



Aspects of the demography of two *Podarcis muralis* populations in anthropogenic modified habitats in western France, based on a non-invasive sampling method

Roger Meek¹, Luca Luiselli^{1,2,3} & Roger A. Avery⁴

¹Institute for Development, Ecology, Conservation and Cooperation, via G. Tomasi di Lampedusa 33, I-00144 Rome, Italy

²Department of Animal and Environmental Biology, Rivers State University of Science and Technology, P.M.B. 5080, Port Harcourt, Nigeria

³Laboratoire d'Ecologie et d'Ecotoxicologie, Faculté des Sciences, Université de Lomé, Togo

⁴British Herpetological Society: c/o Zoological Society of London, Regent's Park, London, NWR 4RY, UK

Urbanisation impacts on both abiotic and biotic characteristics of the environment and is likely to bring new selective pressures on animal species living within these areas. The common European wall lizard *Podarcis muralis* adapts well to urbanisation and indeed may be described as the archetypical urban lizard. In this paper we investigated some aspects of the demography of two populations of *P. muralis* from western France, one living in a hedgerow system situated in an agricultural area on the edge of a village and a second in an urban garden. The active year in both populations was from February–March until October–December, the latter in the urban garden where temperatures were higher. Numbers decreased from around June then increased again during September but this varied annually and between populations. Diversity and equality indexes for both populations were high, especially in females, indicating a range of individuals and their frequency of presence. Both populations were therefore stable despite only limited numbers of lizards being present for more than one year. Male lizards with high presence were more frequently seen in the company of females than males that were seen less frequently. Hatchling lizards were seen from June after the spring mating period with a second period of hatchlings appearing during autumn. This supports the notion that females annually deposit two clutches of eggs in the area.

Keywords: lizards, *Podarcis muralis*, demography, western France, non-invasive sampling

INTRODUCTION

Whereas many reptile populations have been monitored in order to analyse their demography (e.g. Guiller et al., 2022; Kusriani et al., 2022), quantitative data on reptiles living in anthropised landscapes, especially at the level of the individual, are still limited (French et al., 2018; Doherty et al., 2020). For example, since reptiles have a limited ability for dispersal and relatively small home ranges, they are more likely to be exposed to increased risk of population decline and collapse due to habitat modifications (Doherty et al., 2020; Guiller et al., 2022). One species that thrives in urban areas is the European wall lizard *Podarcis muralis* (e.g. Capula et al., 1993; Williams, 2019). This species has successfully colonised many new areas, including urban environments, where they are non-natural due to pet trade escapes or deliberate introductions (e.g. Gherghel et al., 2009; Allan et al., 2011; Kolbe et al., 2013; MacGregor et al., 2017; Williams, 2019; Williams et al., 2021) and can be regarded as a model species to understand how urban lizards are able to colonise and persist in anthropogenic environments.

Several studies have examined *P. muralis* population ecology within its natural range (e.g. Barbault & Mou, 1988) including in urban environments (e.g. Edsman, 1990; Meek, 2014a; 2014b; 2020; Heym et al., 2013; Lazic et al., 2017; Williams, 2019). Edsman (1990; unpublished PhD thesis) described a five-year study of behaviour and territoriality of individual lizards living on an ancient stone wall in Fiesole, central Italy. The study was primarily focused on the causes and consequences of male territoriality in *P. muralis* based on individually marked lizards. The results showed that males defended long term territories encompassing the home ranges of resident reproductive females. Females were evenly distributed on the wall and hence larger male territories contained more females. Edsman concluded that females remained in male territory because it offered access to optimal basking places, which is important for reproduction.

In this paper, we describe the results of a three-year study in western France on two populations of *P. muralis* situated less than 1 km from one another, a hedgerow in an agricultural area and an urban garden. This means that both populations experienced a similar climate but occupied structurally different habitats,

Correspondence: Roger Meek (rogermeek85@aol.com)

