

Living in Patchy Habitats: Substrate Selection for Basking by Sympatric Lizards in Contrasted Anthropogenic Habitats in Western France

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Abstract

The influence of temperature on the physiological processes in reptiles is well known, for example growth, reproduction, muscular energy are all largely temperature dependent and therefore temperature is a key aspect of reptilian ecology. However, there may be constraints on the ability of reptiles to harness thermal energy, particularly during cold seasons in the temperate zones. Substrate selection is a key aspect in thermoregulation and can enhance 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 two species of lizard, *Lacerta bilineata* and *Podarcis muralis* in a hedgerow and suburban garden in western France compared against a null model of substrate availability. When different substrates were pooled based on their 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 substrate availability (fallen tree branches, tree stumps, open ground etc), *P. muralis* showed strong substrate selection for basking, whereas *L. bilineata* did not depart significantly from the null model. We speculated that intra-specific aggression in *L. bilineata* was a possible cause of this result due to dominant individuals limiting smaller or female lizards from accessing prime basking sites. Differences in communal basking between the two species supported this notion.

Introduction

The expansion of urban areas and modification to natural environments by agriculture is a key cause of reptile population declines (e.g. Jellinek et al. 2004; Audsley et al. 2006; Böhm et al. 2013; Keinath et al. 2016). Major changes to vegetation structure may impact upon a reptiles 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 and this in turn depends on the thermal quality of the substrates (Huey and Slatkin 1976; Huey, 1991; Castilla et al. 1999). Adaptation therefore requires a habitat offering a suitable thermal environment with basking opportunities to raise body temperatures and also access to shaded areas for cooling (e.g., Avery 1979; Basson et al. 2019). The costs of moving to and from optimum basking areas in terms of both energy costs and predation risk during movement 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 the quality of the habitat (Carrascal et al. 1992; Herczeg et al. 2008; Basson et al. 2017). Therefore, population persistence in altered habitats, including patchy habitat and suburban areas is subject to the same thermal and other ecological constraints/requirements.

Lacertid lizards regulate body temperatures by selecting thermally favourable microhabitats (via appropriate substrates) and adjusting activity times and behaviour that alter heat exchange with the environment (e.g., Bauwens et al. 1996; Castilla et al. 1999). Two of the most common lacertids in

Western Europe, the wall lizard (*Podarcis muralis*) and the green lizard (*Lacerta bilineata*), occur in a wide range of environments that include suburban gardens and agricultural areas (e.g. Corti et al. 2011; Speybroeck et al. 2016). Both are lacertid lizards that differ substantially in terms of body size (*L. bilineata* being much larger; see Corti et al. 2011), primarily consume a range of insects (Barbault and Mou 1986; Angelici et al. 1997; Speybroeck et al. 2016) and *P. muralis* is essentially an active forager whilst *Lacerta bilineata* is a sentinel predator (Verwajen and Van Damme 2008). Body temperatures of up to around 36° C have been recorded by *P. muralis* in the field (Avery 1978; Bauwens 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 therefore of particular interest because of (i) their contrasted life-histories and (ii) the highly modified landscapes they inhabit typically impact on physical structure, micro-climates and the species composition of natural vegetation, thus potentially isolating populations (e.g. Germaine and Wakeling 2001). For example, agricultural mono-cultures have little value to most wildlife and the remaining usable habitat in such landscapes is often hedgerow systems (Saint Girons 1996; Luiselli and Capizzi 1997). Hedgerows are typically linear habitats that may be used as permanent home ranges for some species, whilst for others they function as connection pathways to more usable habitats (Saint Girons 1996; Vignoli et al. 2009; Meek, 2014a 2014b; Rugerio et al. 2018). Suburban gardens are also typically highly altered in structure compared to natural habitats but many species of lizard, especially *P. muralis*, are capable of adapting to these anthropogenic environments including having the 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 such habitats using data on substratum selection.

