

Patterns of reptile road-kills in the Vendée region of western France

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Road mortalities of two lizard and four snake species were recorded in the Vendée region of western France over a period of four years. Road-kills were more frequent in the foraging snakes *Hierophis* (= *Coluber*) *viridiflavus* and *Natrix natrix* as well as the lizard *Lacerta bilineata*, and lower in the small lizard *Podarcis muralis* and the sedentary snakes *Vipera aspis* and *Natrix maura*. Road-kills were found throughout the active year, with differences in size class and monthly frequencies in *H. viridiflavus*, *N. natrix* and *L. bilineata* commencing in June. Pearson rank correlation coefficients revealed a significant positive association between monthly road-kill and monthly live counts of *H. viridiflavus* and *N. natrix*, suggesting regular road crossings in these species. Road traffic volume was related to the number of road deaths using regression analysis of the log-transformed data. This gave an allometric equation with an exponent of 0.75, which was not significantly different from 1, the exponent required if road-kills increase in direct proportion to increasing road traffic volume. The highest traffic volume route showed lower than expected mortalities, but fewer numbers of species living in the vicinity. Models of road-kill vulnerability in *H. viridiflavus* and *N. natrix*, derived from the integration of size frequencies of road-kill and live distributions, predict high vulnerability in small and large individuals. In lizards, particularly *L. bilineata*, road basking is probably the main factor determining mortality, in addition to species velocities, traffic volumes, road widths, abundance at the sides of roads, and behaviour and activity patterns.

Key words: behaviour, lizards, snakes, traffic volumes

INTRODUCTION

Reptiles suffer natural mortality for many reasons, including effects of the environment, predation and disease, but evolutionary forces have enabled species to respond to natural mortality with a variety of compensatory mechanisms. However, anthropogenic activities are in evolutionary terms sudden, and knowledge of the impact of road building programmes and associated road traffic on reptile ecology is limited (Rudolph et al., 1999). Road effects are in theory twofold: they fragment the landscape, isolating key resources from species that treat roads as barriers (Wymen, 1991; Spellerberg, 2002; Andrews et al., 2006), and inflict casualties on species that cross roads.

Patterns of reptile road-kill vary, from cases where bulldozers have been employed to scrape the carcasses from the road (e.g. *Thamnophis sirtalis*, Shine & Mason, 2004) to others where road-kills are negligible despite high abundance of individuals in the vicinity of roads. To explain the differences, researchers have drawn attention to several potential variables, and identify abundance at roadsides, behaviour and the influence of the environment on behaviour as crucial factors (e.g. Bonnet et al., 1999; Andrews et al., 2006). Velocities when crossing roads, body length (Hels & Buchwald, 2001; Gibbs & Shriver, 2002), movement patterns, sensitivity to vehicles (Jaeger et al., 2005), traffic intensity (Foreman et al., 2003) and habitat changes associated with road construction (Kjoss & Litvaitis, 2001) also contribute to patterns of road-kills.

Road-kills potentially impact on all species, but are a particular threat to those with slow population turnover (Goodman et al., 1994; Haxton, 2000; Gibbs & Shriver, 2002; Szerlag & McRobert, 2006; Row et al., 2007) and with time could ultimately change mortality–recruitment ratios (Rosen & Lowe, 1994). The potential effects on population dynamics are critical, and lead to the key questions of to what extent anthropogenic activities add to natural mortality, and which species are most vulnerable and when. Interspecific differences in movement patterns are one of the potential causes determining road-kill frequencies (Bonnet et al., 1999). For example, sit-and-wait predators may be abundant in roadside habitats but have limited locomotory activity and low road crossing frequency, whilst a wide-ranging forager with relatively high activity levels may cross roads more frequently and be subject to greater risk. This is an important conservation issue since foraging species may potentially suffer greater population impact from roads. If movement is a key contributing factor, then it can be assumed that if a species is living alongside road corridors and frequently crosses roads, it will suffer road-kill in proportion to its roadside abundance. Part of this study tests this prediction by examining the strength of the association between monthly mortality and monthly roadside sighting/capture frequencies. The study also seeks to examine the effects of differing traffic volumes on road deaths and to determine which species and sections of the populations are at risk. The area surveyed was in the Vendée region of western France, where the activity period of reptiles lasts around eight or nine months.

