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LIVING IN PATCHY HABITATS: SUBSTRATE SELECTION BY BASKING SYMPATRIC LIZARDS IN CONTRASTED ANTHROPOGENIC HABITATS IN WESTERN FRANCE

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The influence of temperature on the physiological processes in reptiles is well known, for example growth, reproduction and muscular energy are all temperature dependent. However, there may be constraints on the ability of a reptile to harness thermal energy, particularly during cold seasons in the temperate zones. Substrate selection is a key factor in enhancing thermoregulation since it can enhance rate of heat uptake. For example, wood substrates are known to increase rates of heat gain in basking reptiles enabling earlier attainment of optimum body temperatures compared to other substrate types, which enables increased time available for other activities. In this paper we describe substrate use for basking in populations of *Lacerta bilineata* and *Podarcis muralis* in a hedgerow and a population of *Podarcis muralis* in a suburban garden in western France. The proportions of substrate used were compared against a null model of substrate availability. When different substrates were pooled based on material similarities both species were recorded in greater frequency on wood based materials in comparison to their availability compared to non-wood substrates. However at a finer level, in comparison to the null model of substrate availability (fallen tree branches, tree stumps, open ground etc), *P. muralis* showed strong substrate selection whereas *L. bilineata* did not depart significantly from the null model. We speculate that intra-specific aggression in *L. bilineata* was one possible cause of this result due to dominant individuals limiting access to prime basking sites in smaller or female lizards. Differences in communal basking between the two species supported this notion.

Keywords: urban lizards; basking; substrate selection.

INTRODUCTION

The expansion of urban areas and subsequent modification to natural environments by agriculture is a key factor in reptile population declines (e.g., Jellinek et al., 2004; Audsley et al., 2006; Böhm et al., 2013; Keinath et al., 2016). This involves, among others, the changes to vegetation structure that may impact upon a reptile eco-physiological performance (Keinath et al., 2016; Yang Hu et al., 2020). For example, reptile body temperature levels determine whether they can perform at optimum physiological levels, which in turn depends on the thermal quality of the substrates (Huey and Slatkin 1976; Huey, 1991; Castilla et al., 1999). The ability to adapt to urban environments requires habitats that present suitable thermal environments with basking opportunities to

raise body temperatures and shaded areas for cooling (e.g., Avery, 1979; Basson et al., 2019). In addition the costs of moving to and from optimum basking areas in terms of both energy costs and predation risk should be lower than the benefits gained (Huey and Slatkin, 1976; Huey, 1991). Abundance of both prey and retreat sites is also critical and hence reptiles are constrained to balance these factors, which will have different ratios of cost-benefits depending on habitat quality (Carrascal et al., 1992; Herczeg et al., 2008; Basson et al., 2017). Therefore, population persistence in altered habitats, including presence of patchy habitat is subject to the same thermal and ecological constraints/requirements as in pristine environments.

Lacertid lizards are common species in Europe and regulate body temperatures by selecting thermally favourable microhabitats (via appropriate substrates and basking sites) and adjusting activity times and behaviour that alter heat exchange with the environment (e.g., Bau-

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wens et al., 1996; Castilla et al., 1999). Two of the most common species are the wall lizard (*Podarcis muralis*) and the green lizard (*Lacerta bilineata*). They both occur in a wide range of environments that include suburban gardens and agricultural areas (e.g., Corti et al., 2011; Speybroeck et al., 2016) but differ substantially in terms of body size, *L. bilineata* is much larger (Corti et al., 2011). They both primarily consume a range of insects (Barbault and Mou, 1986; Angelici et al., 1997; Speybroeck et al., 2016), but whilst *P. muralis* is essentially an active forager, *Lacerta bilineata* is a sentinel predator (Verwajen and Van Damme, 2008). Body temperatures of up to around 36°C have been recorded in *P. muralis* in the field (Avery, 1978; Bauwens et al., 1995) with *L. bilineata* (= *L. viridis*) around 34°C (e.g., Rismiller and Heldmaier, 1988). The success of these lizards in anthropogenic environments is of particular interest because (i) their contrasted life-histories and (ii) the highly modified landscapes they inhabit are potentially impacted by physical structure, micro-climates and species composition of natural vegetation, thus potentially isolating populations (e.g., Germaine and Wakeling, 2001). For example, agricultural monocultures have little value to most wildlife with the remaining usable habitat often hedgerow systems (Saint Girons, 1996; Luiselli and Capizzi, 1997). Hedgerows are typically linear habitats that may be used as permanent home ranges or function as connection pathways to more usable habitats (Saint Girons, 1996; Vignoli et al., 2009; Meek, 2014a, 2014b; Rugerio et al., 2018). Suburban gardens represent a second example of highly altered environments but many species of lizard, especially *P. muralis*, are capable of adapting to these including an ability to colonize completely new areas (e.g., Allan et al., 2006; Mole 2010; Corti et al., 2011; Heym et al., 2013). Evidence of anthropogenic impact on reptiles is perhaps the least understood of vertebrates (e.g., McCoid et al., 1994; Walker et al., 1996; Jellinek et al., 2004) and here we examine one aspect of how these two species of lizard utilize disturbed habitats using data on substratum selection.

