



Juveniles are different: substrate selection in juvenile green lizards *Lacerta bilineata*

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The relationship between a reptile and its thermal environment is a key feature of habitat use, which may be impacted by, among others, the requirements for food, avoidance of competitors and predators. Juvenile lizards are subject to the same ecological pressures, but may additionally experience predation or exclusion from prime basking site by adults and hence their capacity to achieve preferred body temperatures. In this paper, we examined basking site selection in juvenile western green lizards, *Lacerta bilineata* and compared them to basking site availability. Secondly, measurements of morning substrate temperatures at different basking sites were compared to basking site selection over the same period. The results indicated that juveniles selected substrates with fast heating surfaces, for example fallen branches for basking, in greater frequency than their availability but in even greater than expected frequency on the cooler surfaces of clusters of bramble plant. This finding contrasted with basking site selection in adult *L. bilineata* in a previous study where wood surfaces was preferred over non-wood surfaces whilst avoiding basking on bramble. This illustrates the different ecological requirements between adults and juveniles.

KEY WORDS: juvenile green lizard, *Lacerta bilineata*, substrate selection, thermal ecology, intraspecific competition.

INTRODUCTION

It has long been understood that habitat selection is a critical component of reptilian ectothermy influencing the biophysical relationship of heat exchange between body mass and the immediate environment. Irregular heat distribution in habitats, due to different thermal qualities of microhabitats/substrates, influences a reptile's ability to select the most favourable basking sites to attain preferred body temperatures (Huey & Slatkin 1976; Castilla & Bauwens 1991; Huey 1991). Resource

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foraging in reptiles (Dingle 1996), includes foraging for heat resources (Meek 1988), which is driven by the Q_{10} effects on body temperatures. This is where increases in body temperature increase the rate of physiological processes by an approximate rate of 2 to 3 times, for example running speeds, oxygen, food consumption and heart rates (Avery 1979; Beebee & Griffiths 2000). In cooler temperate climates, this is a key driver of behaviour and habitat use (Reinert 1984; Adolph 1990). Basking in sunlit areas is the principle behaviour reptiles inhabiting temperate climates employ to attain appropriate body temperatures (Avery 1979). However, sun basking in open locations increases risk of predation and risk is further increased the longer the time spent in these areas (Christian & Tracy 1981). Therefore reducing basking duration will be adaptive if the reptile individual is able to select basking areas that maximise rates of heat gain whilst minimising detection by predators. Substrate selection is an important aspect of this selection process since the heat properties of different substrate types can influence heating rates (e.g. Avery 1979; Beebee & Griffiths 2000). However, this aspect of reptile ecology has been less studied in lizards (Beebee & Griffiths 2000).

The western green lizard *Lacerta bilineata* is one of the largest lizard species found in Europe where it occurs in a variety of habitats from woodland edge and scrubland to fragmented landscapes in hedgerows and suburban gardens (e.g. Saint Girons et al. 1989; Speybroeck et al. 2016). It is a typical basking heliotherm elevating body temperatures to around 34 °C (e.g. Rismiller & Heldmaier 1988). In a previous paper (Meek & Luiselli 2022) we found that the differences in the thermal properties of potential basking sites influenced substrate use for basking in *L. bilineata* and the sympatric smaller, but more sociable, *Podarcis muralis*. Both species selected wood-based materials (for instance fallen branches, tree stumps or tree trunks) in preference to stone, concrete and bare soil substrates (Meek & Luiselli 2022). However, the result was highly significant only in *P. muralis*. To explain the differences it was proposed that an absence of communal basking and intraspecific aggression in *L. bilineata* (Holec & Kminiak 1970; Beebee & Griffiths 2000) repressed a section of the population from accessing optimum basking sites (Meek & Luiselli 2022). This is an important behaviour in an ecological context because when prime basking sites are limited some individuals in the population may be constrained to operate at suboptimal body temperatures, which has an impact on their physiology including key aspects such as growth due to Q_{10} effects. Additionally ontogenetic differences in habitat use and differences in preferred body temperatures between adults and juveniles are known in other species of lizards (e.g. Ferguson & Fox 1984; Castilla & Bauwens 1991; Jenssen et al. 1998; Civantos & Forsman 2000). Similar pressures might be expected in juvenile *L. bilineata* but predation risk and aggression from larger size classes, especially male *L. bilineata* may result in differences in basking strategy (Holec & Kminiak 1970; Meek & Luiselli 2022). If so, how does the behaviour of juveniles differ from that of adults? Understanding these aspects of reptile thermal ecology is central towards understanding the adaptive significance of ontogenetic differences in the thermal ecology traits (e.g. Heatwole & Taylor 1987; Bauwens 1999; Radder et al. 2005).