MATERIALS AND METHODS

Study area

Information was collected over a four-year period beginning in 2005 from a series of roads in the Vendée region of western France (46°27'N; Fig. 1). A single observer using a pushbike carried out most of the road surveying at a maximum speed of around 5–10 km/hour. A feasibility study undertaken beforehand indicated that surveying by car or motorcycle at around 20 km per hour failed to locate many of the smaller individuals; walking is probably more effective but cycling enables greater areas to be covered. The road segments sampled (Fig. 1) connect the town of Lucon to the village of Chasnaïs (D949, approximately 1.2 km), Chasnaïs to Lairoux (D44, approximately 1.2 km), La Bretonniere-La-Clay to St Denis-Du-Payre (D60, approximately 6.1 km), Chasnaïs to Triaize (D127, approximately 1 km), and include the rue de Bourneau in Chasnaïs village (approximately 0.5 km) and an unnamed road running from St Denis-Du-Payre to Chasnaïs (from rue de Moulins in the village of St Denis-Du-Payre to Chasnaïs, approximately 6 km). Between four and six surveys per month on each road section were undertaken. The surveys were spaced 3–4 days apart, one series mid-week and the other

at weekends. For logistical reasons, D949, D127 and rue de Bourneau were surveyed on different days to those on the D44, D60 and St Denis-Du-Payre to Chasnaïs road. Sampling usually commenced at midday and required 5–7 hours for the D44, D60 and St Denis-Du-Payre to Chasnaïs road and around two hours for the D949, D127 and rue de Bourneau. The roads are all two lane but differ in width from 5 to 7 m. Simultaneously, short sections of other roads running off the main study roads were systematically searched. Data on 42 monitored road-kills of both snakes ($n=33$) and lizards ($n=9$) gave a mean of 7.9 days ($SD=10.4$) for a carcass to remain on the road. However, the frequency distribution was heavily biased toward low persistence time ($S=1.86$), suggesting that inevitably some carcasses were missed. The bordering habitats have a largely flat topography that includes woodland, grass-covered fields with occasional ponds and extensive arable land, but also houses with gardens and hedgerows of varying heights as well as marshlands, some of which form part of La Reserve Naturelle, St Denis-Du-Payre.

Sampling methods

To test predictions about vulnerability to road-kill, road-kill frequency was compared with corresponding numbers of live animals found at the roadsides. Individuals living within a distance up to about 100 m from the roadsides were captured and measured or counted if capture was not possible. This included animals in the process of a road crossing, those located whilst searching under rocks and logs and during locomotory movement or basking. This method reduces bias since it does not rely totally on activity for detection. Direct observations of road-crossing snakes were low (three *Hierophis viridiflavus*, three *Natrix natrix*, one *Vipera aspis* and one *Natrix maura*).

The live animal surveys were conducted on the same days as those for road-kills and were essentially concurrent in the sense that areas were also searched on foot during the road surveying. Capture of live animals was not always possible, in which case information, particularly from lizards, was taken from photographs with a digital camera and approximate size then assessed using objects in the immediate environment for scale. After measurement any captured animals were released. Since no animals were marked, some live animals could have been counted more than once. However, the counts were relatively low and over a four-year period, and it is thus assumed that multiple counts of individuals were limited. Additionally, the two snakes *H. viridiflavus* and *N. natrix* are known foragers covering extensive distances during activity (see below). There was no evidence of reptiles suffering road-kill as a result of being disturbed.

Carcasses were not removed from the road but locations were noted to avoid double counts. Measurements of all individuals were made using a flexible tape. In snakes, total body length (TL) was measured since it is possible for a lethal collision to result from being attached to the road by the tail and rendered immobile after an initial non-lethal collision. In lizards, snout–vent length (SVL) was measured, on the assumption that tail damage during a collision would have minimal or no effect.

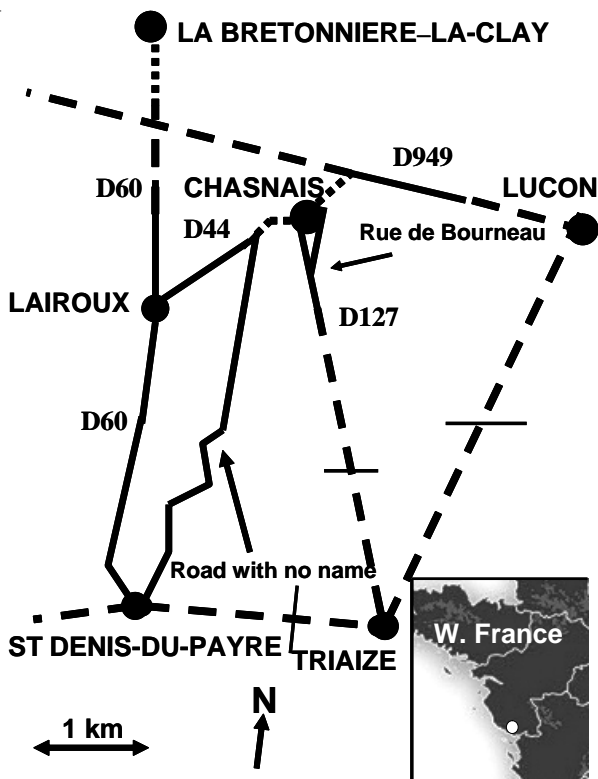


Fig. 1. Map of the study area showing sampled roads (heavy lines) and major towns or villages in the vicinity. Broken lines indicate non-sampled road segments and double lines across roads indicate roads that are not to scale. The white circle in the insert represents the study site.

