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Temporal distributions, habitat associations and behaviour of the green lizard (*Lacerta bilineata*) and wall lizard (*Podarcis muralis*) on roads in a fragmented landscape in Western France

Roger Meek

rue Georges Clemenceau 7, Chasnais, France. E-mail: rogermeek85@aol.com

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Abstract. Observations of the green lizard (*Lacerta bilineata*) and wall lizard (*Podarcis muralis*) on roads in Western France indicated that basking close to the road edge was the predominant activity in *L. bilineata* but *P. muralis* mostly foraged. Spatial locations of road mortalities in both species reflected this with the median distances from the road edge greater in *P. muralis.* Temporal differences in road presence, based on mortality counts and those of live lizards, indicated significantly more lizards were present on roads during late summer and autumn, especially in *P. muralis*. A significant correlation was found between the monthly presence of live lizards and monthly road mortalities in *P. muralis* (r = 0.73) but not in *L. bilineata* (r = 0.64). Numbers of *L. bilineata* found on roads bisecting low-density urban areas and roads bordered by hedgerows were higher than expected in relation to the occurrence of these habitats at roadsides. In *P. muralis* higher than expected numbers were found alongside low-density urban areas and roads bisecting woodland. Generally both species were less commonly seen on roads alongside agricultural areas with no hedgerow border.

Keywords. Lizards, roads, behaviour, habitat associations, temporal distributions.

INTRODUCTION

Habitat selection is a key aspect of animal ecology that can influence their behaviour and physiology (e.g. Huey, 1991). Reptiles are ideal organisms with which to understand habitat selection (Smith and Ballinger, 2001), as they are often numerous and adapted to a wide range of habitats and hence may provide insight into the effects of human alterations on the environment for wildlife. For example, urban and agricultural landscapes may constrain reptiles to live alongside roads due to the unsuitability of the surrounding habitat (Spellerberg, 2002) and although numerous studies have now been undertaken on these effects on reptiles, most have concerned snakes. Fewer works have examined lizard presence on roads perhaps in part because of detection difficulties due to their frequent small size and rapid carcass degradation (e.g. Koenig et al., 2002; Delgado Garcia et al., 2007; Lebboroni and Corti, 2006; Fahrig and Rytwinski, 2009; Meek, 2009). Additionally, if lizard populations fluctuate across both temporal and spatial scales this may necessitate long-term research to gather an adequate database for effective analysis. The present paper attempts to increase understanding of lizard road presence using the results of a 9-year study of two lizard species in an agricultural landscape in western France.

In Western Europe, two species of lizards that are frequently seen on roads are the western green lizard *Lacerta bilineata* and wall lizard *Podarcis muralis* (e.g. Lebboroni and Corti, 2006; Meek, 2009). Both species are heliothermic and found in a variety of habitats but *P. muralis* is more often associated with human habitations, including on walls and the sides of buildings in town centres (Arnold and Burton, 2000). Both species

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are primarily insectivorous but there are differences in lifestyle; *P. muralis* is essentially a foraging species whilst *Lacerta bilineata* is a sentinel predator (Verwaijen and Van Damme, 2008). Although road mortalities have been documented (Lebboroni and Corti, 2006; Meek, 2009) little information is available on how these lizards interact with roads, either on temporal or spatial scales or indeed their behaviour when they move onto road surfaces. The present study was prompted by observations that both species, in contrast to sympatric snakes, may attempt to use roads as a resource, for instance for securing prey and thermal resources. This paper addresses the following questions: 1) Does the presence of lizards on roads change seasonally? 2) How do the lizards behave when they are on roads? 3) What are the habitat associations of the places where lizards enter or cross roads?