In this paper we describe juvenile *L. bilineata* substrate selection in an attempt to understand these ontogenetic differences in habitat use (Castilla & Bauwens 1991; Shanbhag et al. 2006). Our questions are underpinned by the different heating properties of potential basking substrates, for example wood surfaces have higher specific temperatures than stone which enables faster heating rates in lizards when they use them (e.g. Meek & Luiselli 2022). Therefore if substrate selection in juvenile lizards is

driven purely by the heat properties of different substrate surfaces then selection should be for wood-based materials.

We asked the following questions:

- (1) Do juvenile *L. bilineata* exclusively select substrates that have the optimum heat properties for basking to attain optimum body temperatures?
- (2) Is there a differential selection of basking substrates between juveniles and adults?

MATERIALS AND METHODS

Study areas and protocol

The study was carried out in a hedgerow situated in a fragmented landscape in western France. Field data on *L. bilineata* were gathered during 2020, 2021 and 2022, in a hedgerow on the edge of the village of Chasnais with a length of approximately of 190 m (46°27'38"N; 1°13'42"W) (Fig. 1A). The hedgerow fits the paradigm of a low-cost thermal environment in the sense of Huey and Slatkin (1976) in that it is structurally relatively simple, and formed of low-growing trees *Fraxinus excelsior* (Ash), *Fraxinus excelsior* (Oak) and *Rubus fruticosus*, and *Hedera helix* bushes that give abundant shaded areas along with open sunlit patches enabling basking opportunities.

Lizard sampling

Sampling was during most days between late March and October and was approximately even across seasons, allowing for inclement weather. Juvenile lizards are defined as lizards with snout to vent lengths of 70 mm or less and identified by key body proportions (for example head and eye dimensions) and the dorsal colouration which is different from that of adults (Meek 2014a). This means that we sampled lizards in their 1st year after birth or early in their 2nd year. Sampling frequency was from 32.5 to 30 hr each month for around 45–70 min daily from between around 08:30 up to 11:00 hr depending on season and weather. All lizards were detected by slowly walking along the hedgerow (see Fig. 1) and photographed. This enabled identification of each individual lizard (Dustin et al. 2020; Welbourne et al. 2020) but only one photograph of each lizard was used per day. Photographs also enabled estimates of lizard SVL's. Basking sites are defined as those observed used by lizards for more than 1 min and hence by definition do not include lizards seen in shaded areas or those moving across open patches.

Estimating substratum availability

Available substratum, is here defined as the surface areas of wood or stone and open ground areas and estimated by using a tape measure to calculate approximate surface areas of all basking sites that were used by lizards. This is defined as the locations where at least one basking lizard was observed on at least one occasion. However, only the curved surface areas of fallen branches or tree trunks exposed to sunshine were measured since these were the areas where lizards basked. Bramble leaf density was high (Fig. 1) so calculating the area of the leaves exposed to sunshine was a good approximation of basking availability.

The surfaces areas of all basking locations, for example stones, open ground or bramble leaves exposed to sunshine, were calculated as near possible (through repeated measurements) to an approximate estimated $\pm 5\%$ error.