Table 1. Size frequencies of road killed (DOR) and live samples in six species of reptile in the Vendée region of western France.

Species	Category	Mean total	Length	<i>n</i>
		length ±SD (mm)	range (mm)	
<i>H. viridiflavus</i>	DOR	678.5±458.2	175–1445	70
<i>H. viridiflavus</i>	live	708.7±351.3	210–1430	32
<i>N. natrix</i>	DOR	524.1±297.1	90–965	57
<i>N. natrix</i>	live	593.8±223.3	180–960	27
<i>N. maura</i>	DOR	392.3±119.0	200–640	13
<i>N. maura</i>	live	342.2±86.3	190–500	9
<i>V. aspis</i>	DOR	278.6±92.0	120–410	12
<i>V. aspis</i>	live	461.1±84.0	356–572	7
<i>L. bilineata</i>	DOR	90.3±15.7	60–115	37
<i>L. bilineata</i>	live	97.6±14.5	75–115	12
<i>P. muralis</i>	DOR	53.2±13.0	24–73	10
<i>P. muralis</i>	live	46.1±14.0	26–70	20

Weather conditions within a day or so of each location were recorded. Air temperature was measured with alcohol thermometers 15 cm above ground.

Defining size classes

Frequent heavy body damage generally prevented the sexing of road-kills accurately and hence this was not employed in the analysis, but a note was made of whether the animal was adult, subadult or neonate. Size and age categories (when known) were derived from information given in Street (1979), Arnold & Ovenden (2002) and other sources (see below). Adult *H. viridiflavus* were animals exceeding 500 mm TL, which is approximately the size at which there is a change to adult coloration. Neonates were up to 250 mm TL, subadults 250–500 mm TL. Neonate *N. maura* and *V. aspis* were below 200 mm TL, and subadults were 200–350 mm and 200–400 mm respectively. Size categories for *N. natrix* are those described by Gunther & Volk (1996) and Ciesiolkiewicz et al. (2006). Maturity was defined as above 500 mm TL; animals of 250–500 mm were classed as subadults and those less than 250 mm as neonates. Adult *Lacerta bilineata* were defined as animals exceeding 80 mm SVL. No neonate *L. bilineata* were seen dead on the road or living close to the road and so only subadults (below 80 mm) and adults were defined. *Podarcis muralis* lizards exceeding an SVL of 50 mm were classed as adults, subadults were 25–50 mm SVL and neonates were less than 25 mm SVL.

Statistical analysis

Data collected from March/April to October/November were analysed, depending on the activity period of the species. Traffic volume was counted in both directions in 30-minute periods on the same days as the road-kill surveys, and adjusted to traffic volumes per hour. Road-kills were measured as casualties per kilometre, unless stated otherwise. When constrained by non-parametric data sets, Mann–Whitney *U*-tests were used. For percentage

comparisons a *z*-test for independent proportions was employed. To test for road traffic volume effects on the number of road-kills, regression analysis was applied to the data after transforming to logarithms. The resulting allometric equation was tested for significant departure from a theoretical exponent of 1 using a *t*-test at *n*–2 degrees of freedom (Bailey, 1981).

For monthly road-kills, the frequencies were tested for departure from regularity using a χ^2 test set at the 95% interval. The null hypothesis was no significant monthly differences during the active season (April to October). The data from all species were pooled but excluded March and November, when very low numbers were recorded.

RESULTS

General counts

In total, 152 snakes of four species and 47 lizards of two species were found dead on the road (Fig. 2, Table 1). The highest numbers of road-kills were recorded in the snakes *N. natrix* and *H. viridiflavus*, followed by the lizard *L. bilineata*. Lower road-kills were recorded for *V. aspis*, *N. maura* and *P. muralis*. Adults suffered the highest road-kill in all species except in *V. aspis* where subadults predominated. After adults (*H. viridiflavus* = 48.6%; *N. natrix* = 54.4%), neonates were the most common in *H. viridiflavus* (35.6%) and *N. natrix* (29.1%), although in *N. maura* and *L. bilineata* subadults were the next frequently found size class. There were no differences in size class proportions found dead on the road between the foraging snakes *H. viridiflavus* and *N. natrix* (i.e. comparisons of proportions of neonates, subadults and adults; *z*-values 0.23–0.79, *P*-values 0.42–0.91). Sample sizes were small in the sedentary species, but the percentage of adult road-kill in *V. aspis* (8.3%) was significantly lower than in the foragers *H. viridiflavus* and *N. natrix* (*z*-values 4.1 and 4.4, *P* = 0.01), with the majority (91.7%) of *V. aspis* consisting of subadults and neonates. However, adult road-kill was relatively high in the sedentary *N. maura* (adults, 69.2%; subadults, 23.1%; neonates 7.7%)

