolmogorov-Smirnov one sample test. Agreement with the null model is assumed to support road-crossings, departure towards positive skewness indicating roadside basking.

RESULTS

The data set comprises 484 snakes in total: *H. viridiflavus, n*=262, including 7 crossing roads, TL range 175–1562, mean=570 mm; *N. natrix, n*=140, including 19 crossing roads, TL range 90–990, mean=453 mm; *N. maura, n*=49, including 4 road crossings, TL range 125–643, mean=362.7 mm; *V. aspis, n*=35, including 5 road crossings, TL range 120–621, mean=311.2 mm). One

hundred and ninety-seven live snakes were captured or sighted in roadside habitats: *H. viridiflavus*, n=63, TL range 210–1430, mean=786.8 mm; *N. natrix*, n=55, TL range 170–960, mean=554.3 mm; *N. maura*, n=22; TL range 190–500, mean=342.2 mm, *V. aspis*, n=57, TL range 109–572, mean=398.7 mm.

In the three species tested, carcass position on the road was skewed towards the side of the road (*L. bilineata*, s=1.21; *N. natrix*, s=0.84; *H. viridiflavus*, s=0.52). However, the Kolmogorov-Smirnov one sample test indicated no significant departure from the null model in *H. viridiflavus* (D_{max}=0.097, p>0.05, df=2) and *N. natrix* (D_{max}=0.145, p>0.05, df=2), whereas the distribution deviated significantly from uniformity for *L. bilineata* (D_{max}=0.296, p<0.01, df=2), supporting the notion that snakes were attempting to cross roads before being killed.

Snakes were observed in higher than predicted numbers on road segments bordered by woodland and low-density urban areas. The deviations from expected frequencies were significant in all four species. The mean multiple deviation (±standard deviation) of woodland edge from random was 2.1±0.55, and highest in *V. aspis* (3.0). Crossings alongside light urban areas were 2.2±0.47 higher than expected. However, road crossing frequencies were not more frequent than expected alongside hedgerows (mean multiple=-0.13±1.18) and less frequent than expected alongside dense urban areas (mean=-2.5±0.62) and monocultures without hedgerow border (mean=-2.6±0.75, Table 1A, Fig. 1).

Tests against abundance at roadsides were significant in all species (Table 1B). Crossings were more frequent than expected alongside woodland (mean=1.8±0.39) and high-density urban areas (mean=2.6±0.1.35) in agreement with expectations alongside low-density urban areas (mean=-0.5±1.04), and less frequent than expected for hedgerows (mean=-1.67±0.28). Only *N. natrix* showed a positive value for crossings in relation to abundance alongside monocultures, with strong negative values in the two sentinel species *V. aspis* and *N. maura*. The mean was negative but with a wide standard deviation (mean=0.55±1.66).

DISCUSSION

As expected, the most frequent crossings were made by the two foraging species *H. viridiflavus* and *N. natrix*, although all study species crossed or attempted to cross roads non-randomly at locations with similar habitat characteristics. The observed association of crossings with woodland may involve using cover to minimise predation risk, including from raptors on telegraph poles at roadsides (Meunier et al., 2000). Predation pressure on snakes by raptors, especially *Buteo buteo*, is high in the region (e.g., Lelievre et al., 2013) and increases when snakes enter more exposed habitat (*V. aspis*: Naulleau et al., 1997). Many species of snake perceive roads as high-risk environments, and minimise the time spent on the roads by crossing at a perpendicular angle (Shine et al., 2004; Andrews & Whitfield Gibbons, 2005) or avoiding crossing roads altogether (Fitch, 1999). Cover-dependent

road crossings are also known in mammals and have been attributed to life history traits (Clevenger et al., 2003; Clevenger & Waltho, 2005; Dickson et al., 2005).

Negative values in the roadside abundance tests indicated that fewer than expected crossings were made alongside hedgerows (Table 1B). Hedgerows facilitate snake movement between prime habitat patches (Saint Girons, 1996). However, examination of road segments where crossings or attempted road crossings were made often involved sections where physical barriers interrupted the hedgerow and hence the movement pathways. Examples were open plan unwalled gardens, road T-junctions or the forecourts of commercial premises. If minimising risk underlies movement, a snake should select the shortest distance through any open terrain (i.e. the least cost path; Fahrig, 2007). If the road width at these locations is less than the open sections interrupting the hedgerows, then an optimal decision would be to cross the road rather than attempting to cross the wider expanse of, for example, a garage forecourt. This decision might also reduce the risk of overheating in smaller or slower moving snakes (e.g., Shine & Fitzgerald, 1996).

Perhaps unexpectedly, no snakes were found basking on roads, which contrasts with studies elsewhere (e.g., Andrews & Gibbons, 2005; Shepard et al., 2008a) and with sympatric lizards *L. bilineata* (Meek, 2014). Road basking increases the time reptiles spend on roads but factors other than predation risk may be involved. For instance, crossings at habitat with cover may reduce thermal stress during the hottest months, when road surface temperatures may reach 50 degrees Celsius (personal observation).

Surveying for snakes is known to be difficult (e.g., Fitch, 2001), and snake detectability might vary depending on time and habitat. This questions the accuracy of VEF as a method for estimating snake abundance, although reasonable results can be obtained if sampling is homogeneous (Scali et al., 2008). The present results cannot unequivocally demonstrate that more snakes crossed roads at non-random locations because certain roadside habitat represented less risk from predators or because those habitats had higher numbers of snakes present. This study does nevertheless provide an empirical understanding that road crossing locations in snakes were associated with roadside habitat.

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