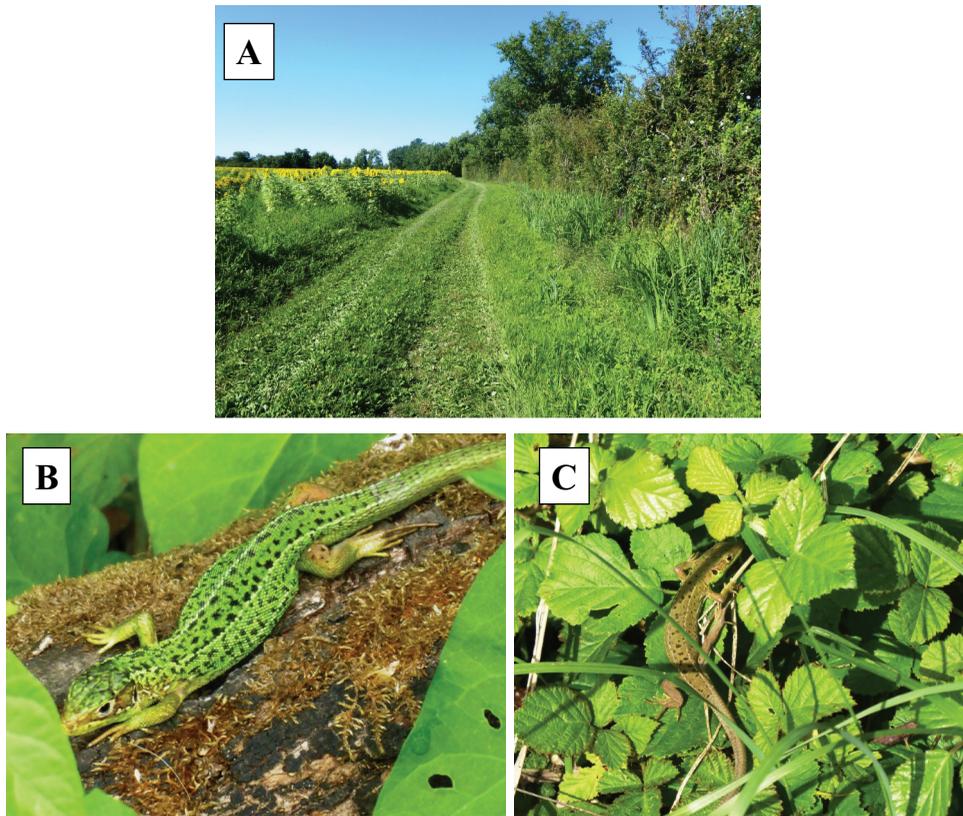


Fig. 1. — Study area (A) shown with examples of juvenile lizards basking at the two most frequently used substrates, fallen branches (B) and bramble (C).

Estimating substratum temperatures

We assumed that juvenile lizards should select substrates that optimise heating rates, in a low cost thermal environment, in terms of both access to optimum basking substrates and risk of predation. To give insight into substrate temperatures at the basking site, surface temperatures at the various basking locations were measured during 3 days of sampling on 27th, 28th and 29th July 2022 between 09:30 and 10:45 hr, during cloudy weather (26th) and mixed sunny and light cloud. Because of the specific heating rates of different materials we expected, for example, wood always to heat up faster than stone under the same climatic conditions. Temperatures were measured using a lazer digital thermometer (Workzone, PANA, France) pointed at the material surfaces, which gave an instant read-out.

Statistical analysis

To determine potential thermal optimum basking substrates, we assumed that those sites offering both high heating rates and wide temperature ranges would be selected for in greater frequencies. Data collected during both sunny and cloudy weather was analysed by a non-

parametric Kruskal-Wallis ANOVA test for multiple comparisons which was followed by a Dunns post-hoc test. This compares medians of the ranked data using a χ^2 statistic with a null hypothesis:

$$H_0: = H_1 = \dots = H_k$$

Variance of substrate surface temperatures was assessed by Leven`s test for homogeneity of multiple variances, that uses the F -distribution. Post-hoc test was by Tukey HSD. The null hypotheses is equality of variances:

$$H_0: \sigma^2_1 = \dots = \sigma^2_k$$

Alpha was set at 0.05 in both tests.

To examine whether lizards non-randomly used different substrates for basking we constructed null models that would indicate a random use of basking sites (Gotelli & Ellison 2004). To do this, we estimated the various substratum types that were available to the lizards and then compared these proportions to those used by the lizards. The assumption was if substratum use by lizards for basking was proportional to its availability, then selection would be considered random and non-selective. Significant deviations from the null model are indicative of substratum selection. The test used was the Kolmogorov-Smirnov Goodness of Fit test (D_{max}), which is distribution-free, and not sensitive to cell counts. It evaluates the maximum difference between the cumulative proportions of the two patterns, here the observed lizard substrate use compared with the expected use based on substrate availability or, in a third test, substrates used for basking in adult *L. bilineata* derived from data in Meek and Luiselli (2022). For analysis the observed and expected probabilities were converted to decimal fractions since the Kolmogorov-Smirnov test requires that $\sum n = 1$, where n is the decimal proportions. The hypothesis is

$$H_0: P = P_o, H_1, P \neq P_o$$

where P is the observed distribution of substratum use by the lizards and P_o the distribution of available substrates or that used by adults. A D_{max} value of 1 indicates random selection (see Table 1). The null model of expected proportions were: tree stump = 0.02; fallen tree branches = 0.22; open areas with no vegetation = 0.40; tree bark = 0.11; limestones = 0.07; bramble growth = 0.17.