The size difference between *L. bilineata* and *P. muralis* is an important factor in their thermal biology by impacting primarily on differences in rates of heating and cooling due to differences in skin surface area and body mass with size (e.g., Corti et al., 2011). Indeed, the smaller *P. muralis* heats around 1.5 times faster than *L. bilineata* (e.g., Hailey, 1982) and hence time spent basking could also be expected to impact on time budgets for other daily activities. In addition microhabitat/substratum selection can also influence heating rates (e.g., Hailey, 1982) and hence time taken to achieve optimum body temperatures. For example, heat conduction from substrates can even be important during sunny weather

and especially during cloudy weather (Avery, 1979; Beebe and Griffiths, 2020). In a study of basking substrates used by the cold adapted lacertid lizard *Zootoca vivipara*, Hailey (1982) found that wood surfaces were mostly selected for basking during overcast or changeable weather compared to grass but there was non-selection of wood during sunny days. This was attributed to the costs (energy costs of movement and risk of predation) of moving to warm substrates for basking during sunny weather compared to the lower benefits of more rapid body temperature increases from using wood substrates (Hailey, 1982).

The present study was prompted by observations of basking behaviour and substratum selection by lizards in two contrasted anthropogenic habitats in west France: (i) a hedgerow with sympatric *L. bilineata* and *P. muralis*, and (ii) a suburban garden, situated at a relatively short distance (0.9 km) from the above-mentioned hedgerow. In the garden habitat only a *P. muralis* population is present. Because of the close vicinity of these habitats, the climate was nearly identical (and thus comparable) between areas but the vegetation structure and the ecological conditions were very different. Hailey's (1982) study was undertaken in the cooler climate of the south of England, approximately 650 km north of our study area, where temperatures are lower with greater cloud cover and fewer sunshine hours. We therefore posed a general question of whether substratum selection for basking would have equal importance in more southerly species with greater sunshine hours and higher temperatures. Specifically we attempted to answer the following questions:

- 1) Are there any species-specific preferences for substratum selection in basking wall and green lizards in the hedgerow? We ask this question because the substratum and perching materials available to the lizards in diverse habitats may differ in specific heat capacity. For example, wood in general is around 1.17 J/(g · °C), Ash wood very similar at 1.6 J/(g · °C), concrete 0.88 J/(g · °C) and limestone 0.75 J/(g · °C). Therefore in a theoretical low cost thermal environment, lizards should select substrates for basking that are low cost in terms of rates of heat gain if the costs of reaching or using them outweigh the risks. In this study the presence of trees and fallen branches in the hedgerow and also deadwood in the garden habitat were within reasonably short distance of each other (Fig. 1) and we predicted that wood-based materials should be selected for in terms of the advantages gained in heating rates in achieving optimum body temperature relation to their availability.

- 2) Do lizards adjust substrate selection for basking with season and are there differences in this respect be-

tween the two species? We ask this question because as summer progresses and the environment warms lizards may be less dependent on substrates that offer greater heating rates. We therefore predicted that selection for the high $1.17 \text{ J}/(\text{g} \cdot ^\circ\text{C})$ wood based substratum would decline.

3) Does communal basking occur in and if so is there a difference in frequency for this behavior between *L. bilineata* and *P. muralis*? We ask this question because competition for prime basking sites may enhance thermoregulatory capability in some lizards if they can exclude potential competitors from optimum basking sites (e.g., Huey and Slatkin, 1979).