METHODS

Surveying was carried out over a 9-year period between April 2005 and November 2013 on six roads in Vendée, Western France with additional observations on road behaviour made until 31 July 2014. The roads surveyed differed in width from 5 to 7 metres with one lane in each direction. The surveyed sections ranged in length from 1 to just over 6 km and totalled around 16 km. They connected the town of Lucon with four villages; Chasnais, St Denis-Du-Payre, Lairoux and La Brettoniere-La-Clay (46º27`N, 1º53`W). Figure 1 shows the location of the study locality. All road surfaces were tarmac based but apart from town or village centres only the D2949 (previously the D949 see Meek, 2009) between Lucon and Chasnais had a sidewalk. During the study period land changes along roadsides were minimal and mostly concerned woodcutting at woodland areas (for fuel), but re-growth was normally well underway the following year. New house construction was often present in villages but this had little or no impact on measurement of roadside habitats, as it mainly concerned buildings replacing buildings or new constructions that were at not actually on the roadside. Surveying was between 4 and 6 times per month at around 4 day intervals by a single observer usually between 1000-1700hrs on a bicycle at a maximum speed of around 5-10 km/hour. Data are based on point observations of individual lizards that were either present on roads or found as road-kill. When a live or road-killed lizard was observed or found, snout to vent length (SVL) in mm, approximate location where found, proximate roadside habitat and distance from the road edge were recorded. Distance from road edge is to the centre of the road irrespective of the side of the road the carcass was found. If it was suspected that a carcass had been displaced from the original point of the mortality (i.e. by being subsequently run over by other vehicles) the measurement was discarded. Most measurements of live lizards were approximate (± 10mm) and derived from photographic records, which were then compared with some object in the immediate vicinity for length comparison, for instance wood debris or distances between sections of larger stone aggregate on roads. Measurements of road–killed lizard SVL had a maximum estimated error of 5mm depending on body condition.

Behaviour

The behaviour records were determined using VEF (Visual Encounter Frequency; Latham et al 2005) and were only of animals actually on the road surface. Behaviour of each lizard was ascertained at its initial sighting. When there was any uncertainty, for example if the observer disturbed the lizard before behaviour could be determined, the observation was discarded. In general it was possible to identify three behaviours; basking, foraging and road crossing. Examples are shown in Fig. 2 (Avery, 1979). Foraging was defined as a moving lizard where the head was closer to the ground than when running. This also included making frequent direction changes and sometimes chasing and securing prey. Basking was defined as a lizard sitting on the road with no significant locomotory movement often with the body flattened laterally and the limbs sprawled sideways. The flattened body and sprawled limbs can be seen particularly clearly in Fig. 2C. However, these postures probably represent a combination of sentinel and/or thermoregula-

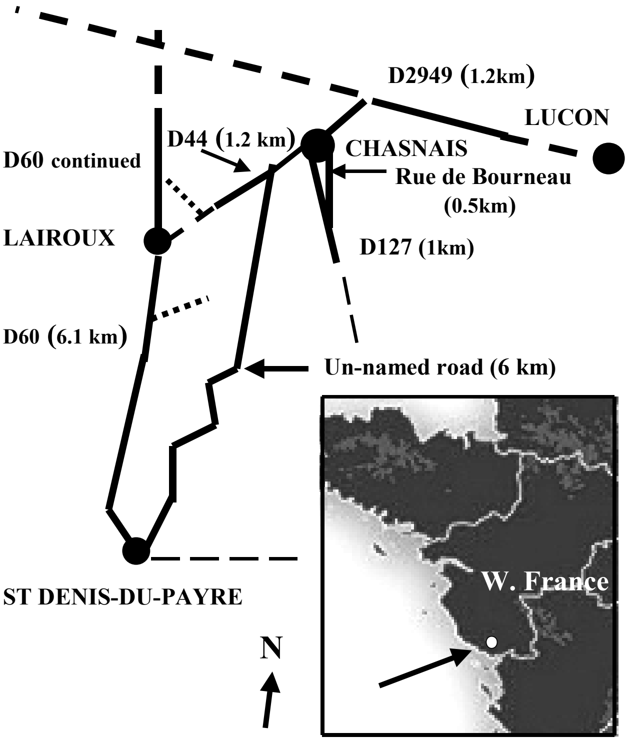

Fig. 1. Schematic diagram showing survey roads with approximate distances surveyed on each road in parenthesis. Broken lines represent road segments not surveyed. Map insert indicates location of the study locality.