In a second test we constructed a more general null model of expected basking proportions based on material similarities comparing wood-based substrates, with tree, tree stump and fallen branches = 0.036, non-wood (stones, bare soil) = 0.47 and bramble = 0.17.

The third test compared the juveniles with the adult *L. bilineata* selection, based on the results found by Meek and Luiselli (2022). In Meek and Luiselli (2022), basking site selection in adult lizards gave expected probabilities of: tree stump = 0.078; fallen tree branches = 0.37, bare soil (open areas with no vegetation) = 0.52; tree bark = 0.022; limestones = 0; bramble growth = 0.

The tests were set at the 95% interval with deviations from the expected probabilities indicated if the 95% intervals were attained or exceeded. Statistics were carried out using Minitab V17 and Internet sites Statskingdom and Socscistatistics.

RESULTS

A total of 85 juvenile *L. bilineata* were photographed along with four observed but not photographed lizards during the 3-year study period (in 2020, $n = 17$; in 2021, $n = 40$; in 2022, $n = 28$). Fallen branches ($n = 34$) and bramble bush ($n = 31$) were the most frequently used basking sites whether in terms of absolute counts or as proportions to their availability with the differences significant. Less used was tree bark and tree stump ($n = 3$ frequency for both patches). Open ground, frequently used by adults, formed only 10.7% ($n = 9$) of the sample in juveniles. The differences in use and availability were significant ($P = 0.001$)

Table 1.

Results of the Kolmogorov-Smirnov one-sample Goodness of Fit tests (D_{\max}) comparing juvenile *L. bilineata* substratum use for basking against expected basking frequencies under a null hypothesis of substratum availability. Values of 1 would indicate substratum use in agreement with availability; negative values indicate less use than expected, positive values greater use. NA = Absence of plant and stone use in adults renders comparison with juveniles invalid.

Expected versus observed	Tree stump	Tree	Fallen branches	Bramble	Stones	Soil
$D_{\max} = 0.301$, $P = 0.001$	0.16	- 0.6	3.4	3.9	1.7	- 0.5
Pooled data (see text)	Wood (all)	Stones/soil	Plants	-	-	-
$D_{\max} = 0.187$, $P = 0.01$	2.5	- 1.5	3.9	-	-	-
Adults as a null model (see text)	Tree stump	Tree	Fallen branches	-	-	
$D_{\max} = 0.210$, $P < 0.01$	1	3.0	2.4	NA	NA	- 2.2

When the data were pooled and based on materials of wood versus stone versus bramble the result was significant ($P = 0.01$) with wood and bramble used in greater frequency. The pattern of juvenile substrate selection also differed significantly when the adult pattern was employed as the null model (Table 1 and Fig. 2).

The Kruskal-Wallis ANOVA test showed that, during sunny weather, significant differences were found between median substrate surface temperatures at the basking sites [χ^2 (5 df) = 21.21, $P < 0.0007$]. The post-hoc Dunns test with Bonferroni correction indicated significant differences between fallen branches (median rank score 52.3) and both bramble (mean rank score 20.6) and stones (median rank score 18.8). The Levene's test detected differences between variances ($F = 5.65$, $P < 0.0001$), with Tukey HSD indicating the significant differences were between bramble and fallen branches and also between bramble and stone.

During cloudy weather the Kruskal-Wallis ANOVA test indicated a significant difference between median temperatures of the basking sites [χ^2 (5 df) = 11.59, $P = 0.04$]. However, the P -value was just inside the 95% interval and the post-hoc multiple comparison test was unable to identify statistical differences between any pair of groups (Fig. 3). During cloudy weather there were no statistical differences in temperature variance of basking sites ($F = 0.013$, $P = 0.98$).

DISCUSSION

This study found clear examples of differences in microhabitat and substrate selection between adult and juvenile *L. bilineata* using three different tests. The results indicated that, although both age classes were found to occupy the same area of hedge-row, their use of basking sites differed significantly, with juveniles selecting areas of