The size differences between *L. bilineata* and *P. muralis* is an important factor in their thermal biology impacting primarily on differences in rates of heating and cooling size (e.g. Corti et al. 2011). Indeed, *P. muralis* heats around 1.5 times faster than *L. bilineata* (e.g. Hailey 1982). Time spent basking could also be expected to impact on time budgets for other daily activities but microhabitat/substratum selection can also influence heating rates (e.g., Hailey 1982). For example, heat conduction from substrates can be important during sunny weather but especially during cloudy weather (Avery 1979; Beebee and Griffiths 2020). In a study of basking substrates used by the cold adapted lacertid *Zootoca vivipara*, Hailey (1982) found that for basking wood surfaces were mostly selected 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, risk of predation) of moving to a warm substrate for basking during sunny weather compared to the 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 (0.9km) from the above-mentioned hedgerow, where only a *P. muralis* population is found. 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 650km north of our study area, where temperatures are lower with also 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. 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 represent 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 basking substrate selection with season and are there any differences in this respect between the two species? We ask this question because as summer progresses and the environment warms lizards may be less dependent on substrates offering greater heating rates. We therefore predicted that selection for the high 1.17 J/g°C wood based substratum would decline.

3) Does communal basking occur in different species and if so is there a difference in frequency for this behaviour 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 *Lacerta bilineata* were studied in a hedgerow (PH) system on the edge of the village of Chasnais (46° 27' N; 1° 53' 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 1197m². The hedgerow can also be described as a low cost thermal environment in the sense of Huey and Slatkin (1976) in that it is structurally relatively simple consisting 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 (area 1197m²) is also low cost (sensu Huey & Slatkin 1976)

but 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 Figs. 1A and 1B).

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 0900hrs) 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 15hrs to 1800hrs. Sampling frequency ranged from 32.5 to 30 hours from April to October and November in the garden population but fewer during March and December (7.35–15 hrs respectively). Data were collected by systematically 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 when sighted several photographs of each or groups of lizards were usually taken, but only one for each sighting used which was the best quality example. Using one photograph per sampling session also minimized the risk of pseudoreplication. Sampling effort was 5–6 days each week for around 45–60 minutes daily, usually from around 0830hrs but up to around 1300hrs in the hedgerow but occasionally until evening in the garden population, especially when the weather was cloudy. Photographs enabled identification of each individual lizard (Welbourne 2020) but only one per day was included in the analysis, giving a total of 39 for *L. bilineata* and 107 for *P. muralis* in the hedgerow, and 361 photographs of *P. muralis* out of a total of 844 taken in the garden. Basking sites are defined those observed used by lizards. For example shaded areas where lizards might be seen were not by definition basking sites. Additionally lizards crossed areas of open ground when moving from one location to another but these were not basking sites and hence the substrates types the moved across were not included in the analysis.

Estimating substratum availability. Available substratum proportions were estimated by simple measurement using a tape measure to calculate surface area of all potential basking sites. Potential basking sites were defined as those sites where at least one basking lizard was observed on at least one occasion. 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 irregular surfaces of stones or open ground patches when in 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, we compared the substratum use with substratum availability. This required constructing models that produced patterns of expected probabilities (Gotelli and Ellison 2004). The proportions of various substratum types considered available as basking locations were calculated and used as the random model. This random model was then evaluated against the frequency that lizards actually used these habitats. The assumption was that if substratum use was proportional to its availability, then selection would be considered random and non-selective; deviations from the null model were instead an indication that substratum selection was non-random. In Table 1, a value of 1 indicates that observed substratum use is random and hence proportional with its availability. The test used was the Kolmogorov-Smirnov Goodness of Fit test (D_{max})

that has value in that it is an exact and distribution-free test, and hence robust and not sensitive to cell counts. In this study the test hypothesis is $H_0: P = P_0$, $H_1, P \neq P_0$, where P is the observed distribution of substratum use and P_0 the distribution of available substrates.

Table 1

A. Results of the Kolmogorov-Smirnov one-sample D_{max} tests of observed substratum use for basking tested against expected frequencies under a null hypothesis of substratum availability in the hedgerow. Values of 1 indicate substratum use in agreement with availability, negative values less use and positive values greater use. See text for further details. No *L. bilineata* was observed basking on stones.

	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

Table 1

b. Results of the Kolmogorov-Smirnov one-sample D_{max} tests of observed substratum use for basking tested against expected frequencies under a null hypothesis of substratum type availability in the garden habitat. Ivy (*Hedera*) was the only plant used by lizards as a basking surface. Other details as Table 1A.

<i>P. muralis</i>	limestone	Red tiles	wood	Hedera	concrete	D_{max}	P n
Mar-June	1.62	1.21	6.64	-0.69	-1.22	0.201	= 0.01 63
July-Sept	-2.02	1.24	3.83	1.37	1.33	0.265	<0.01 69
Oct-Nov	-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

Table 2

Communal basking composition of individuals in *P. muralis* at both study localities. Additional communal basking of one *L. b* and *P. m* sharing fallen branches as basking substratum was observed on two occasions.