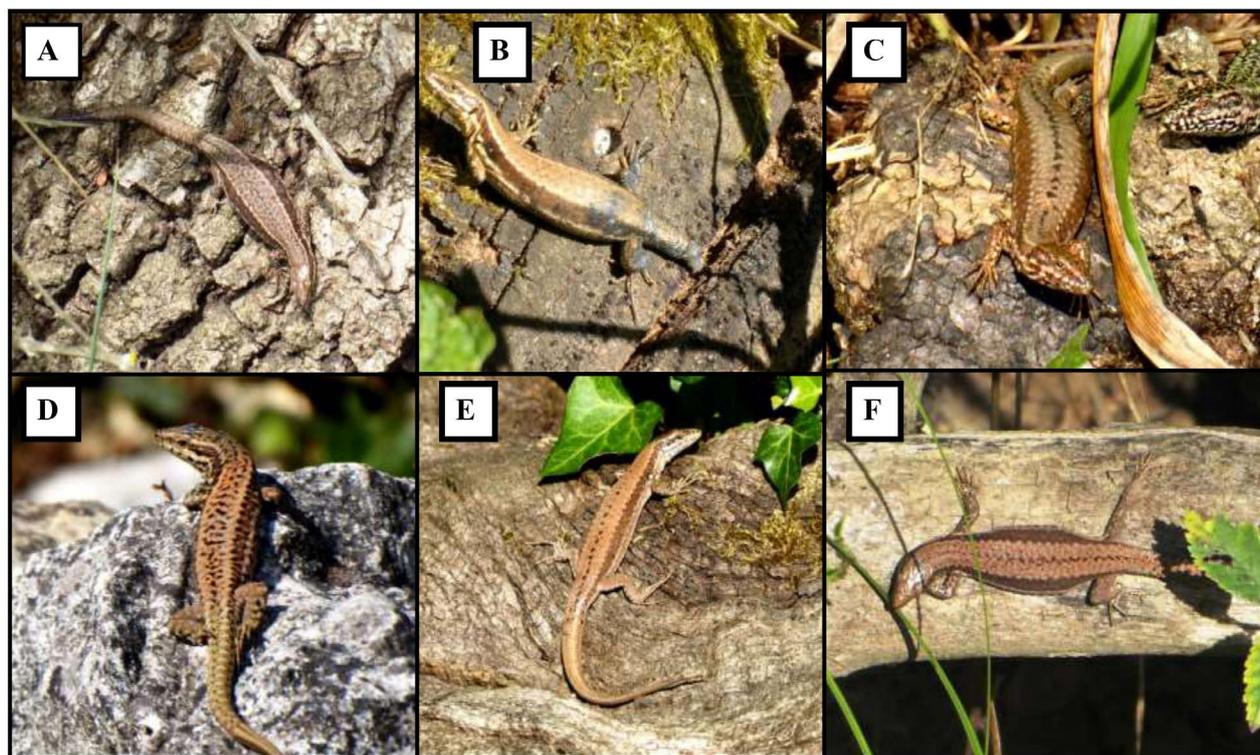


Figure 1. Examples of patterns and colours of females from the two populations. Lizards **A, B, C** and **F** recorded in the hedgerow, **D** and **E** in the garden. Lizards A-E have all experienced autotomy with B also experienced some injury.

for example floral composition and different thermal regimes (e.g. Battles & Kolbe, 2019; Campbell-Staton et al., 2020). Most demographic studies rely on the capture-mark-release-recapture (CMRR) method that provides robust information, for example capture enables direct measurement on growth rates and age structure. However, it is also time-consuming and invasive necessitating disturbance to the subject animals, which potentially risks dispersal and distortion of population characteristics including behaviour and survival rates of individuals (Wilson & McMahon, 2006). So, when possible, it would be useful and important to employ alternative methods than CMRR, which are those that do not require the capture and handling of individuals of the target species. The densities and unique individual dorsal pattern markings of *P. muralis* enabled the tracking of individuals over time (Figs. 1 & 2). Thus, we employed for data collection a photographic-mark-recapture method that minimises disturbance to the lizards and once they become adapted to the researchers presence (Dustin et al., 2020) facilitates data collection. Although errors in identification have occurred using photographic identification they have usually concerned animals with poorly defined markings (e.g. Choo et al., 2020). However, individual *P. muralis* often vary greatly (Figs. 1 & 2) and when numbers are relatively low identification errors are minimised. Non-invasive methods, including photographic-mark-recapture, have in recent years gained importance as a research tool to minimise these effects (Choo et al., 2020). Here we employ the method to ask the following questions:-

1. When collecting data on the duration of presence of individuals in the two populations, we noticed that some individuals remained within the population over

the entire three-year study period but that others did not. We also noticed that there was a correlation between the number of times that an alpha male was sighted and the likelihood that it would be seen basking in the presence of females. These two aspects of the demography of the two populations are analysed further here. Is high male presence (= high sighting frequencies) associated with male-female presence? We answer this question by comparing counts of individual males and their corresponding frequencies in the company of females.

2. In a previous study, Meek & Luiselli (2022a) showed that *P. muralis* were generally social lizards with high frequencies of communal basking. This might suggest that tail breaks and their frequencies are due to predation pressure and not primarily a result of intra-specific conflicts. We then asked the question, what are the tail breakage levels and are there differences between populations and between males and females?
3. What was the long-term presence of individual lizards in the study areas?

MATERIALS & METHODS

Study areas

The study was carried out during 2020, 2021 and 2022 on two populations of *P. muralis* in a hedgerow (PH) and urban garden (PG). The study area lies on the edge of the village of Chasnaix (46° 27' N, 1° 53' E), western France and was selected because of the numbers of lizards present that also quickly habituated to observer presence minimising observer effect (e.g. Diego-Rasilla, 2003b). The garden area was rectangular shaped with an area of 1197 m² and

hedgerow 190 m in length (Meek & Luiselli, 2022a). Both habitats were structurally relatively simple. The hedgerow consisted of mostly low growing bush *Rubus fruticosus* and *Hedera helix*, ash tree *Fraxinus excelsior* and oak *Quercus robur*, with open sunlit patches and shaded areas that facilitated thermoregulatory opportunities (Meek & Luiselli, 2022b) and detection. The urban garden had more open areas with approximate 40% cover compared to around 90% cover in the hedgerow but many plant species were non-natural. Both areas had water present, a drainage ditch running parallel to the hedge and several small man-made ponds in the garden. By June the drainage ditch alongside the hedgerow was usually devoid of water but was present in the garden ponds all year. Both study areas are open systems with no barriers preventing lizards from entering or moving outside the study areas.