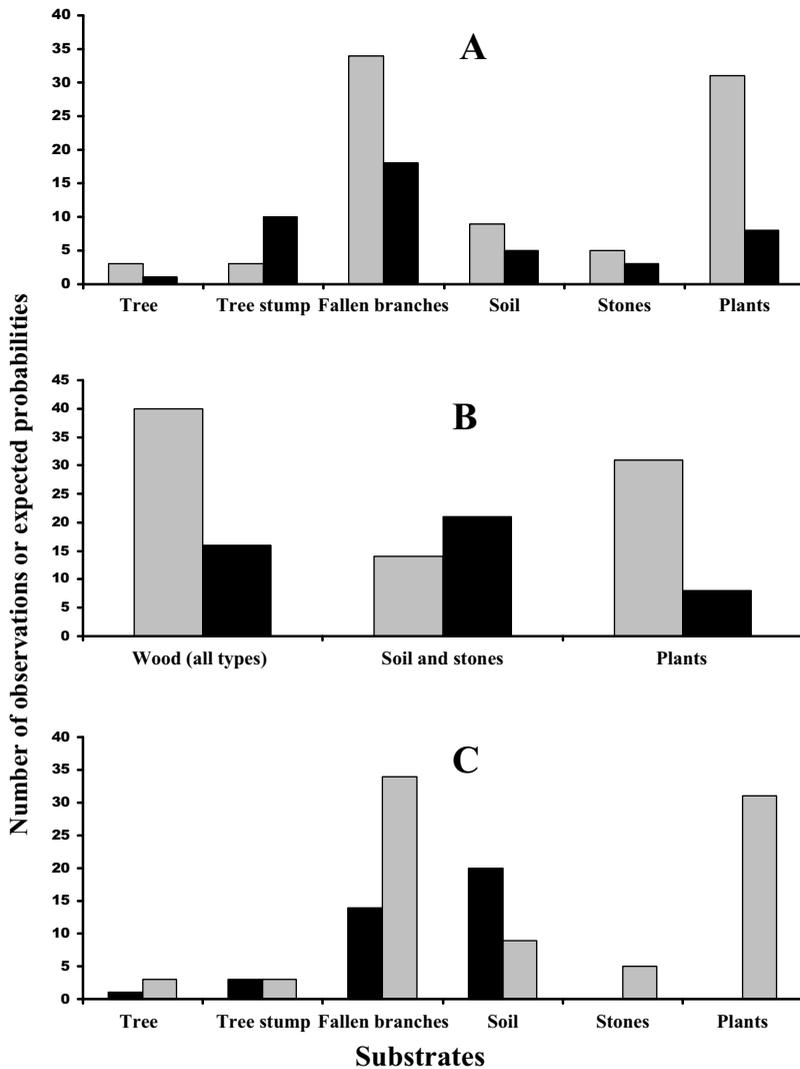


Fig. 2. — Observed substrate use as basking areas (grey bars) plotted against substrate availability (black bars) in juvenile *L. bilineata*. (A) Shows selection plotted against substrate availability as a null model, (B) against pooled substrates based on materials and (C) when adult substrate selection has been used as a null model.

bramble bush and fallen branches more frequently than adults. These differences in selection very likely reflect different ecological requirements and are predicted by the competition – avoidance hypothesis that various age-classes should select different habitat to reduce competition for similar prey size (Andrews 1976). This has been observed in a more general context in Italian populations of *L. bilineata* (Angelici et al. 1997). The potential intraspecific conflicts observed in this study and previously in adults (Meek 2014a; Rugiero et al. 2021) supports the interference hypothesis, which

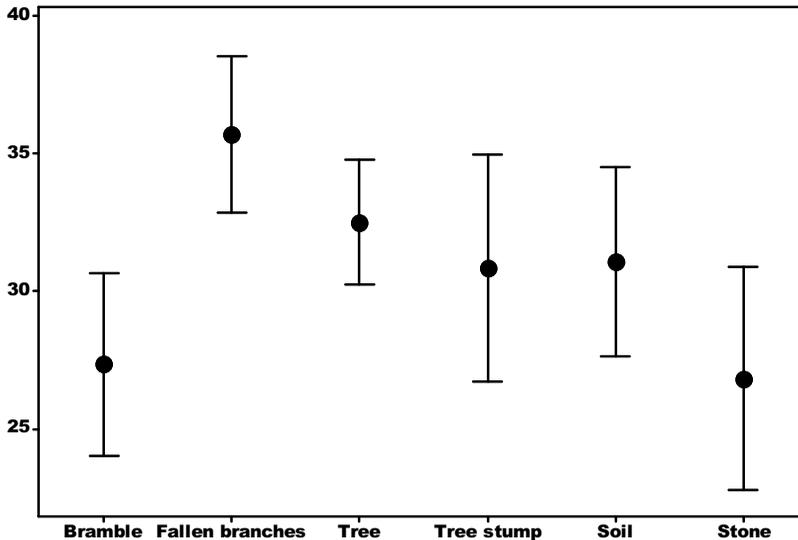


Fig. 3. — Median temperatures (circles) with 95% confidence intervals of basking substrate temperatures during sunny weather.