METHODS

Study areas and protocol. From March to October 2020, sympatric populations of *P. muralis* and *L. bilineata* were studied in a hedgerow (PH) system on the edge of the village of Chasnais ($46^\circ 27' \text{ N } 1^\circ 53' \text{ W}$), and a population of *P. muralis* in a urban garden in the same village in Western France until November 29 (Fig. 1). The garden area was 1197 m^2 . Both habitats can be described as low cost thermal environments in the sense of Huey and Slatkin (1976) in that it is structurally relatively simple consisting in the hedgerow of mostly low growing bush (*Rubus fruticosus* and *Hedera helix*) with open sunlit areas that facilitate basking opportunities and shaded areas presented by ash tree (*Fraxinus excelsior*) and oak (*Quercus robur*), the latter tree being in greater proportion. The urban garden habitat had more open areas and slightly less cover than the hedgerow: approximate areas of cover were 40% in garden habitat and in excess of 90% in the hedgerow (see Fig. 1A, B).

Lizard sampling. Sampling was approximately even across seasons, allowing for inclement weather. In the hedgerow habitat sampling was confined from morning (first lizards seen around 9:00 a.m.) to midday due to the habitat being in shade after this period. In the garden habitat, which was south facing and in sun most of the day sampling was also from around 3 p.m. to 6 p.m. Sampling frequency ranged from 32.5 to 30 h from April to October and November in the garden population but fewer during March and December (7.35 – 15 h, respectively). Data were collected by slowly walking along the hedgerow and garden area and photographing any lizards detected. A total of 631 photographs (*L. bilineata*, $n = 258$; *P. muralis*, $n = 373$) were taken in the hedgerow. When possible several photographs of each or groups of lizards were usually taken, but only the best quality example used for each sighting. Using one photograph per lizard per sampling session also minimized the risk of

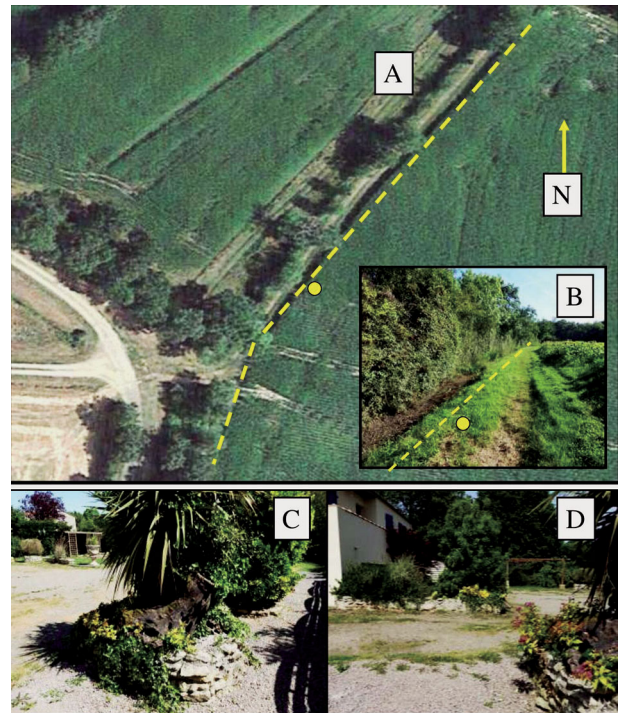


Fig. 1. Google Earth map with (A) showing hedgerows with agriculture land either side. The broken line represents the sampling area and insert a ground view of a section of the sampling area (B). Examples of basking areas used by *P. muralis* in garden habitat are also shown with limestone wall (C) and deadwood and raised bed created from limestone (D).

pseudo replication. Sampling effort was 5 – 6 days each week for around 45 – 60 min daily, usually from around 8:30 a.m. but up to around 1:00 p.m. Photographs enabled identification of each individual lizard (Welbourne, 2020) but only one per day was included in the analysis, giving a total used photographs of 39 for *L. bilineata* and 107 for *P. muralis* in the hedgerow and 361 photographs of *P. muralis* in the garden. Lizard identification was by color, presence and location of tail breakage points, dorsal markings and especially in *L. bilineata* distribution of dorsal spots (see examples in Fig. 2). Basking sites are defined as those observed used by lizards and hence by definition not lizards seen in shaded areas. Additionally lizards crossed areas of open ground when moving from one location to another but these also were not basking sites and hence the substrates types they moved across were not included in the analysis.

Estimating substratum availability. Available substratum proportions were estimated by using a tape measure to calculate surface area of all potential basking sites. These were defined as those sites where at least one basking lizard was observed on at least one occasion.