Lizard sampling

Allowing for inclement weather, sampling was approximately even across seasons and carried out 5–6 days each week for around 45–60 minutes daily, usually from around 08:30 h but up to around 13:00 h. In the hedgerow habitat, sampling was mostly confined to the morning (first lizards seen around 09:00 h) until midday

due to the habitat being in sun most of the day. Sampling was between February to December in the garden and February to October in the hedgerow. Data were collected by a single observer walking along the hedgerow covering 1140 m (= 6 x 190 m) and around six times around the garden area and photographing any lizards detected. All sighted lizards were photographed using a Lumix DMC-TZ70 camera set on Intelligent-Auto for rapid use. However, a number were discarded due to low quality identification (e.g. out of focus), which was expected using this setting. Identification was by colour, markings, tail loss and the position of loss, and abnormalities of re-grown tails if present (See examples in Figs. 1 & 2). When possible several photographs of each lizard were taken, but only the best quality used for each daily sighting. Using one photograph per lizard per daily sampling session was adequate to register that the lizard was present on that day (Welbourne et al., 2020).

Statistical analysis

The Shannon-Weiner index (Spellerberg & Fedor, 2003) was repurposed to calculate lizard diversity based on individual presence. The method is normally used to quantify diversity in species assemblages and is based



Figure 2. Examples of male lizards. Lizard **A** was a male recorded in high frequencies in the hedgerow during the three-year study period. Lizard **B** a male recorded in high frequency in the garden from 2020 into early 2021 and known from 2018 indicating a minimum five years in age. Lizard **C** is an example of a male from the garden population with a likely viral papilloma on the flank (Baxter & Meek, 1988). Lizards in **D** were two of the four males that entered the garden after the disappearance of lizard B, photographed here in a territory dispute.

on the probability of sighting a single lizard two or more times in succession if the lizards in the population were encountered at random. It evaluates the numbers of individual lizards that were present in each study area and their sighting frequencies. In theory the method has no limit with high scores indicating high diversity (many lizards and high frequency of presence) and a zero score when only a single lizard is present. The index is calculated from

$$H = -\sum[(p_i) \times \log_e(p_i)]$$

where the Shannon-Weiner index score H is derived from p_i the numbers of individual lizards and their sighting frequencies. The H -values were then employed to calculate the degree of equability E of individual presence derived from

$$E = H / \log_e(K)$$

where H are the Shannon index values and K the number of individuals in the sample. Equability values range from 0 to 1, where a theoretical value of 1 indicates all individuals were sighted an equal number of times. Low E -values indicate individual lizard presence was unequal. Values of H and E were found for males and females separately and for pooled samples of males, females and juveniles.

We then compared the distributions of female sighting frequencies between years for both populations using a Kruskal-Wallis non-parametric test. This pools and ranks the number of lizards and sighting frequencies in each population and then returns the ranked data to their original columns and compares the rankings using a χ^2 test. The null hypothesis is that female numbers and individual frequency of presence is the same for each year. Post hoc, when appropriate, is by Dunn's test.

Regression analysis was used to compare count frequencies of solitary males with numbers of males in association with females. To improve the fit, males in association with females were treated as the dependent variable y after transformation to logarithms (\log_e) and male counts as the independent variable x . If a zero count was present in the y -array, $\log_e y(+1)$ was applied. This gives an equation of the form

$$\log_e y = m \pm \epsilon x + b$$

where $\log_e y$ (or $\log_e y(+1)$) is the number of males with females and x the number of corresponding solitary male counts in linear form with ϵ white noise error (Gotelli & Ellison, 2004). The null hypothesis is $m = 0$, which would indicate no relationship between solitary male numbers and males with females; significant positive departures from m indicative of males with high presence counts are more likely to be seen with females. Departures from $m = 0$ were evaluated using a t -test at $n-2$ degrees of freedom (Bailey, 1995).

If it is assumed that males have a greater chance of having access to females they should be present over most of the active time period. If so, are all lizard sighting frequencies a measure of the length of time they were present in the study area? This notion was tested by

Table 1. Summary statistics for two *P. muralis* populations during the three-year study period based on identified lizards. For juveniles only counts of sighting are given due to difficulties of individual identification

	# of lizards	# of sightings (photo-graphs)	Ratio of individual females to males	Ratio of female to male sighting frequency counts	Ratio of adult to juveniles sightings (m+f)/j
Garden					
2020 Males	2	83			
2020 Females	15	122	7.5	1.46	7.32
2020 Juveniles	-	28			
2021 Males	5	62			
2021 Females	13	95	2.6	1.37	11.21
2021 Juveniles	-	14			
2022 Males	3	59			
2022 Females	13	88	4.33	1.49	14.7
2022 Juveniles	-	10			
Hedgerow					
2020 Males	4	37			
2020 Females	12	66	3.0	1.78	12.87
2020 Juveniles	-	8			
2021 Males	5	84			
2021 Females	13	113	2.6	1.34	49.25
2021 Juveniles	-	4			
2022 Males	4	92			
2022 Females	17	135	4.25	1.46	28.37
2022 Juveniles	-	8			

regressing the number of days (N_{days}) each lizard was observed between first and last annual sightings against the numbers of times they were counted (N_{mc}). In the regression, days between first and last sighting were arbitrarily treated as the independent variable x (N_{days}) and sighting frequencies as the dependent variable y (N_{mc}). No relationship between the two would be indicated if the regression coefficient did not differ significantly from 0. In all tests alpha was set at 5%, with Minitab V17, and various internet statistical sites used for data analysis (e.g. Rain, 2023).