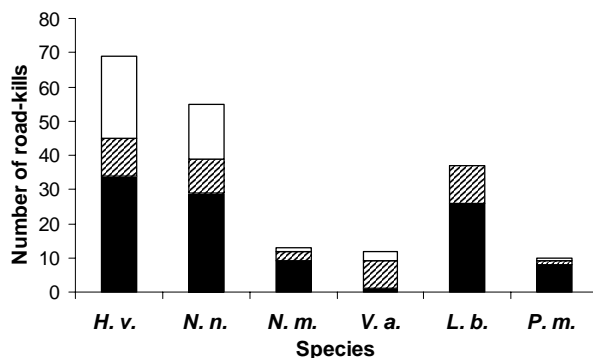


Fig. 2. Number of reptile roadkills in the Vendée region of France. Hv = *Hierophis viridiflavus*, Nn = *Natrix natrix*, Nm = *Natrix maura*, Va = *Vipera aspis*, Lb = *Lacerta bilineata*, Pm = *Podarcis muralis*. Solid, cross-hatched and open areas represent adults, subadults and neonates respectively.

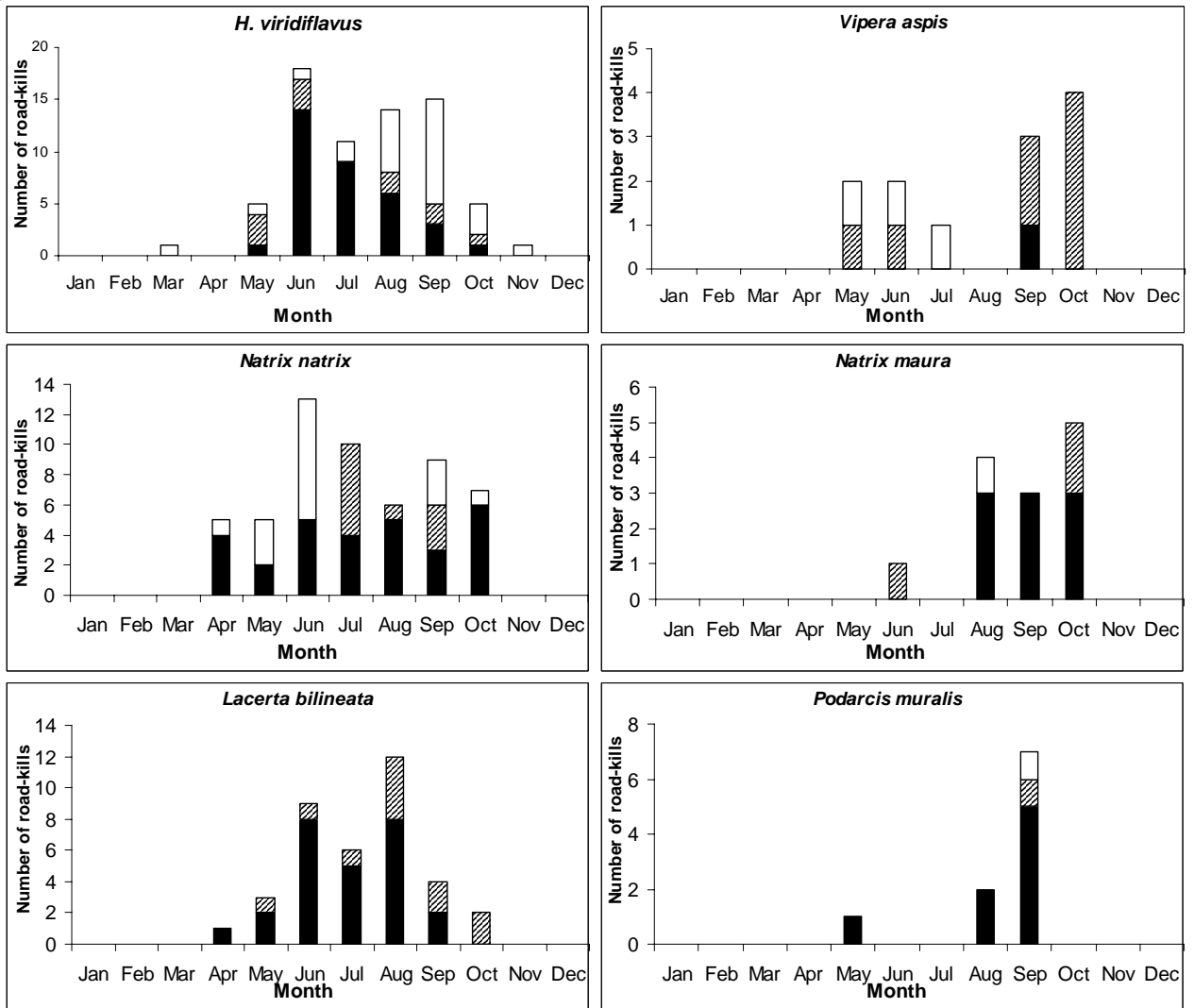


Fig. 3. Monthly frequencies in road kills in four snake and two lizard species. The histograms on the left show species with the highest road-kills. The graphs show monthly changes in adult and neonate road kill, particularly in *H. viridiflavus*, but similar levels in adult *N. natrix* from April through to October. Also indicated is late summer and autumn road kills in *N. maura* and the apparent lack of any clear pattern in *V. aspis* other than a low number of adults. Also indicated is higher *L. bilineata* road kill than found for *P. muralis*. Definitions of age categories as in Fig. 2.

when compared to *V. aspis*, $z=4.03$, $P=0.01$. Adult road-kills were similar in both species of lizard (*L. bilineata* = 70.2%; *P. muralis* = 80%; $z=0.66$, $P=0.51$) despite the differences in absolute road-kill ($n=37$ versus $n=10$).

Monthly road-kill

Road-kill frequency is related to season (Fig. 3, $\chi^2=39.77$, $P<0.001$, $df=6$). For example, road-kill in *N. maura* and *P. muralis* was largely from late summer through to autumn. In *H. viridiflavus*, *N. natrix* and *L. bilineata*, high levels of road-kill began in June with lower numbers in April (*N. natrix*) and May (*H. viridiflavus* and *L. bilineata*). Taken as percentages of seasonal road-kills, adult *H. viridiflavus* suffered higher road-kill during