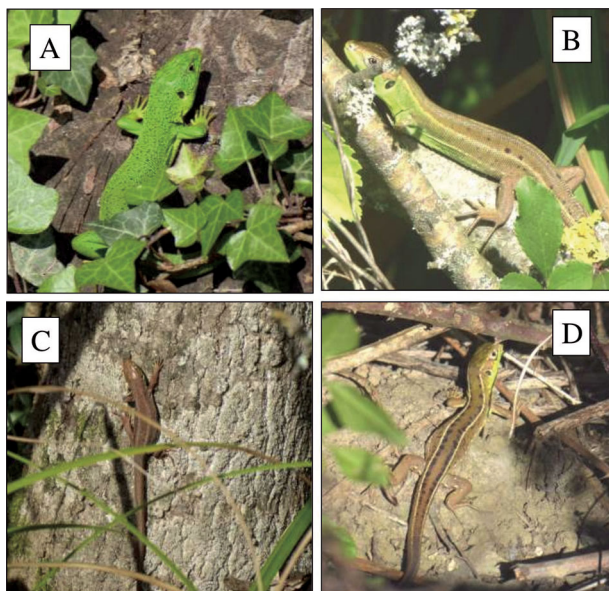


Fig. 2. Examples of *L. bilineata* basking on various surfaces: (A) a male basking on tree stump; (B) female on fallen branch; (C) female on bark of a tree trunk, and (D) female on bare soil.

Only the curved surface areas of fallen branches or tree trunks exposed to sunshine were measured since these were the areas where lizards basked. The surfaces areas of stones or open ground patches exposed to sunshine were calculated as near possible to an estimated $\pm 5\%$ error.

Statistical analysis. To examine whether lizards non-randomly used different substrates for basking requires constructing a null model of random selection (Gotelli and Ellison, 2004). To do this a random model was constructed by estimating the proportions of various substratum types that were available to the lizards and then comparing the proportions to those actually used by the lizards. The assumption was that 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 an indication that substratum selection was non-random. The test used was the Kolmogorov – Smirnov Goodness of Fit test (D_{\max}). This test has value in that it is exact and

distribution-free, and not sensitive to cell counts. The hypothesis is $H_0: P = P_0$, $H_1: P \neq P_0$, where P is the observed distribution of substratum used by the lizards and P_0 the distribution of available substrates. A value of 1 in the goodness of fit test indicates that observed substratum use is random and hence proportional to its availability (see Tables 1 and 2).

The expected probabilities were derived from the summed substratum availability after conversion to decimal fractions. The Kolmogorov – Smirnov test requires that $\Sigma n = 1$, where n is the decimal proportions. The expected proportions for the garden habitat were: Limestone (walls), 0.526; red tiles, 0.0525; wood, 0.0454; concrete, 0.349.

In the hedgerow expected proportions were: Tree stump, 0.027; fallen tree branches, 0.270; open areas with no vegetation, 0.487; Tree bark, 0.135; limestones, 0.081.

In a test for monthly frequency of communal basking in *P. muralis* (frequency of groups of lizards basking together), the Kolmogorov – Smirnov Goodness of Fit Test was again used. The null hypothesis is monthly equality of communal basking derived from,

$$\text{Expected} = 1/(N_1 N_2),$$

where N_1 is number of months and N_2 the total sample size. This gave an expected value of 4.875 groups of lizards (up to three individuals) in each cell (month).

The tests were set at the 95% interval with deviation from the expected probabilities indicated if the 95% intervals were attained or exceeded. Tests for independent proportions were made using z -tests to test for seasonal differences comparing basking on different surface types, which had wood surfaces (trees, fallen branches, and a tree stump) versus areas composed of bare soil or stones and concrete.

RESULTS

Hedgerow. Basking *P. muralis* were observed on fallen branches (50.4% of, $n = 107$ observations), tree stump (23.4%), trees (13.1%), bare soil (7.7%) and stones (5.6%). Basking in *L. bilineata* was greater on bare soil substrates (52.6% of, $n = 38$ observations),

TABLE 1. Results of the Kolmogorov – Smirnov One-Sample D_{\max} Tests of Observed Substratum Use for Basking Tested Against Expected Basking Frequencies Under a Null Hypothesis of Substratum Availability in the Hedgerow

Species	Fallen branches	Tree	Tree stump	Stones	Soil	D_{\max}	P	n
<i>P. muralis</i>	1.86	-1.03	8.65	-1.45	-6.51	0.439	<0.01	103
<i>L. bilineata</i>	-0.73	-5.13	2.92	–	1.08	0.189	0.18	39

Notes. Values of 1 would indicate substratum use in agreement with availability; negative values indicate less use than expected, positive values greater use. No *L. bilineata* was observed basking on stones. See text for further details.