RESULTS

General overview

Number of identified lizards and their sighting frequencies for both populations are shown in Table 1 and graphically in Figures 3A and 3B. During the three-year period a total of 54 adults were identified in the hedgerow, which were sighted 541 times, with 51 adults sighted 577 times in the garden. Most sightings were from late February to March, with usually the alpha male appearing first (see below), but sightings declined from June to August then increased during September. Alpha male sightings (black cells in Figures 3A and 3B) were greater than other males (cross hatched cells) but were fewer late in the year, especially compared to females.

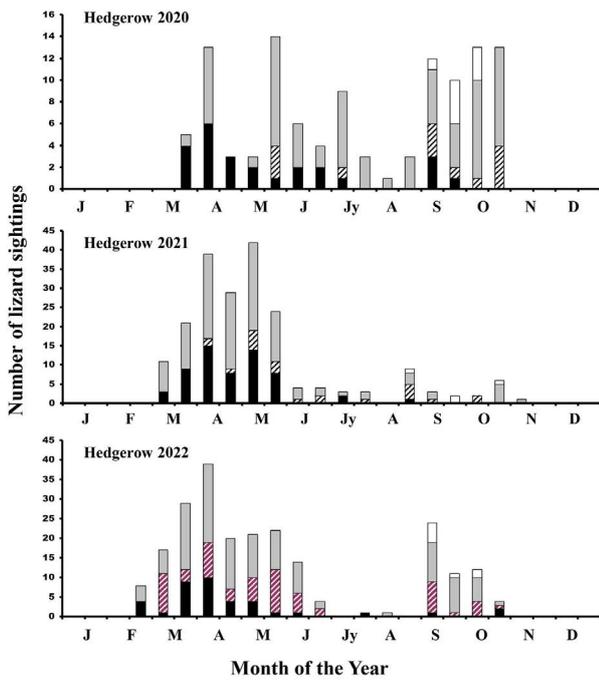


Figure 3A. Annual sightings (15-day intervals) in the hedgerow. Black cells represent male lizards with high sightings, crosshatched other males, females grey cells and open cells hatchling/juveniles. See text for further details

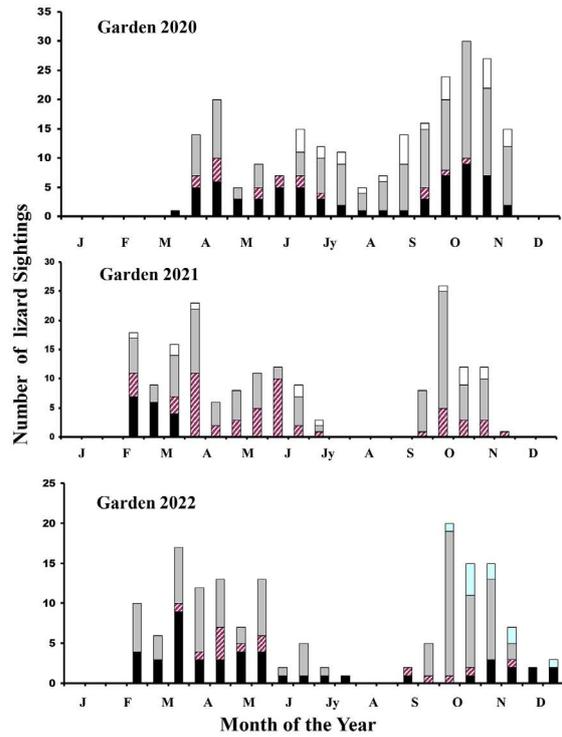


Figure 3B. Annual sightings (15-day intervals) in the garden. Cell differentiation is given in Fig. 3A. See text for further details

Table 2. Results from the Shannon-Weiner analysis (H) of numbers of individuals and their relative abundance derived from sighting frequencies (Σn). E values indicate equality of presence is in part calculated from the Shannon-Weiner results (see text). The evenness score ranges from 0 to 1 with 1 indicating equal individual presence. Pooled results indicates males, females and juveniles. The low E values for males reflect alpha male presence. See text for further details.

	Males	Σn	Females	Σn	Juveniles	E (pooled)	H (pooled)	E (males)	H (males)	E (females)	H (females)
Hedge											
2020	4	37	12	66	8	0.92	2.62	0.69	0.96	0.97	2.41
2021	5	84	13	113	4	0.85	2.46	0.59	0.82	0.93	2.38
2022	4	92	17	135	8	0.90	2.77	0.91	1.27	0.91	2.57
Garden											
2020	2	83	15	122	28	0.86	2.49	0.73	0.51	0.95	2.57
2021	5	62	13	95	14	0.92	2.65	0.99	1.59	0.86	2.15
2022	3	59	13	88	10	0.85	2.40	0.65	0.71	0.88	2.27

Females (grey cells in Figs. 3A and 3B) were present in greater numbers than males with female/male ratios (in terms of individuals) in the hedge from 2.6 to 4.25/1 and in the garden from 2.6 to 7.5/1. These ratios changed when adjusted for female/male sighting frequencies with the hedgerow population female/male ratios from 1.34 to 1.78/1 and the garden 1.37 to 1.49/1. The full results are shown in Table 1.