July and August (67.4%) compared with September to November, when it was 19.1% ($z=4.37$, $P<0.01$). Most neonate road-kill in *H. viridiflavus* was from August to October (55.8% of 34), with lower levels from May through to July (11.8% of 34); the difference between the two periods was significant ($z=4.33$, $P<0.01$).

Relationship of road-kills to live samples

Mann–Whitney *U*-tests showed no significant differences between medians of the live and road-kill size distributions in either *H. viridiflavus* or *N. natrix* ($w=3629.0$ and $w=2718.5$, P -values 0.37 and 0.89 respectively). Two-sample *t*-tests for the remaining species indicated a significant difference between road-kill and live samples only in *V. aspis*, with live individuals significantly longer ($t=4.41$, $P=0.001$, $df=13$). The *t*-tests for the remaining species were from 1.14, to 1.48, P -values from 0.18–0.26. These results show size-class frequencies of road-kill are in agreement with size-class frequencies of live individuals in *N. maura*, *L. bilineata* and *P. muralis*.

Tests for a relationship between monthly road-kills and monthly live samples were made using Pearson rank correlation coefficients. The results indicated an association in *H. viridiflavus* ($r_s=0.77$, $P=0.02$, $n=9$) and *N. natrix* ($r_s=0.71$, $P=0.03$, $n=9$) but not in *N. maura* ($r_s=0.52$, $P=0.24$, $n=7$), *V. aspis* ($r_s=0.15$, $P=0.74$, $n=7$), *L. bilineata* ($r_s=0.39$,

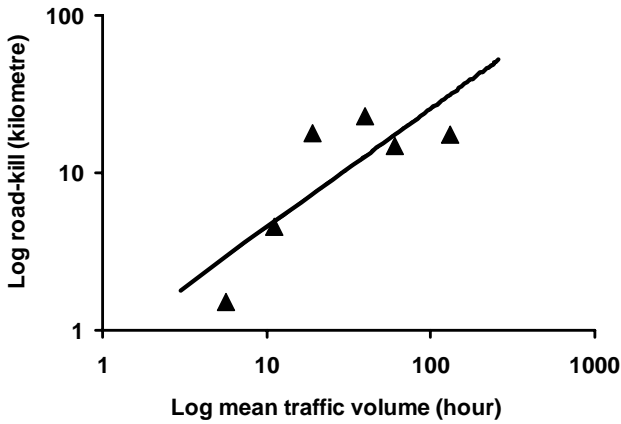


Fig. 4. Logarithmic coordinates of traffic volumes on six surveyed roads plotted against corresponding levels of roadkill. The line running through the data points was calculated from equation 1. See text for further details.