	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
Hedge	2	2	0	0	0	0	0
Garden	16	4	7	2	0	1	3
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The expected probabilities were derived from the summed substratum availability after conversion to decimal fractions. The Kolmogorov-Smirnov test requires that $\sum n = 1$, 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) in the garden population, the Kolmogorov-Smirnov Goodness of Fit Test was used. The null hypothesis is monthly equality of communal basking. This was 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) 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 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), fallen logs (36.8%), tree stump (7.98%) and tree trunks (2.6%) (see examples in Fig. 2A & 2B). However, in terms of availability there were inter-specific differences in basking substratum use with *P. muralis* showing significantly different selection from the null model of expected probabilities (Fig. 3). In contrast *L. bilineata* showed no significant departure of substratum use from substratum availability ($D_{\max} = 0.189$, $P = 0.18$). Table 1a shows the full results of the D_{\max} Goodness of Fit tests.

Seasonality tests. Sample sizes in the hedgerow constrained the seasonality tests to 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 $n = 22$) 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 $n = 17$); $z = 4.76$, $P < 0.001$). However, both *P. muralis* and *L. bilineata* increased time spent on bare soil/stones during July – October (*L. bilineata* 31.8 to 76.5%; *P. muralis* 6 to 20.3%) (Fig. 4).

Garden habitat

The *P. muralis* garden population (total $n = 361$) 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. 5). 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 1b.

Seasonality tests Tests for seasonal differences in proportions between 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 these frequencies were not significantly different ($z = 1.83$, $P = 0.07$). Therefore the data for *P. muralis* were pooled and indicated 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 (x 2.05), October (x 1.64) and November (x 3.28). Figure 6 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 *Z. vivipara*. Careful thermoregulation in terms of the benefits of selecting wood-based substrates will be economical when such sites are in relatively close proximity and will be more likely to be achieved in low cost habitats both in terms of thermal opportunities and predation risk (e.g. Huey 1991). Increased thermoregulations in low cost habitats enable body temperatures to more closely reach optimum levels (e.g. Huey and Slatkin 1976) indicating the present day importance of, not only suburban gardens, but hedgerow systems in fragmented landscapes. Predators were rarely seen in both our study sites (n = 5) but various sized individuals of the saurophagus snake (*Hierophis viridiflavus*) were the most frequent. We observed both hatchling and subadult *H. viridiflavus*, both categories preying actively upon *P. muralis* (e.g., Rugiero and Luiselli 1995; Capizzi et al. 2008), and given the secretive behaviour 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), as we felt also happened at our study sites.

Our observation of lower use of wood based surfaces in *P. muralis* during the hotter summer months supports our prediction based on Hailey's (1982) results. For example, fallen log use declined as summer progressed into autumn in both species (*P. muralis* 94 to 79.7% versus *L. bilineata* 68.2 to 23.5%) with basking on open ground increasing over the same time period (*P. muralis* 6 to 20.3% versus *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 involved in substratum/microhabitat selection, perhaps enhanced prey and predator detection. *Podarcis muralis* also showed a similar but less evident trend (Fig. 3). For example, *P. muralis* selected substrates to scan horizontal surfaces for potential prey species (Avery et al 1993; Avery 1994). Fallen branches and tree stumps in our study may serve this purpose and also enable enhanced detection of potential predators. *Lacerta bilineata* is well known for intra-specific aggression with minimal (or rare) communal basking (Beebee and Griffiths, 2000), including cannibalistic acts (Angelici et al., 1997; Rugiero et al., 2021). This interference competition may constrain some individuals in the population to avoid accessing optimum basking sites by the presence of other lizards, especially large males. For example, 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 such sites may reduce shuttling, which increases risk of predation and optimizes detection of insect prey and the approach of predators. Greater home ranges in *L. bilineata* may influence familiarity with prime basking locations. Individually identified *P. muralis*, for example, were present in all months of the active year in both habitats, which might enable greater habitat familiarity.