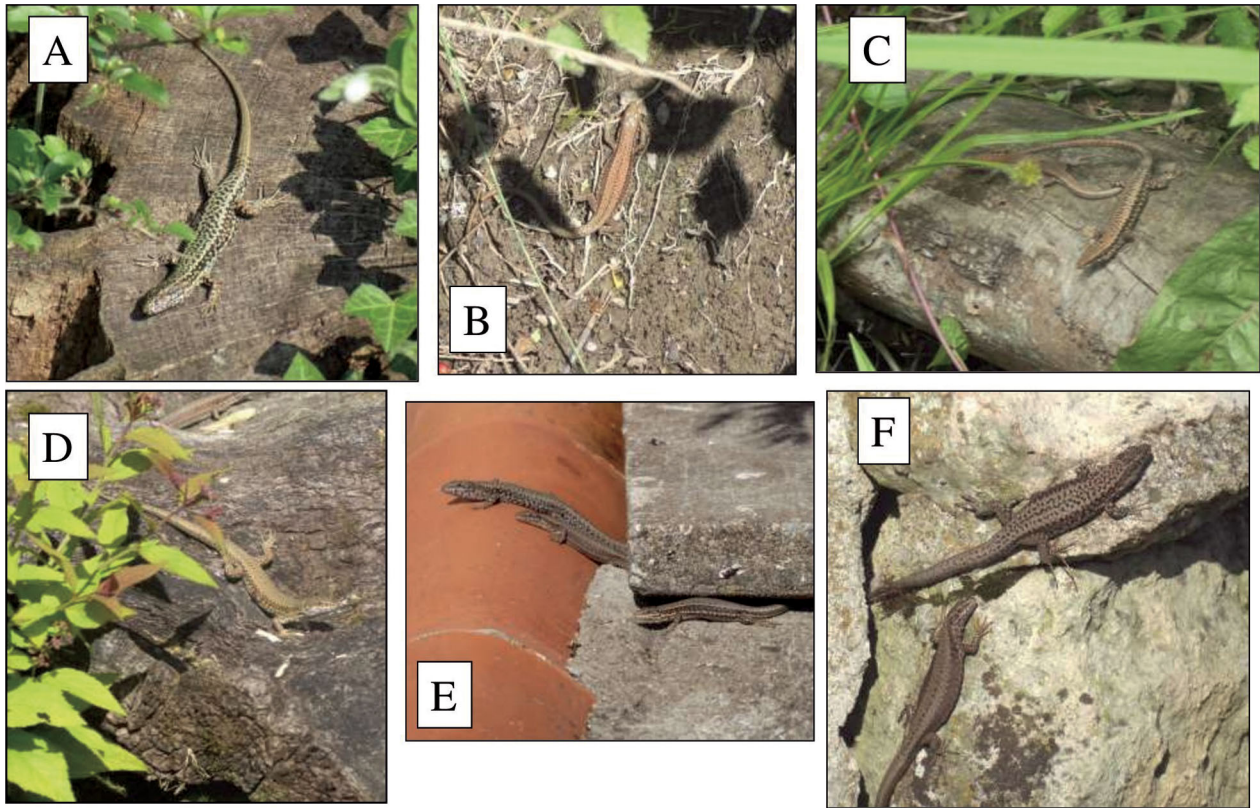


Fig. 3. Examples of *P. muralis* basking. A, B, and C show lizards in the hedgerow with: (A), a male basking on tree stump; (B) female on bare soil; (C) male (right) and female communal basking on fallen branch; (D) male and female on wood; (E) three lizards communal basking on red tile (male left, female right) a female on concrete and (F) communal basking with male (top of photograph) on concrete and female on limestone. Photographs (D) – (F) show lizards in the garden habitat.

fallen logs (36.8%), tree stump (7.98%) and tree trunks (2.6%) (see examples in Figs. 2 and 3). However, in terms of availability there were inter-specific differences in basking substratum use with *P. muralis* showing significant differences from the null model of expected probabilities (Fig. 4). In contrast *L. bilineata* showed no significant departure of substratum use from substratum availability ($D_{\max} = 0.189$, $P = 0.18$). Table 1 shows the full results of the D_{\max} Goodness of Fit tests.