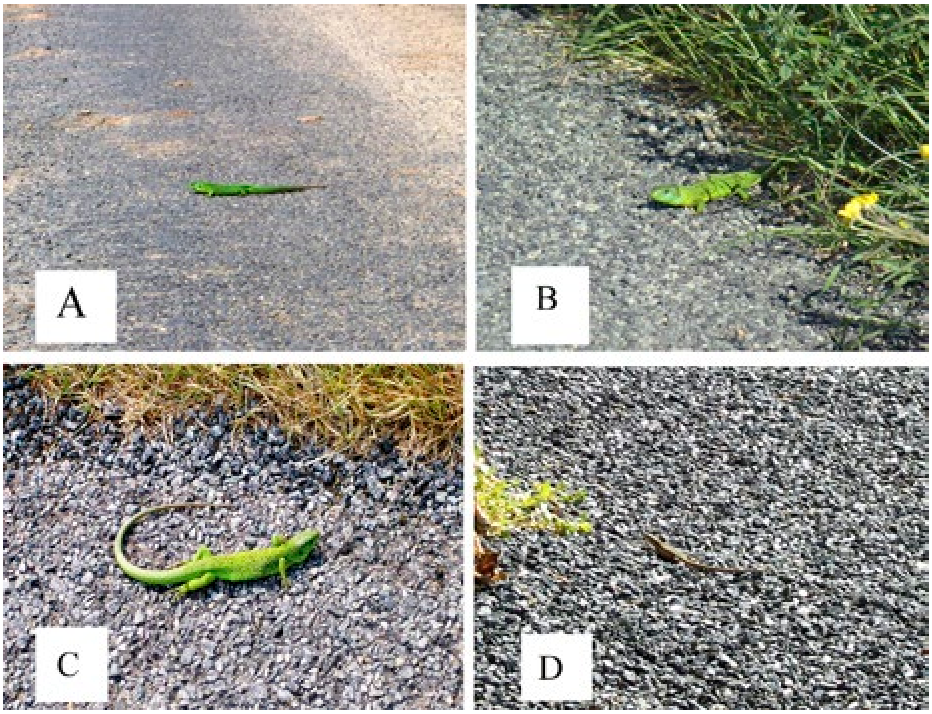

Fig. 2. Examples of *L. bilineata* and *P. muralis* road behaviour. Foraging in *L. bilineata* is shown in A, basking/sentinel behaviour in B and C. D shows a road basking *P. muralis* to illustrate potential differences in detection on roads compared to *L. bilineata*. See `Methods` for definitions of behaviour.

tory behaviour (Figs. 2B and C). Road crossings were when a lizard was observed making a complete crossing from one side of the road to the opposite side with little or no changes in direction. Usually the head of the lizard was held higher off the ground than when foraging and usually involved running very fast. Since crossings were sometimes made at high speeds and hence of limited duration, it opens up the possibility that the frequency of road crossings may be underrepresented due to having less chance of being observed, potentially introducing some bias in the behaviour results. The photographs in Fig. 2 also illustrate the good contrast with the road surfaces in *L. bilineata*, but less distinct in *P. muralis*.

Estimating habitat proportions

The relevant (major) habitat parameters alongside roads were identified and quantified in linear terms. The various habitats were continuous and hence assumed potentially available to both species. Because of low counts in certain habitats and hence potential bias, male and female data were pooled. Habitat segments were broadly defined as roads with hedgerow borders (33.6% of roadside habitat), monocultures without hedgerows (18.2%) woodland edge (16.5%), high-density urban areas – i.e. villages (25.0%) and low-density urban areas (6.7%). Low-density urban areas were defined as a small number of houses or buildings (usually no more than three) with high density urban defined as villages or towns. Due to crop rotation and the presence or absence of grazing animals, monocultures are transient environments and hence although their composition varied over time they were always agricultural areas. However, over the 9-year study period roadside habitat generally varied little except for some roadside woodcutting during 2013, which reduced woodland cover by around 10m along the roadside. Sample effort in each habitat type was approximately proportional to habitat availability since observer movement along each road was at a reasonably constant speed. However, some bias will have resulted from pauses to gather data and from occasional searches into roadside habitats, for instance to confirm species identification. The latter were confined to around 5 times per year and not expected to introduce significant bias.

Statistical analysis

To determine whether lizards were associated with particular roadside habitat requires selection analysis, which compares habitat use with habitat availability. Statistically this requires models that will produce patterns of expected probabilities that can be compared with real data (Gotelli & McGill, 2006). A null model was constructed by determining roadside habitat occurrence defined as their linear distances along road edges using the distance-measuring tool on *Google Earth* (http://www.google.co.uk/intl/en_uk/earth/). *Google Earth* applies an average of many sampled points in order to smooth the data in the horizontal plane and ignores undulations in the landscape. A comparison using the trip meter of two different cars and a motorcycle indicated reasonable agreement with the *Google* estimates; likely due to the limited distances being surveyed and relatively flat topography of the study locality.