Sightings of hatchlings/juveniles - the latter are defined as offspring born late the previous year, were greater in the garden area (52 versus 20), possibly due to ease of detection. First sightings were usually from June in the garden although most were detected during September/

October with September the main month of sightings in the hedgerow.

Diversity of individual presence

Results from the Shannon-Weiner analysis (H) of males, females and the pooled sample are shown in Table 2 along with the E values indicative of population equality. The lower E and H -values for males reflect fewer male numbers and their skewed presence but females showed high scores in both indexes and thus higher equality of presence compared to males (Fig. 4). The χ^2 Goodness of Fit tests comparing the rankings of individual lizard sightings indicated the annual counts of females and their individual

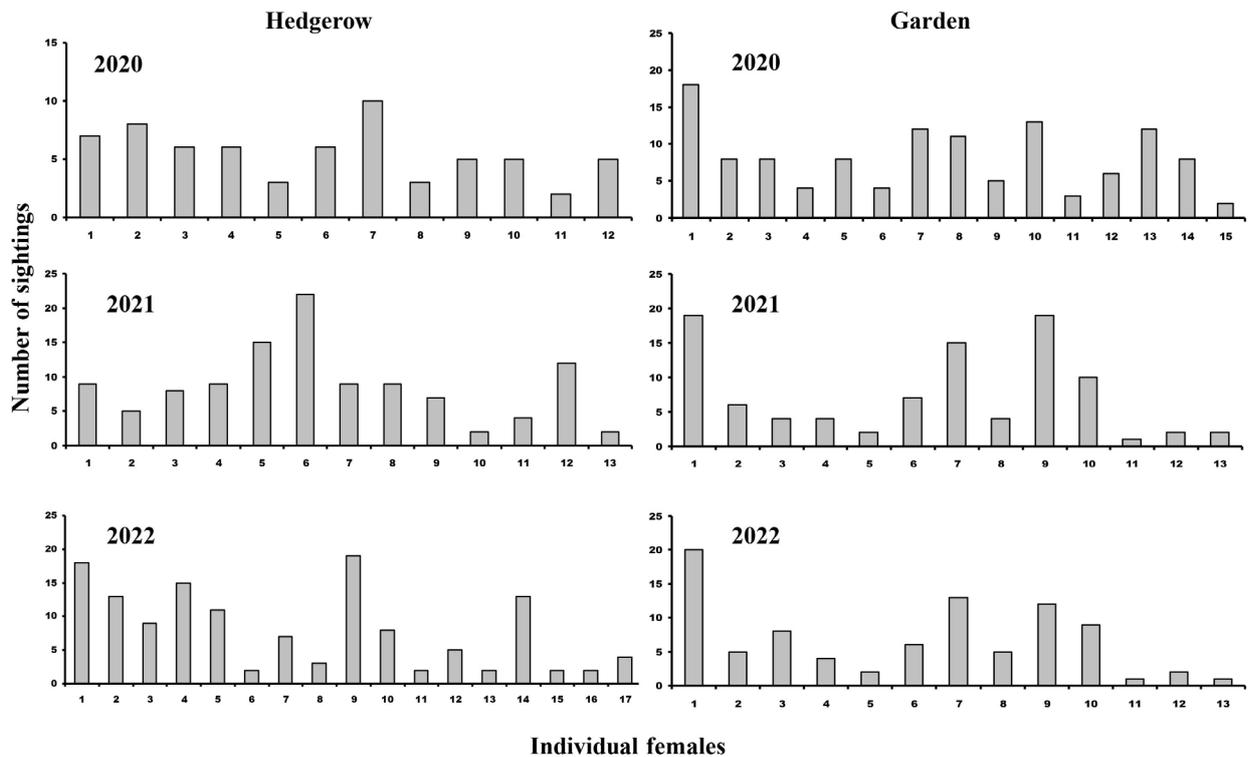


Figure 4. Number of individual females and their frequencies. Details are given in Tables 1 & 2.

frequencies were in good agreement; Garden $\chi^2 = 1.3$, $P = 0.52$, Hedgerow $\chi^2 = 1.93$, $P = 0.38$. When year counts for individual females in each study locality were pooled and compared, sighting frequencies between populations were consistent; $\chi^2 = 3.41$, $P = 0.64$, d.f. = 5 supporting the *E*-score results. This suggests healthy populations in both study populations' in all years.

The Kruskal Wallis χ^2 Goodness of Fit tests indicated that differences in annual male counts were significant; Garden (2020) $\chi^2 = 27.7$, (2022) $\chi^2 = 49.2$ both $P < 0.0001$;

Hedge (2020) $\chi^2 = 36.6$, (2021) $\chi^2 = 106.1$, 2022, $\chi^2 = 21.6$ all $P < 0.0001$. The exception was during 2021 in the garden population when each male was sighted in approximately similar frequencies that ranged from 13–21 times ($\chi^2 = 2.77$, $P = 0.6$, 4 d.f.). This latter result was likely due to the early disappearance in 2021 of the 2020 alpha male, which was not seen after 28 March (Fig. 2B). Four males subsequently appeared in the study area and although sighted in approximate equal frequency this was generally during different time periods (see Fig. 2D).