In a study of *L. bilineata* in Germany morning basking was observed on $f * - heat \in gstructures$ such as moss or compact layers of grass and tracked lizards sometimes moved over long distances (up to 205m within an hour) when 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. Interaction with *P. muralis* was rarely observed except on two occasions when two 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 skewed presence of communal basking occurrence in the garden population of *P. muralis* was likely due to (i) emergence and mating behaviour in spring and (ii) individuals clustering around winter den areas in autumn (Fig. 5 and Table 3). The latter may constrain microhabitat/substratum selection during November, when the colder days increase risk of movement around the environment. Communal basking may also facilitate early female - male contact for reproduction in Spring. One group of seven lizards (including just one male) used the same den for hibernation during late November.

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 extra demands on thermal ecology are present. For instance, it might be expected that optimum patch selection would also operate in these newer 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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Author contributions - RM and LL initiated the study and wrote the manuscript. RM carried out the field work and data analysis. Both authors agreed on the final submitted version of the manuscript.

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Figures



Figure 1

Google Earth map showing hedgerow with agriculture land either side (A). Insert is sampling area.
 Examples of basking areas used by *P. muralis*. A shows limestone wall and B deadwood and raised bed
 created from limestones.



Figure 2

(A) Examples of *L. bilineata* basking on various surfaces. Fig 2A shows *L. bilineata* male basking on tree
 stump, B female on fallen branch, C female on bark of tree trunk and D female on bare soil. (B) Figure 2B.
 Examples of *P. muralis* basking; A, B and C show lizards in the hedgerow with A male basking on tree
 stump, B female on bare soil and C male (right) and female communal basking on fallen branch.

Photographs D, E and F show lizards in the garden habitat D male on wood, E three lizards communal basking on red tile (male left, female right) and female on concrete and F communal basking with male (top) on concrete and female on limestone.