The proportions of roadside habitat types x in metres were calculated as fractions of total available roadside habitat in y in metres from x/y. The common fractions were then converted to decimal fractions and compared with the proportion of lizards found or observed alongside each of the corresponding habitat types. The null hypothesis predicts lizards will be randomly distributed when their habitat associations do not depart significantly from habitat availability and therefore no selection is involved; habitat selection requires a significant departure from the null model.

The tests employed were one-dimensional χ^2 Goodness of Fit statistics that were then subject to Monte Carlo randomisations of 5000 iterations. The simulated χ^2 values this produced where then compared with the true χ^2 values. The test for significance is the number of the simulated χ^2 values that equalled or exceeded the true values should not exceed 5%. If this interval was surpassed the true values would be considered unreliable and potentially due to random chance. This is a useful test when the true χ^2 is close to the 95% interval.

Since the reliability of the χ^2 statistic is proportional to the number of values in the cells, the tests for temporal distributions, where low cells counts were present, were made using the Kolmogorov-Smirnov test (D_{max}). This test avoids cell re-binning, is robust and importantly not sensitive to cell counts. The null model employed is equality of cell counts across months and applies only to months when lizards were observed/road-killed on roads, which was from April to November. This test has also been used to examine for annual deviations of monthly road presence from the general 9-year trends. The expected probabilities were derived from the summed yearly trends after conversion to decimal fractions. The test is set at the 95% interval with deviation from the expected probabilities indicated if the 95% intervals were attained or exceeded. No departure from the null model indicates annual monthly presence was in agreement with the 9-year trend.

Two tailed *z*-tests for independent proportions were used to test for differences in behaviour and non-parametric Mann-Whitney *U*-tests for differences in carcass location on roads after testing for normality using the Anderson-Darling Test. Leven`s test (L) was used to determine homogeneity of variances with the null hypothesis $\sigma^2{}_1 / \sigma^2{}_2 = 1$ and $\alpha = 0.05$. All ± values represent 1 standard deviation from the mean.

RESULTS

Annual counts of lizards on roads were relatively low and mostly seasonal. A total of 369 lizards were recorded as mortalities or observed active on roads; 175 *P. muralis* (50 live and 125 road mortalities) and 194 *L. bilineata* (47 live and 147 mortalities). This result suggests greater road presence in *L. bilineata* than the more locally abundant *P. muralis* (see below). All size classes were observed as mortalities; *L. bilineata* s.v. range 41-135, mean = 97.01±18.3mm, *P. muralis* s.v. range 24-73, mean = 51.99±11.7mm and had comparable size ranges to live lizards on roads; *L. bilineata* s.v. range 55-121, mean = 102.2±11.4mm, *P. muralis* s.v. range 22-61, mean = 47.4±11.1mm.

Temporal aspects

Monthly road activity and mortality occurrence was irregular in both species and deviated significantly from monthly equality, whether for mortalities (*P. muralis*, $D_{max} = 0.339$, $P < 0.01$; *L. bilineata*, $D_{max} = 0.115$, $P < 0.05$) or mortalities and live counts pooled (*P. muralis*, $D_{max} = 0.3$, $P < 0.01$; *L. bilineata*, $D_{max} = 0.12$, $P < 0.01$). Significantly higher deviations were found in both species during August and September compared to other months and were respectively (mortalities and live) 2 and 4.5 times greater in *P. muralis* and 1.81 and 1.47 times in *L. bilineata*. Correlation of monthly road presence of live lizards and monthly road mortalities was significant in *P. muralis* ($r = 0.73$, $P = 0.04$) but not in *L. bilineata* ($r = 0.64$, $P = 0.08$). A relatively high number of live *L. bilineata* were observed on roads in April, which was in agreement with mortality counts.

Can these general trends predict annual monthly road presence? The Kolmogorov-Smirnov tests indicated deviations in annual monthly presence from the general 9-year trends were found only in *L. bilineata* during 2012 when the test statistic reached the 95% interval ($D_{max} = 0.234$, $P = 0.05$). Monthly road presence of *L. bilineata* in 2012 was 1.6 times less than expected during June and 1.65 and 1.36 times greater than expected during August and September respectively compared to the general trends. The distributions on which these statistics are based are shown in Fig. 3.