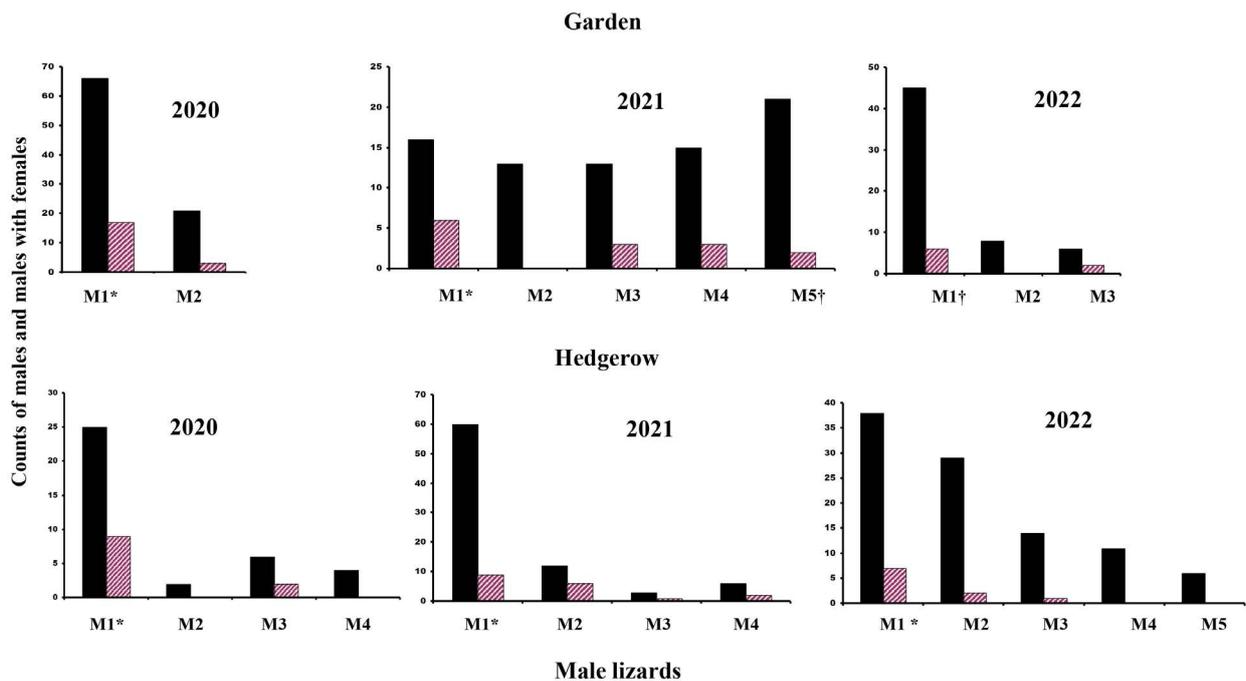


Figure 5. Male sightings (black cells) and their frequencies with females (cross hatched). Asterisk indicates same individual males in each population, with crosses a male that entered the garden in 2021 and was present in 2022.

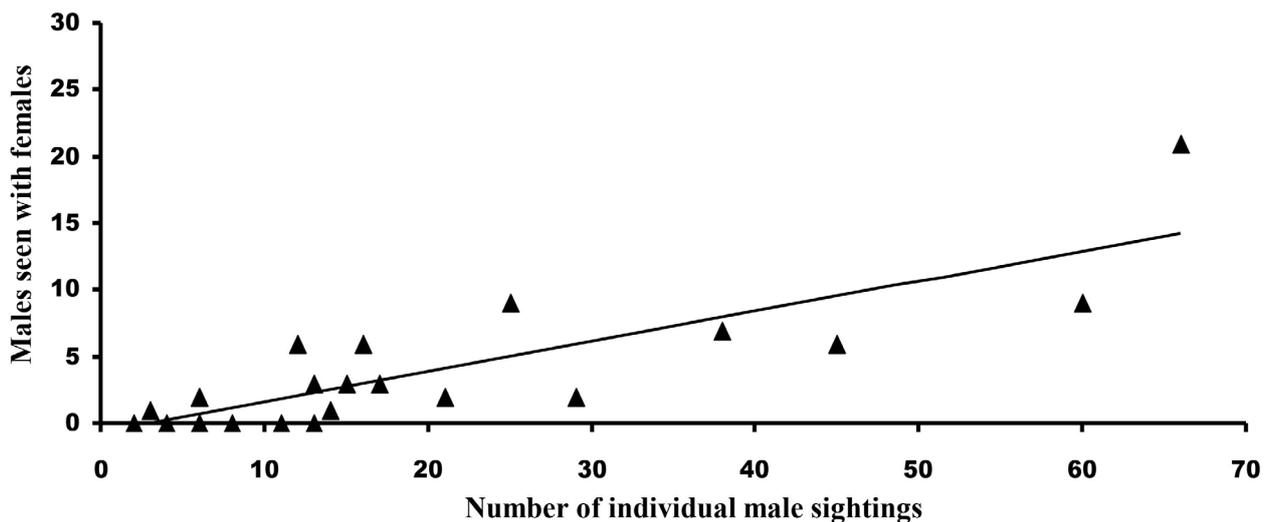


Figure 6. Graph of the general relationship (data from years and study sites data pooled) of male count frequencies and their presence with females. The line running through the data represents the regression equation given in the text. Data points situated on the x-axis indicate individuals not seen in female presence.