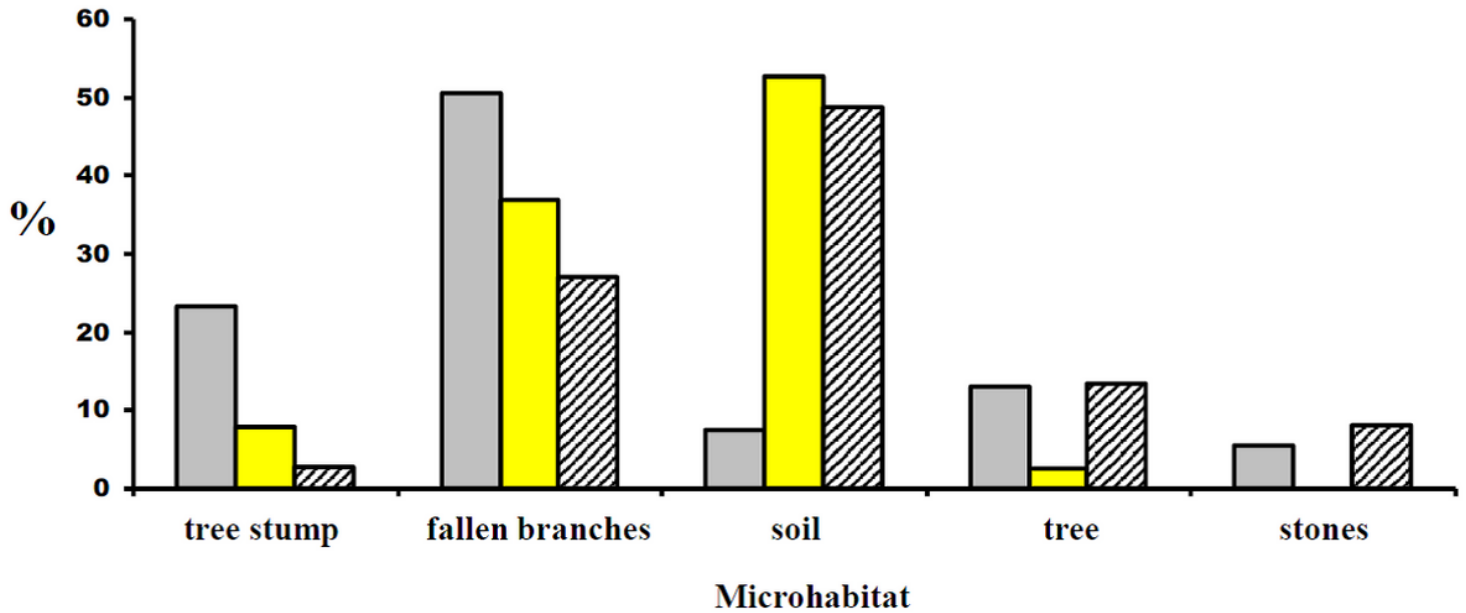


Figure 3

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

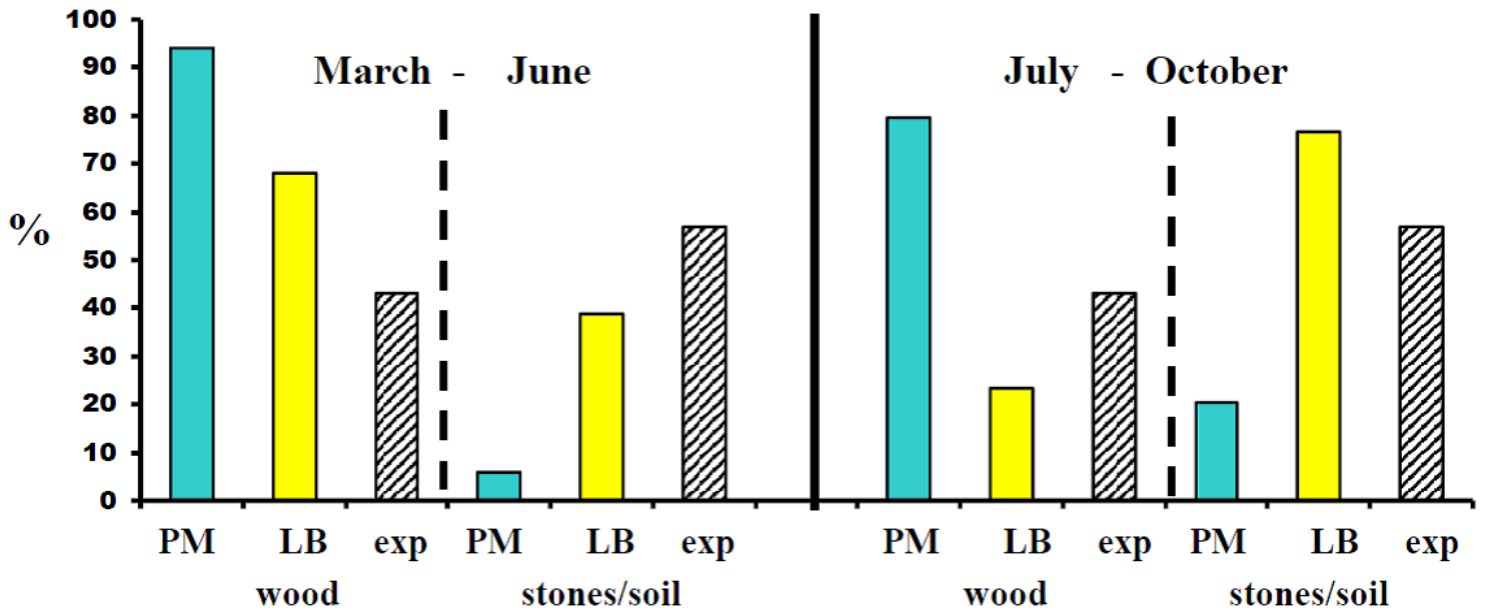


Figure 4

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.