Road behaviour

Basking / sentinel behaviour on roads was more frequent in *L. bilineata* (72.3%) than *P. muralis* (42%), with the latter spending more time foraging (51.1 versus 12.5%). The differences between species were significant (basking $z = 3.013$, $P < 0.001$; foraging $z = 4.017$, $P < 0.0001$). Fewer lizards of both species were observed crossing roads and in similar frequency (*P. muralis* 10% versus *L. bilineata* 17.1%; $z = 1.01$, $P > 0.05$). The data are summarized in Fig. 4.

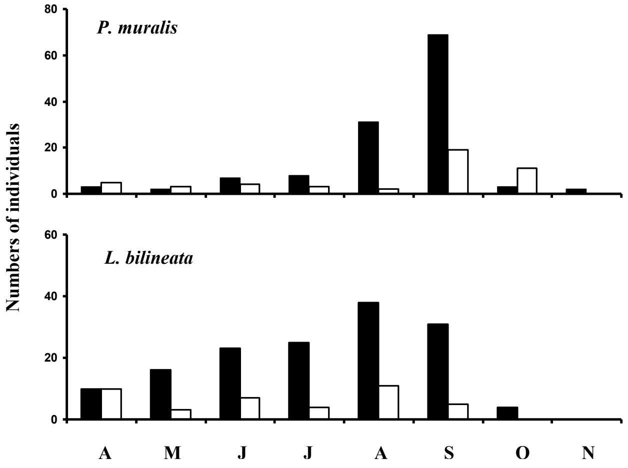

Fig. 3. Monthly distributions of lizard mortalities (solid histograms) and live lizards (open) on roads.

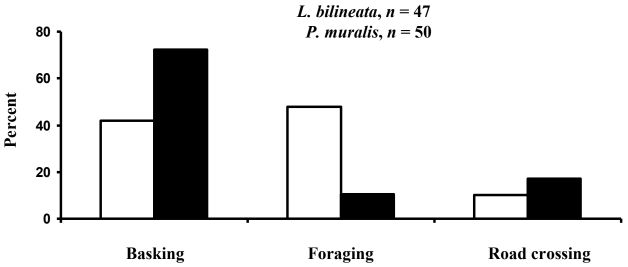

Fig. 4. Road behaviour of *L. bilineata* and *P. muralis*. Solid and open histograms represent *L. bilineata* and *P. muralis* respectively.

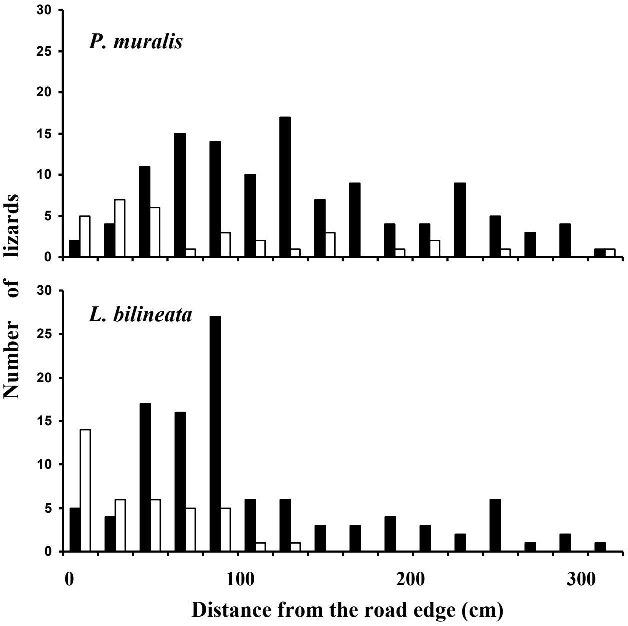

Fig. 5. Distances from the road edge of lizard mortalities (solid) and live lizards when first sighted (open). For live lizards road crossings are omitted. Increments on the x-axis are 20cm. See text for further details.