$P=0.33$, $n=8$) or *P. muralis* ($r_s=0.23$, $P=0.55$, $n=9$). The n values represent number of paired months. In general, the ratios of road-kill to living samples (road-kill/live sightings + captures) were lowest in the lizards *P. muralis* (0.03) and *L. bilineata* (0.42). In snakes, the ratios were greater than 1 (*H. viridiflavus*: 1.29, *N. natrix*: 1.42; *V. aspis*: 1.09, *N. maura*: 1.18).

Relationship of traffic volume to road-kill numbers

There was a non-linear trend when road-kill numbers were related to traffic volume on the six main roads surveyed. With road-kill treated as the y-variable and road traffic volume as the x-variable, the best fit to the data was provided by the allometric equation:

$$\text{road-kill} = 0.79 \text{ traffic volume}^{0.75 \pm 0.26} \quad (1)$$

($r^2=66.0\%$), with the coefficient of determination significant ($P=0.02$). This approach assumes that habitat structures or traffic noise do not act as deterrents for different reptiles. Although the exponent indicates negative allometry, it is not significantly different from 1 ($t=0.96$, $P>0.05$), the exponent required when road-kills are increasing in direct proportion to increasing road traffic volume (Fig. 4). Low traffic roads such as D44 and D127 recorded higher than expected road deaths, perhaps due to surrounding favourable habitat where all six species occurred. However, the D949, with high traffic volume, had less road-kill than expected, with *N. natrix* and *H. viridiflavus* forming 84% of the sample; *V. aspis* and *L. bilineata* were apparently absent.

Size class vulnerability in *N. natrix* and *H. viridiflavus*

If individuals suffer from road-kill in equal size-class frequencies, then it is a reasonable assumption that road-kill size frequency should be in approximate agreement with live sample frequency. In *H. viridiflavus* and *N. natrix*, the size distributions differed with a bias towards small and large animals in road-killed individuals. To clarify this bias, both distribution frequencies were integrated to calculate vulnerability models. The differences in

percentage frequencies between the histogram cells were treated as $f_m - f_l$, where f_m is the road-kill size frequency and f_l the corresponding live sample frequency, plotted against size class frequency f_s . Vulnerability to road-kill V was then determined from a second-degree polynomial:

$$V(f_m - f_l) = b + m_1 f_s + m_2 f_s^2$$

where b , m_1 and m_2 are the constants. This gives:

$$V(f_m - f_l) = 28.54 - 0.1f_s + 0.00006f_s^2 \quad (2)$$

($r^2=79.2\%$) for *H. viridiflavus*, and

$$V(f_m - f_l) = 24.46 - 0.1f_s + 0.00009f_s^2 \quad (3)$$

($r^2=65.8\%$) for *N. natrix* (Fig. 5; the x-axis on the graphs represent vulnerability to road-kill in equal proportion to size-class frequency). The r^2 value is higher for *H. viridiflavus*, as is the size range, but a good fit was also found for *N. natrix*. The equations predict lower than expected vulnerability in snakes from around 400 mm to around 1000 mm in *H. viridiflavus* and from around 300 mm to slightly more than 900 mm in *N. natrix*. Adults and neonates in both species therefore have higher than expected vulnerability.

DISCUSSION

Roads were not avoided by any of the species found living at the road margins and crossings resulted in frequent mortalities. The majority (76%) of road deaths concerned snakes, of which 83.5% were the foraging species *H.*