Seasonality tests. Sample sizes in the hedgerow constrained the seasonality tests from April to the end of

June and from July to October. The results showed that *P. muralis* spent a significantly greater time basking on wood surfaces (94%, total, $n = 44$ compared to *L. bilineata* (68.2%, total sighting, $n = 22$) during April – June ($z = 2.47$, $P = 0.007$) and also during July – October (*P. muralis*, 79.7% (total, $n = 59$) vs *L. bilineata*, 23.5% (total sighting, $n = 17$); $z = 4.76$, $P < 0.001$). However, both *P. muralis* and *L. bilineata* increased the time they basked on bare soil/stones (stones were not seen used by *L. bilineata*) during July – October (*L. bilineata* 31.8 to 76.5%; *P. muralis* 6 to 20.3%) (Fig. 5).

TABLE 2. Results of the Kolmogorov – Smirnov One-Sample D_{\max} Tests of Observed Substratum Use for Basking Tested Against Expected Substrate Frequencies Under a Null Hypothesis of Substratum Type Availability in the Garden Habitat

<i>P. muralis</i>	Limestone	Red tiles	Wood	<i>Hedera</i>	Concrete	D_{\max}	P	n
March – June	1.62	1.21	6.64	–0.69	–1.22	0.201	=0.01	63
July – September	–2.02	1.24	3.83	1.37	1.33	0.265	<0.01	69
October – November	–5.79	1.41	4.71	2.79	–0.95	0.221	<0.01	175
Pooled	–5.68	1.33	4.91	2.01	1.01	0.227	<0.01	307

Notes. Ivy (*Hedera* sp.) was the only plant used by lizards as a basking surface. Other details as Table 1.

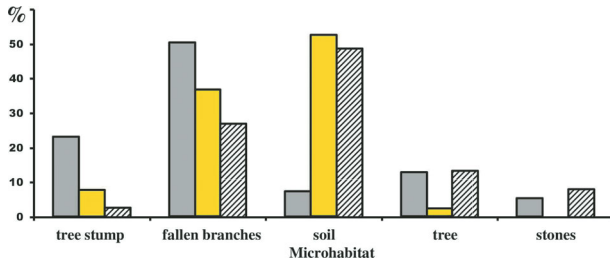


Fig. 4. Observed vs. expected substratum use in the hedgerow indicating selection in *P. muralis* but non-significance in *L. bilineata*. Gray histograms are *P. muralis*, and yellow *L. bilineata*. Cross-hatched are the expected probabilities based on basking area availability.

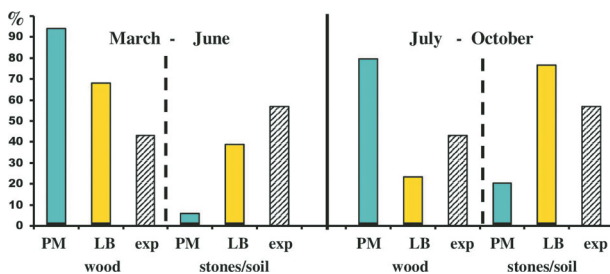


Fig. 5. Seasonal substratum type selection when types of surface are pooled, for instance wood consists of trees, fallen branches and tree stump data, soil is open bare soil patches with little or no vegetation cover or stones. Cross-hatched cells are the expected probabilities.

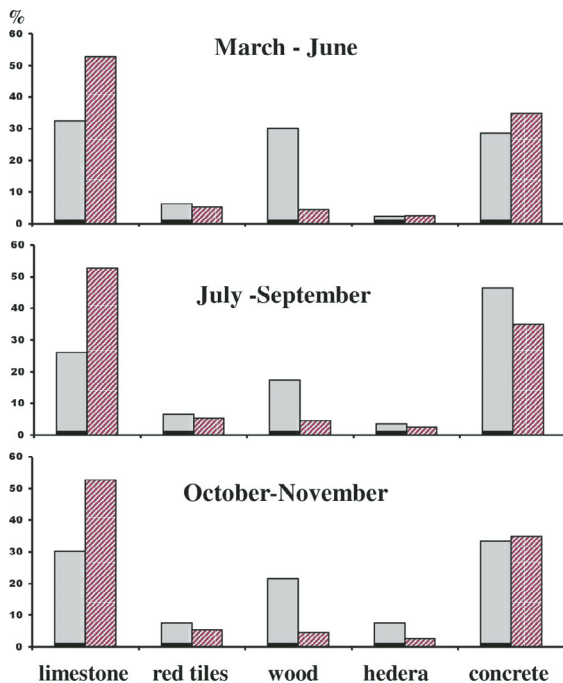


Fig. 6. Observed and expected frequencies of substratum type selection for basking *P. muralis* in the garden population during 3 periods of the active year. Crosshatched areas are the expected probabilities based on basking area availability.