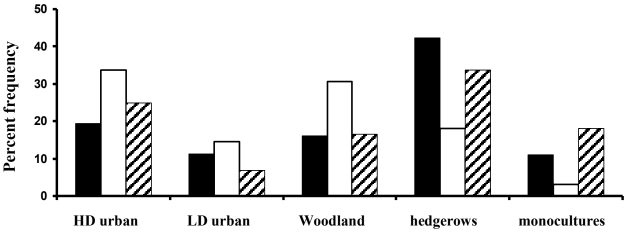

Fig. 6. Roadside habitat associations based on data from both live lizards and mortalities. Solid histograms represent *L. bilineata* and open *P. muralis*. Cross-hatched represents the expected proportions if lizards were randomly distributed alongside available roadside habitat. See text for details.

Road location of mortalities and live lizards

Median distances of carcass location on roads were positively skewed towards the road edge in both species (*P. muralis* S = 0.56, *L. bilineata* S = 1.1) but *P. muralis* carcasses were found at significantly greater distances (measured in mm) from the roadside (medians ± 95% confidence intervals; *P. muralis* = 1240±114.5 versus *L. bilineata* 900±70.4mm; w = 10342, P = 0.0024). Live *L. bilineata* were observed closer to the road edge than the location of their mortalities (w = 8689.0, P < 0.00001) with live lizard locations also having significantly smaller distributions (L = 6.4, P = 0.012). *P. muralis* mortalities were also found further from the road edge than live lizards (w = 9926.5, P = 0.0002) but had similar variances (L = 0.105, P = 0.74). These results are what might be expected in a lizard that was foraging across a road surface compared to one that was operating as basking/sentinel species sitting mostly at the roadside. Histograms of the distributions on which these statistics are based are shown in Fig. 5.

Roadside habitat associations

Both species departed significantly from the null model of a random distribution across roadside habitats. *P. muralis* was found in greater than expected frequency alongside low-density urban areas and woodland, whilst greater than expected numbers of *L. bilineata* were found on roads bisecting low-density urban areas and hedgerow bordered roads. Lower than expected numbers were found alongside monocultures with no hedgerow borders in both species. Table 1 gives the statistics with graphical representations of the observed frequencies against the random model of expected frequencies shown in Fig. 6.

Table 1. Observed versus expected frequencies of habitat-associated presence of lizards on roads. Columns indicate multiples of greater or less (negative values) than expected crossings in relation to habitat availability (a value of 1 indicates observed = expected). Urban HD represents high-density urban areas; Urban LD, low-density urban areas and Mono/no hedge, monocultures with no hedgerow border. Values of p specify levels of significance in χ^2 tests at d.f. = 4. The p-values for Monte Carlo randomisation tests give probability that the true χ^2 statistics were equalled or exceeded after 5000 randomisations. See text for details.

	HD urban	LD urban	Wood	Hedgerow	Mono/ no hedge	χ^2	P	Monte Carlo	n
P. muralis	1.3	2.1	1.9	-0.5	-5.8	50.2	<0.0001	<0.0001	172
L. bilineata	-1.3	1.7	1.0	1.3	-5.9	23.2	<0.0001	<0.0001	187

DISCUSSION

A perhaps unforeseen result of this study was the major temporal differences in lizard road presence with high numbers observed in autumn (August and September) especially in *P. muralis*. A compelling explanation is a comparable temporal presence of the saurophagus snake *Hierophis viridiflavus* on roads or along roadsides (Capula et al., 1997; Van Damme and Quick, 2001). For example, over the equivalent 9 year period monthly road presence in both lizard species was correlated with the presence of hatchling *H. viridiflavus* on roads (based on 165 hatchling road mortalities); versus *P. muralis*, r = 0.95, P < 0.0001, versus *L. bilineata*, r = 0.69, P = 0.04. The correlation is also significant (r = 0.71, P = 0.03) between *L. bilineata* and adult *H. viridiflavus* presence (n = 122), but not with *P. muralis* r = 0.08, P = 0.83. It is recognised that correlation does not necessarily imply causation but this does present several possibilities; for instance that lizards may exploit the absence of visual barriers on roads to enhance snake detection. If road use enables increases in flight initiation distance (Cooper et al., 2009) then the higher running speeds of most lacertid lizards compared to the fastest snakes (Vanhooydonck et al., 2001; Vanhooydonck and Van Damme, 2003; Alexander, 2012) should reduce predation risk (Lima and Dill, 1990). Lacertid lizards are additionally able to detect snake presence using chemical cues (Van Damme and Quick, 2001) and therefore it is conceivable that when *H. viridiflavus* are present in numbers alongside roads, this may initiate lizard movement onto roads. Interestingly, in contrast, no strong association could be found between the life cycles of the lizards and their presence on roads other than a slight increase in basking *L. bilineata* during early spring following emergence from hibernation (April – see Fig. 3). The high autumn road presence of *P. muralis* did not involve juvenile lizards, which contrasts with sympatric *H. viridiflavus* (Meek, 2009).