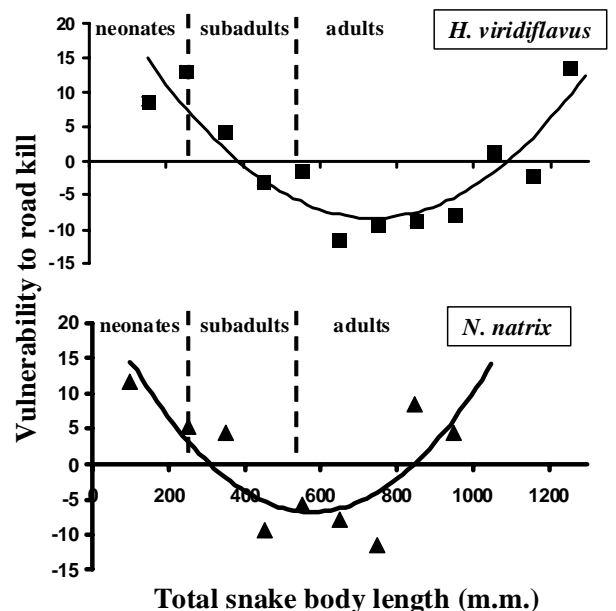


Fig. 5. Probability models of road-kill risk in *H. viridiflavus* and *N. natrix* calculated by integrating the size frequencies of road-killed and live samples. The parabolas have been calculated from equations 2 and 3. The x-axis represents where size-class vulnerability would be in equal proportion to size-class frequency in the live population, above the x-axis where there is higher than expected risk, and below the x-axis where risk is lower than expected. Vertical broken lines delimit size and/or age class (see text).

Table 2. Road specific mortality given as percentages for each species (data from rue de Boureau excluded due to low sample size). Values in parenthesis are mean traffic volumes per hour on each road. Total road kills n on each road and n per kilometre are also given.

	StDen–Chas					Mean±SD
	D60 (60.2)	D44 (39.7)	(rue de Moulins) (11.1)	D949 (130.2)	D127 (19.1)	
<i>H. viridiflavus</i>	38.5	40.0	18.5	53.8	25.0	35.2±12.4
<i>N. natrix</i>	20.5	37.5	37.1	30.7	20.0	29.2±7.7
<i>V. aspis</i>	5.1	3.1	14.8	0.0	5.0	5.6±4.9
<i>N. maura</i>	3.8	6.2	7.4	7.8	20.0	9.0±5.6
<i>L. bilineata</i>	29.5	12.5	11.1	0.0	20.0	14.6±9.8
<i>P. muralis</i>	2.5	6.2	11.1	7.8	10.0	7.5±3.0
Total n	78	32	27	13	20	28.8±26.2
n/km	14.8	22.8	4.5	17.6	18.0	13.2±8.4

viridiflavus and *N. natrix*. Road-kill in *H. viridiflavus* was seasonal, and highest during the period after birth (from August through to autumn). In adults, it peaked in June, persisting throughout summer into autumn. Road-kill in *N. natrix* also peaked in June and was found over a longer period of the active year, with relatively high deaths of neonates in May and June, perhaps indicating dispersal after spring (Fig. 3). This has been observed in other areas, although in Poland, for example, neonate *N. natrix* road-kill was recorded throughout the active season (Ciesiolkiewicz et al., 2006). Apparent from the present study was a high vulnerability in the foraging snakes *H. viridiflavus* and *N. natrix*, and lower vulnerability in the sedentary *V. aspis* and *N. maura*. This agrees with previous studies identifying movement as a key factor in road-kill (e.g. Bonnet et al., 1999; Andrews & Gibbons, 2005; Roe et al., 2006). Road-kill in *V. aspis* was 14.6% that of *H. viridiflavus*, despite being common in the vicinity of roads (e.g. Bonnet et al., 1999; Vijayakumar et al., 2001; Shepard et al., 2008). Low viperid road-kill is apparently common, particularly in adults (Seigal & Pilgrim, 2002). Shepard et al. (2008) found that *Sistrurus catenatus* crossed roads less frequently than predicted. Vipers have lower velocities than colubrids (Andrews & Gibbons, 2005), which must increase their vulnerability to road-kill during crossings (e.g. Hels & Buchwald, 2001), contrasting with actual road mortality levels.

Our understanding of road-kill patterns in reptiles enables us to predict, in a general sense, the probabilities of road-kill for different reptiles, but we lack a full understanding of all the underlying factors involved. It may be self-evident that road traffic is the main causal factor for road-kills, but it has not always been possible to establish a direct correlation with traffic volume due to the complex interactions of a series of variables (e.g. Orłowski, 2007; Shepard et al., 2008). Shepard et al. (2008) attributed an absence of correlation between monthly road-kill levels and traffic volumes to asynchronous patterns of reptile daily activity and traffic volume. Temperature is known to correlate with road-kill (e.g. Ciesiolkiewicz et al., 2006; Shepard et al., 2008), but this was not found in this study across species ($P=0.98$). The highest temperature-associated road-kill was in *H. viridiflavus*; whilst an ability to be

active at high temperatures may confer an ecological advantage, it may also increase road-kill risk by greater exposure to both vehicular traffic and hot tarmac when active. Hot tarmac in summer is a particular hazard for neonates (personal observation). Roadside species abundance is also important (e.g. Vijayakumar et al., 2001), but cumulative road deaths may lead to local extinctions and mask underlying traffic volume effects (Rudolf et al., 1999; Marchland & Litvaitis, 2004), potentially explaining lower than expected mortalities on the high volume D949 (Fig. 4).