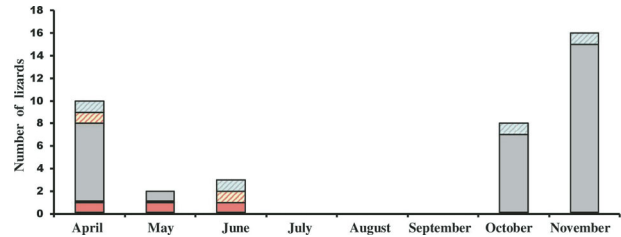


Fig. 7. Communal basking in *P. muralis*. Green sections indicate two lizards together and cross-hatched green areas represent three lizards in the group in the hedgerow. The garden population is shown as gray bars when there were two lizards in the group and cross-hatched gray when three lizards were in a group. Examples are shown in Fig. 2.

Garden habitat. The *P. muralis* garden population (sighting totals, $n = 361$) was seen in greater numbers on limestone walls (52.6%) and concrete based surfaces (34.9%) than other substrates. However, in respect to availability there was a strong preference for wood surfaces but this was much reduced during the hotter summer (Fig. 6). Secondary selection based on availability was for red tiles, which was also greater than expected during all periods of the active year. The full results for this population are shown in Table 2.

Seasonality tests. Tests for seasonal differences in proportions of substratum use in *P. muralis* showed statistically greater use of wood in March – June (30.2%) compared to July – September (17.4%; $z = 1.72$, $P = 0.04$) but not compared to October – November (21.43%; $z = 1.32$, $P = 0.09$). Wood substrate selection was also significantly greater during October – November compared to July – September ($z = 1.87$, $P = 0.03$). These results indicate wood substrates for basking was in greater use during the cooler months compared to mid-summer months.

Communal basking. Communal basking was observed in both species but in significantly greater frequency in *P. muralis* (garden, 9.4%; hedgerow, 4.7%), but the inter-population frequencies in *P. muralis* were not significantly different ($z = 1.83$, $P = 0.07$) and therefore data for *P. muralis* were pooled. This showed greater communal basking in *P. muralis* (pooled data = 8.33%) compared with *L. bilineata* (2.56%; $z = 2.005$, $P = 0.04$). The D_{\max} Goodness of Fit test against equality of months for *P. muralis* communal basking in the garden habitat indicated a significant departure from equality ($D = 0.366$, $P < 0.01$) occurring in greater frequencies during April (2.05× greater), October (1.64× greater), and November (3.28× greater). Figure 7 shows a histogram of frequencies at both study areas.

DISCUSSION

Our study has shown strong preference for wood as a basking substratum in both *P. muralis* and *L. bilineata*, which supports our prediction (1) and is in good agreement with the earlier findings of Hailey (1982) in his study of the cold adapted lizard *Z. vivipara*. Careful thermoregulation in terms of the benefits of selecting wood-based substrates will be economical when basking sites are in relatively close proximity and more likely to be achieved in low cost thermal habitats both in terms of thermal opportunities and predation risk (e.g., Huey, 1991). Increased thermoregulation effort in low cost habitats enable body temperatures to more closely reach optimum levels (e.g., Huey and Slatkin, 1976) indicating the importance of, not only suburban gardens, but hedgerow systems in fragmented landscapes. Predators were rarely seen in both our study sites ($n = 5$) but hatchling and subadult *Hierophis viridiflavus*, a saurophagus snake (e.g., Rugiero and Luiselli, 1995; Capizzi et al., 2008), but given the secretive behavior in snakes they may actually be more frequent than actually seen. The grass snake *Natrix helvetica* was also seen on four occasions (two in each study area) during the study period but these snakes are essentially predators of amphibians rather than lizards (e.g., Luiselli et al., 2005). Lacertid lizards are able to detect snake presence using chemical cues (Van Damme and Quick, 2001; but see Cerini et al., 2020 for different results) and therefore it is conceivable that when *H. viridiflavus* are present the lizards do indeed shift to more safe habitats (Meek, 2014) that we suggest also occurred at our study sites.

Our observation of lower use of wood based surfaces in *P. muralis* during the hotter summer months supports our prediction (2) based on Hailey's (1982) results. For example, fallen log use in the hedgerow declined as summer progressed into autumn in both species (*P. muralis* 94 to 79.7% vs. *L. bilineata* 68.2 to 23.5%) with basking on open ground increasing over the same time period (*P. muralis* 6 to 20.3% vs. *L. bilineata* 31.8 to 76.5%). These changes likely reflect the warmer summer environment but differences between species might reflect different life styles or longer distance movement in *L. bilineata*.