An additional explanation is that the simplified visual environments presented by roads enhance prey detection. Simultaneous surveys through 2011-2012 recorded 626 road-killed/crossing invertebrates on the six roads throughout the active months (April-November). The majority were *Lepidoptera* (31.6%) and *Coleoptera* (26.2%) but also *Gryllidae* (10.6%), *Orthoptera* (3.5%) and non-toxic/hairy *Lepidoptera* larvae (6.1%). Many of these invertebrates were road-killed or injured, which would facilitate easy prey capture. The sample shows similarities with reported diets of *L. bilineata* (Korsos, 1984; Perkins and Avery, 1989; Angelici et al., 1997), especially the presence of *Coleoptera*, suggesting prey opportunities could be one of a suite of factors that attract lizards to roads. Reptile presence on or alongside roads has previously been correlated with potential prey concentrations (Andrews et al., 2008), which supports the patch use model (Gilliam and Fraser, 1987) that predicts animals should select habitat patches offering the lowest predation risk to food harvest ratio (e.g. Martin and Lopez, 1995; Shepard, 2007) and hence is determined by the presence of predators and prey.

Both species were observed to use road surfaces mostly for foraging and basking with greater than expected presence on roads that bisected urban areas, woodland and hedgerows. The former agrees with non-road behaviour of both species (Verwaijen and Van Damme, 2008) and the latter supports the notion that roadside habitat is selected in both species since non-selective animals should use habitats in proportion to their availability (Alldredge et al., 1998). The greater than expected presence alongside hedgerows in *L. bilineata* indicates they use this habitat both for permanent occupancy and for potential connectivity between habitats. Hedgerows have already been identified as important in this respect for sympatric snakes (Saint Girons, 1996; Meek, 2015). The presence of *P. muralis* on roads bisecting urban environments was perhaps predictable given they are often abundant around human habitations (Arnold and Burton 2002), but given that this species is heliothermic, rather less anticipated was their higher than expected presence alongside woodland, which has more limited access to sunlight than other habitat types. Lizards have been found to thrive in human altered habitats, including woodland, as a result of road construction (Koenig et al., 2002; Delgado Garcia et al., 2007) with road and rail networks presenting movement pathways that enable *P. muralis* to colonise new areas in both Europe (Delgado Garcia et al., 2007; Gherghel et al., 2009) and North America, where is it as an introduced species (Hedeen and Hedeen, 1999; Deichsel and Gist, 2004). Road corridors through woodland have previously been identified as important edge habitat enabling other heliothermic lizards to penetrate and exploit unsuitable habitat (Delgado Garcia et al., 2007).

The mismatch between the cues for costs (e.g. mortalities from traffic) and benefits (e.g. enhanced predator detection and increased prey opportunities) for reptiles on roads has resulted in roads becoming ecological and evolutionary traps (Fahrig and Rytwinski, 2009). Understanding the behavioural differences in road behaviour in lizards is critical if conservation measures are to be implemented to reduce mortalities. Nevertheless ascertaining accurate levels of road presence is problematical. For instance, smaller size and greater rapid carcass degradation in *P. muralis* could potentially skew mortality data (see Fig. 1). This is most likely in hatchling and juvenile *P. muralis* that are far more difficult to detect. A previous study found that the frequency distribution of carcass duration of both snakes and lizards on roads was skewed towards low persistence time (Meek, 2009). However, if the present results are a representation of the relative differences between the two species then higher road mortalities of the locally less abundant *L. bilineata* is indicated. This difference has also be observed between the two species in Italy (Lebboroni and Corti, 2006) and is probably due to prolonged basking and/or sentinel behaviour of *L. bilineata* on roads, which increases the potential for a vehicle collision. When roads had paved sidewalks (as on the D2949 segment) lizard mortalities were in general lower (Meek, 2009) indicating the possibility that the construction of sidewalks coupled to the implementation of speed restrictors could offer potentially simple preliminary solutions to reduce mortalities.

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