Male occurrence with females

Frequency counts of each male and the number of times they were present with females (N_{mf}) as the dependent variable was strongly associated with male frequency counts (N_{mc}). The regression equation was

$$N_{mf} = 0.04 \pm 0.007N_{mc} + 0.4$$

with 0.007 the white noise error ϵ . The regression coefficient of 0.04 was significantly different from a theoretical 0 (no-effect) coefficient ($t = 5.73$, $P < 0.001$). This suggests that males with high frequency counts were more likely to be alpha males with greater access to females (question 1). This indirectly supports the findings of Edsman (1990) that females mate mainly with male territory holders. Figure 5 shows histograms of individual males and their frequencies of associations with females. Figure 6 shows the general trends derived from the regression analysis with the line drawn through the data points calculated from the equation.

Sighting frequencies and time intervals

Regression of the number of male lizard sightings (N_{mc}) against time intervals (in days (N_{days})) between first and final sighting produced a positive regression coefficient

$$N_{mc} = 0.096 \pm 0.04\text{time} (N_{days}) + 3.73$$

with the coefficient significantly different from a no-effect ($m = 0$) of N_{days} on N_{mc} ($t = 2.44$, $P = 0.02$). The data for females gave similar positive results with the regression coefficients significantly different from 0: Garden $m = 0.025 \pm 0.01$, $t = 2.53$, $P = 0.02$; Hedgerow $m = 0.33 \pm 0.01$, $t = 3.36$, $P = 0.002$. This result indicates that frequencies of lizard sightings and length of time between sightings are strongly linked. The data are shown in Figure 7 with regression lines calculated from the equations.

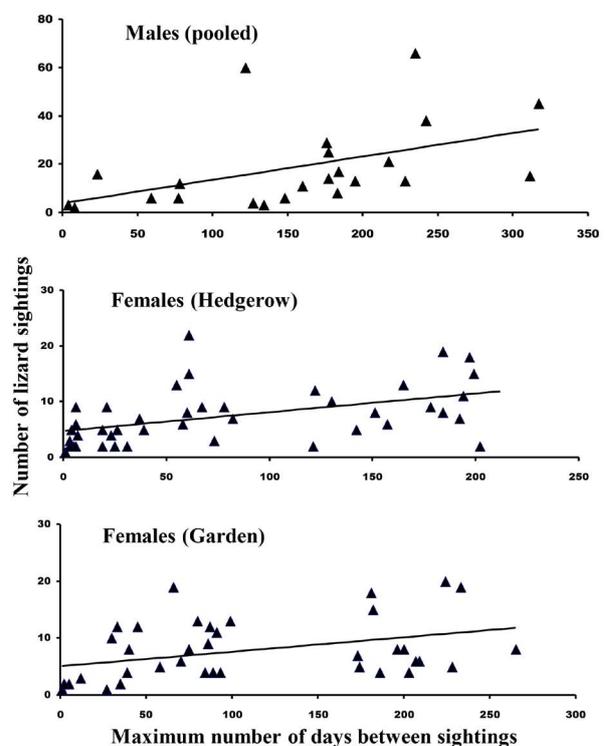


Figure 7. Graphs showing the relationship between lizard sightings frequencies and number of days between first and last sightings

Tail loss

Pooling the year data for male tail loss in both populations gave male tail loss at 66.7% in the hedgerow (12 of 18 males) and 55.5% (5 of 9 of males) in the garden population. These figures are corrected for lizards that were present for 2 or more years with assumed no further instance of autotomy and hence they were only counted as tail loss once. Female tail loss was in good agreement in both populations with 47.7% (21 of 44) in the hedge and 48.6% (18 of 37) in the garden population. However

tail loss varied within years. For example during 2021 all 5 males in the hedgerow had experienced tail loss at some time with 76% (13 of 17) of females showing high numbers in the garden during 2020 (question 2).

Temporal presence

Year to year presence (question 3) indicated that only two males (Fig. 2) in the hedgerow population were present for the three-year study period. Five individuals (2 in the hedgerow and 3 in the garden) were present for two years with four (2 in each study area) detected for just one year. This gives, for both areas 18.2% of males present for the three-year period and 45.5% for two-years. Females were present in greater number than males but in the garden population only three of 15 (20%) of 2020 females were seen continuously for the three-year study period. In the hedgerow four of the 2020 females were present in 2021. It should be noted however that absence of sightings does not necessarily indicate mortalities since both study areas were open habitats with no physical barriers to prevent the lizards going in or out of the study areas.