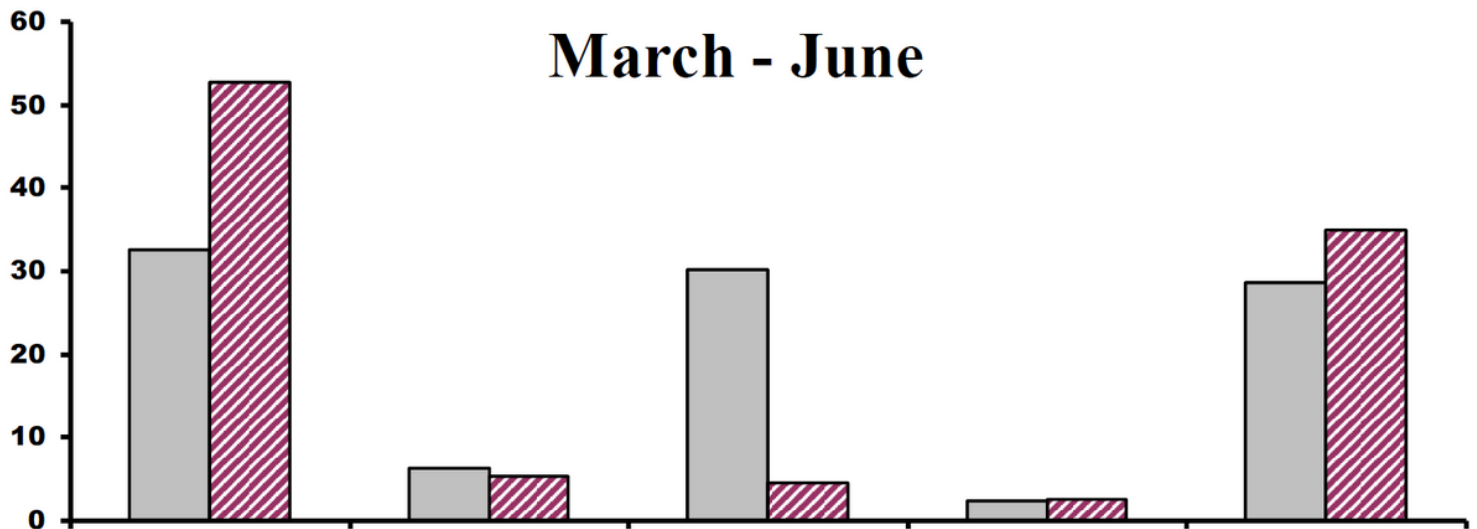


Figure 5

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 indicated expected probabilities based on basking area availability.

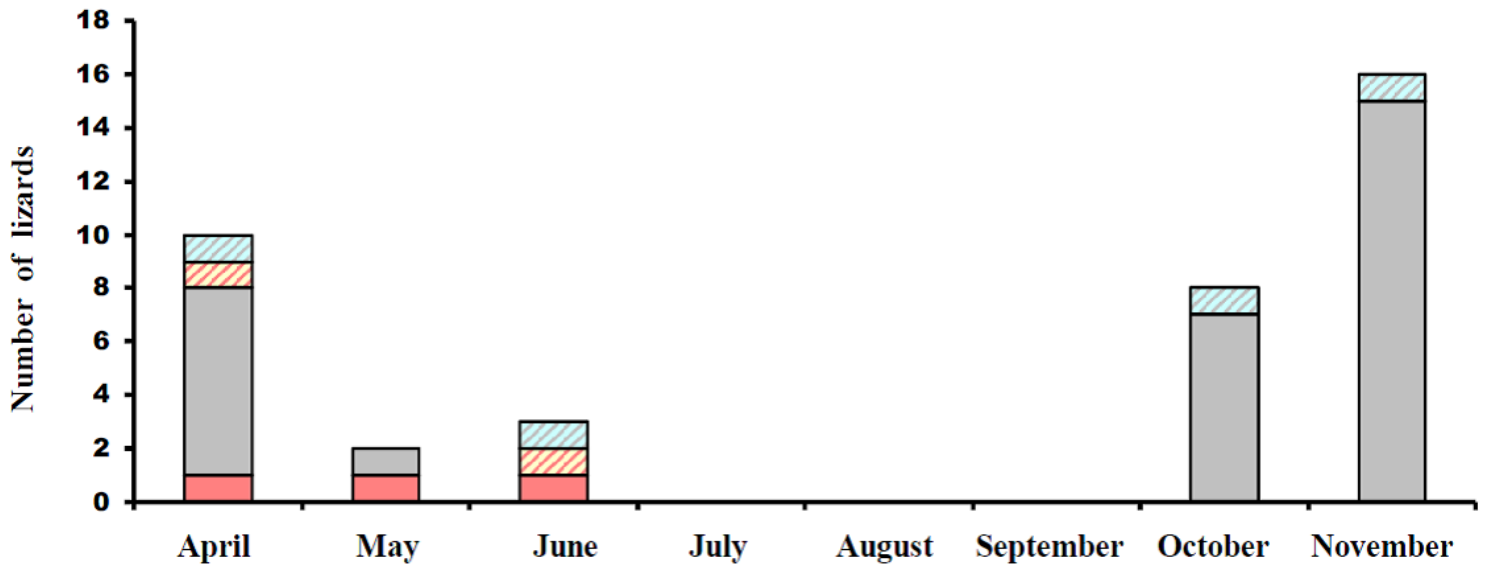


Figure 6

Communal basking in *P. muralis*. Green indicates two lizards together and cross-hatched green areas represent three lizards in the group in the hedgerow. Garden population is shown as grey when there were two lizards in the group and cross-hatched grey when three lizards were in a group. Examples are shown in Figure 2.