Non-significant (random) substratum selection at a finer level in *L. bilineata* was perhaps unexpected but the advantages of reduced basking duration offered by wood was observed when data for wood based materials were pooled and compared seasonally to non-wood (stones, bare soil). Increased movement onto bare soil substrates during the latter part of the year in this species, which is in agreement with a study of *L. bilineata* in northern Italy (Luppi et al., 2020), suggests that other factors were in-

involved in substratum/microhabitat selection, perhaps enhanced prey and predator detection. *Podarcis muralis* also showed a similar but less evident trend (Fig. 4). For example, *P. muralis* selected substrates that potentially enabled the scanning of horizontal surfaces for potential prey species and detection of potential predators (Avery et al., 1993; Avery, 1994). Fallen branches and tree stumps in our study may serve this purpose.

A clear difference between the two species was an almost absence of communal basking in *L. bilineata* in comparison to *P. muralis*. An explanation might be found in the well known intra-specific aggression in *L. bilineata* (e.g., Beebee and Griffiths, 2000), including cannibalistic behaviour (Angelici et al., 1997; Rugiero et al., 2021). This interference competition may constrain some individuals in the population to avoid accessing optimum basking sites due to the presence of other lizards, especially large males. For example, it is known that a lizard can increase net energy gain from careful thermoregulation if it can exclude potential competitors from optimum basking sites (e.g., Huey and Slatkin, 1979). Furthermore securing such sites may reduce the physiological costs of shuttling, a behavior that also increases risk of predation, whilst also optimizing detection of insect prey and the approach of predators. Greater home ranges in *L. bilineata* may influence familiarity with prime basking locations. In our study areas we identified individuals of both species and this indicated that, in both habitats, some individuals of *P. muralis* were present in all months of the active year, which might also enable greater habitat familiarity and knowledge of prime basking sites in this species. In a study of *L. bilineata* in Germany morning basking was observed on "fast-heating structures" such as moss or compact layers of grass and those individuals that were tracked sometimes moved over long distances (up to 205 m within an hour) during which movements were rapid suggesting that the lizards knew the area and exactly where to go (Sound and Veith, 2000). This might also suggest that the lizards were in fact familiar with optimum basking patches. Males also prevented other males entering their territory (Sound and Veith, 2000), which supports our observations of low communal basking frequency in this species. Interaction with *P. muralis* was rarely observed except on two occasions when 2 individuals shared basking sites (both on fallen branches). Other studies have shown niche segregation between sympatric *L. agilis* and *L. viridis* (a species that is closely related to *L. bilineata*; see Böhme et al., 2007) based on fine scale habitat patch use, with *L. agilis* operating in open spaces and *L. viridis* bushy areas, despite generally similar daily activity patterns (Heltai et al., 2015).

The presence of communal basking was confirmed in *P. muralis* (question 3) but showed a skewed monthly

TABLE 3. Communal Basking Frequency and Composition of Individuals in *P. muralis* at Both Study Localities

	1 Male, 1 female	1 Male, 2 females	2 Females	1 Male, 1 subadult	1 Female, 1 subadult	1 Male, 1 female, 1 subadult	2 Subadults
Hedgerow	2	2	0	0	0	0	0
Garden	16	4	7	2	0	1	3

distribution. In the garden population of *P. muralis* this was likely due to (i) emergence and mating behavior in spring and (ii) individuals clustering around winter den areas in autumn (Fig. 6 and Table 3). The latter may constrain microhabitat/substratum selection during November, when colder days and lower body temperatures increase risk of predation by movement around the environment. Communal basking may also facilitate early female–male contact for reproduction in the following spring due to selection of optimum basking sites.

The results of the present study are of additional interest in respect of the ability of both species to colonize areas outside their natural range, for example USA and more northerly areas of Europe, but especially the cooler climate in the south of England where additional thermal constraints are present. For instance, it might be expected that optimum patch selection would also operate in these new cooler habitats given the higher selected body temperatures of *P. muralis* and *L. bilineata* in comparison to native *Z. vivipara* (Avery, 1978). An example of the adaptive capability of *P. muralis* has been shown by non-native females in the south of England where female reproductive investment was shifted into the first seasons clutch which differed from females in their natural (Italy) range (MacGregor et al., 2017).

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