predicts that aggression from adult lizards should result in habitat partitioning, for example, that juveniles will be forcefully excluded by adults from preferred basking sites and constrained to suboptimal basking areas (Mitchell 1986; Keren-Rotem et al. 2006). Juveniles were observed basking on fallen branches but not when adults were basking on one in the vicinity. The active year in *L. bilineata* in the hedgerow was from approximately late March to July (data derived from years 2020, 2021, 2022), similarly to other conspecifics from Italy (Luiselli et al. 2022). During this period adults were primarily involved in territory acquisition and reproductive activity (R. Meek unpublished data). In juveniles the activity period is similar but the key priorities are for growth to attain adult size as rapidly as possible and likely contribute to explain the differences in substrate selection (R. Meek unpublished data).

Occasional basking site disputes with conspecific wall lizards (*Podarcis muralis*) also constrained juvenile *L. bilineata* from accessing optimum basking areas. These conflicts were seen on several occasions, especially with large male wall lizards that drove juvenile *L. bilineata* from basking areas, although the juveniles often quickly returned to use the site after the wall lizards moved on. These are important additional constraints as research on juvenile lizards has indicated that the amount of time a juvenile lizard operates at high optimum body temperatures and accesses food determines its rate of growth (Sinervo & Adolph 1989), that in turn impacts on survivorship (Ferguson & Fox 1984). This is supported by laboratory studies of *Zootoca vivipara*, *Sceloporus occidentalis* and *Sceloporus graciosus* (Ferguson et al. 1983; Avery & Mynott 1990).

Basking on the upper levels of thorny bramble plant by juveniles was unexpected relative to its low availability. During 2021 and 2022 most basking on bramble occurred during short time intervals from the time periods between 24 May 2021 to 10 June 2021 (15 of 18 observation, 83.3%) and between 22 April 2022 to 10 May 2022

(9 of 11 observation, 81.8%). Basking on bramble may involve reducing predation pressures since juvenile green lizards, for example *Lacerta trilineata*, have much slower running speeds than adults and therefore avoiding more open areas, for example on areas of open ground would be adaptive. Bramble as basking sites also represents ease of access to sunlight with minimal distances to cover during shuttling activities. Additionally during the active season there was abundant invertebrate prey (especially spiders and grasshoppers) and only limited snake presence, mostly adult and hatchling *Hierophis viridiflavus* (Meek 2014b; Meek & Luiselli 2021) and a rare sighting of the mustelid *Mustela nivalis*. Bramble probably represents a low cost ecological basking location for juveniles in the sense that it represents access to sunlit and shaded area while offering much reduced contact with adult lizards, which can pose a predation threat (Huey & Slatkin 1976; Huey 1991; Rugiero et al. 2021). Differences in microhabitat selection, body temperatures and basking frequency between adults and juveniles have been observed in other lacertid lizards (Castilla & Bauwens 1991; Civantos & Forsman 2000) including in *L. bilineata* juveniles (Arnold 1987; Mayer et al. 1990). Reducing intra- and interspecific encounters would be expected to increase survival probabilities especially in light of reports of serious injuries and mortalities in adults observed over the wider study area (Rugiero et al. 2021) and hence facilitate population persistence in hedgerows that are effectively narrow linear habitats.

Hedgerows are a prime example of anthropogenic activities that produce fragmented landscape and rapidly changing environments, particularly in terms of animal spacing patterns, levels of predation risk and the thermal environment. In such environments our study illustrates the importance of hedgerows as habitat, not just for lizards, but invertebrates, snakes, amphibians, birds and mammals that were all detected in the study site (Meek 2016; Rugiero et al. 2018; Meek & Luiselli 2021). The linear nature of hedgerows usually incorporates a composite of microhabitats including tree roots, stones, fallen logs and a variety of plants. The diverse thermal environment these produce is particularly important for heliothermic reptiles in temperate areas. For example the approximate North East direction of the study hedgerow provides basking opportunities for most of the day along with suitable egg-laying areas. This supports the conclusions of Lecq et al. (2017) that larger banked area and more ground refuges serve to enhance the abundance and diversity of squamate prey and provide a wider range of thermoregulatory opportunities. In such a special environment the probability of contact between individual lizards of varying size classes may be reduced especially in respect to juveniles impacting on levels of intraspecific mortalities or injuries (Rugiero et al. 2021). This likely contributes to population persistence in a narrow linear environment.

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