A potential difficulty in this type of study is determining whether smaller individuals (particularly snakes) were missed in the live survey counts. However, small-sized road-killed and live snakes were counted in high numbers in late summer and autumn, after the hatching period. Mid-sized road-killed *H. viridiflavus* and *N. natrix* were less common than expected based on their frequency in the live sample counts (Fig. 5), which can be attributed to relatively sedentary behaviour (Bonnet et al., 1999). Nevertheless the velocity and the length of a snake during a road crossing must also be involved, since a large *H. viridiflavus* may represent more than 25% of the road; its survival may depend on whether it is seen by a driver. A small snake will probably not be seen but lower velocity and longer road crossing will increase the chance of a traffic encounter. Attempts have been made to model this problem mathematically (e.g. Hels & Buchwald, 2001). However, Roe et al. (2007) found that the Hels & Buchwald (2001) model overestimated levels of mortality in radio-tracked rat snakes (*Elaphe obsoleta*). Snake velocities have mostly been measured under controlled conditions (e.g. Andrews & Gibbons, 2005; Isaac & Gregory, 2007), but speeds during natural road crossings are measured by chance and rarely reported (Row et al., 2007). On 17 August 2008, a *N. natrix* (TL=690 mm, air temperature = 21°C) was seen crossing the D60. The 7 m wide road was crossed perpendicularly in approximately 13 seconds, indicating a speed of 0.5–0.6 ms⁻¹, which is in good agreement with laboratory measurements (Isaac & Gregory, 2007). A mean traffic volume of 60.2 vehicles per hour gives an estimated chance of vehicle encounter of 1:5, and the higher traffic D949 (see Table 2) increases the

probability to around 1:3. These calculations assume an absence of traffic pulses, but still provide an insight into traffic effects. Road-kills in *L. bilineata* were two thirds that of *N. natrix*, despite having nearly four times greater velocity (data for *Lacerta viridis* (= *L. bilineata*) gave up to 1.7 ms⁻¹; Avery et al., 1987). In theory *L. bilineata* should spend less time on the road for a crossing; however, most road-kill was probably due to road basking. Lebboroni & Corti (2006) recorded high *L. bilineata* road mortalities in comparison to *P. muralis*, and lower mortalities on high traffic roads, which they attributed to a learning effect (see Shepard et al., 2008, for discussion).

A major lack of knowledge is how many times individual snakes cross roads in a season. For instance, a high proportion of *H. viridiflavus* killed on roads were adults, and since maturity is reached at around 4–5 years (Arnold & Ovenden, 2002) many of the large road-killed individuals must be in excess of five years old and the largest animals around 10 years or more. We do not know how frequently this species crosses roads – if an individual snake regularly crosses roads the crossings must be successful for the animal to live to such ages, but equally they could be infrequent but with a high risk of mortality. Roe et al. (2007), from data on radio-tracked rat snakes (*Elaphe obsoleta*), estimated an average number of road crossings of 0.85 in a season, with a maximum of eight and a mortality rate of 0.026 per crossing. Such information would be important for effective management planning for European species. In an area south of the present study, Bonnet et al. (1999) recorded relatively low levels of road mortality in *N. natrix*, which they attributed to limited movement. This contrasts with that found for *N. natrix* in this study, but may be due to differing levels of prey availability and movement behaviour. Although *N. natrix* is largely sedentary when prey is abundant (Nagy & Korsos, 1998), it forages widely when prey is scarce (e.g. Madsen, 1984; Mertens, 1992; Gregory & Isaac, 2004; Wisler et al., 2008).

The effects of roads can be minimized, but the correct placement of mitigation efforts is critical. Simple measures such as temporary road closing or speed restrictions at times when mortalities are greatest could minimize traffic disruption and significantly reduce mortalities. Additionally, the cost of constructing underpasses for animal movement could also be reduced if preferred road crossing sites can be identified – perhaps associated with particular habitats on road margins (e.g. Ciesiolkiewicz et al., 2006). An interesting suggestion, proposed by Bonnet et al. (1999) to reduce female nesting movement in *N. natrix*, is the construction of artificial egg laying sites. However, there is a paucity of information on population dynamics and basic behaviour patterns in many species, highlighting the need for integrated studies that also, for example, include genetic considerations to assess whether roads are acting as isolating barriers (e.g. Shepard et al., 2008).

ACKNOWLEDGEMENTS

James O'Rourke helped with some of the surveying, particularly during 2005 and 2006. Thanks also to Dr Roger

Avery and Dr Donald Shepard for constructive comments on an earlier draft of the manuscript.

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Accepted: 24 July 2009