DISCUSSION

The diversity and equality results showed strong similarities in the numbers of individual lizards and their frequencies, either when comparing habitats or years. This dynamic is likely a key factor in enabling populations to remain stable over time despite general fluctuations in numbers over the wider area (Meek, 2020) and low year-on-year presence. A general trend in both populations was high spring activity followed by declines from around June in both populations (Table 2) with increased sightings from September through to October or December. This is indicative of a bimodal activity pattern due to a midsummer gap in activity as found in the sympatric green lizard *Lacerta bilineata* and other Mediterranean lizards (Luiselli et al., 2022; Meek & Luiselli, 2024) with the hotter dryer midsummer period likely driving the decline in sightings. These observations are similar to those observed in previous studies, including areas where they are non-natural (e.g. Allan et al., 2011; Rugiero et al., 2021; Luiselli et al., 2022). Water availability has been cited as a factor constraining activity during hot and dry periods (e.g. Carneiro et al., 2017; Kearney et al., 2018), with mass-related differences in metabolic rate and fasting endurance contributing to explaining the patterns (Luiselli et al., 2022).

One notable difference between the two populations was times of winter den entrance. This occurred during October in the hedgerow but November and occasionally December (2022) in the garden population and may be examples of climatic and habitat structure influencing activity levels. Measurements of temperatures during spring and autumn showed an approximate 2 °C mean higher ambient air temperatures in the garden, which has a more closed aspect due to a surrounding fence/hedgerow. This supports the urban heat island effect (Alberti, 2015; Campbell-Staton et al., 2020).

Individual female lizards were sighted at wide frequencies from 1 to 20 in the garden and 2 to 22 in the

hedgerow (Fig. 4). However, some lizards that were sighted only a few times also had long intervals between sightings suggesting these were possibly transients moving through the study areas (Fig. 7). Therefore in these lizards, although not present for a second year or third year, such low or absence of counts does not necessarily imply mortality. Recent data on sympatric *L. bilineata* in the hedgerow found low frequency of presence of individual lizards with new individuals appearing after the midsummer gap and an absence of those present earlier in the year. This suggests extensive movement across the hedgerow system (Meek & Luiselli, 2024).

The higher frequencies of females in the company of high prominence males (question 2; Fig. 3) agrees well with Edsman's (1990) study where males held territories and females moved along a wall through these territories resulting in males with larger territories having greater access to females. However Edsman also found that males with smaller territories also had access to females. This is supported here; males with lower annual sighting counts were also observed with females, albeit in lower frequencies (Fig. 3). Edsman (1990) indicated that females only copulated with territorial males and also remained in a male's territory because it offered access to optimal basking sites, important for female reproduction. *Podarcis muralis* is a communal basker with females regularly sharing optimum basking sites with males, other females and occasionally subadults (Meek & Luiselli, 2022a). In the present study, male conflicts were observed only in the garden during 2021, when the resident alpha male that had been present outside the study period since at least 2018 disappeared during late March. Four new males entered the territory and a series of male-to-male conflicts were seen (example in Fig. 2C). Serious conflicts between females were not seen. However it is likely that conflicts, especially between males, were more frequent than observed.

The frequencies of autotomy, defined here as lizards with absent, shortened or regrown tails (examples in Fig. 1), were relatively high in both populations. However given the extent of communal basking (Meek & Luiselli, 2022a) and observed limited incidences of intra-specific aggression, suggests that autotomy is primarily due to predation attempts since there is little evidence that *P. muralis* suffers tail loss during intra-specific conflict (Brown et al., 1995). Males, both in the hedgerow and garden were seen more frequently active and seen to travel over more extensive distances, up to 30–40 m in single bouts of activity. This may partly explain tail loss differences since movement is known to increase predation risk in lizards (Cooper, 2003). Potential predators regularly seen in both study areas were adults and juveniles of the saurophagous snake *Heirophis viridiflavus*, aspic vipers *Vipera aspic* (e.g. Meek, 2014a; Rugiero et al., 2021) and green lizards *Lacerta bilineata*, (Meek & Luiselli, 2022a; 2022b; 2024). Birds and mammals, including mustelids and domestic cats, were occasional sightings. Other studies have shown differences in frequencies of autotomy between lizard populations, for example, between *P. muralis* living in high and low predation sites (Diego-Rasilla, 2003a). Mortalities

from disease are also known in lacertid lizards and several were seen in the garden population with skin disorders (examples in Fig. 1B and Fig. 2C). The latter resembled the papillomas of the skin often observed in lacertid lizards, that are often fatal (e.g. Lopez & Bons, 1981; Baxter & Meek, 1988).

Previous studies of wall lizard populations indicate differences in demography including mortalities and age structures. For example, mortality rates in a Slovenian population were 17% but male-female sex ratio was 1:1 (Vogrin, 1998), this differs from the higher female numbers in this study. Longevity also differs. Two populations in Turkey were reported with life spans from 14–16 years (Eroglu et al., 2018) considerably longer than the estimated age of the two alpha males in Figure 2, which allowing for three years to reach full size was estimated at six or seven years.

Relatively low year-to-year lizard permanence of around 18–20% might suggest high mortality levels or lizards moving out of the study areas to other areas. If this is due to mortalities, long term population stability (Meek, 2020) would be maintained by the capacity of *P. muralis* to recover from very low numbers due to fast generation times (Barbault & Mou, 1988; Bauwens & Díaz-Uriarte, 1997) including involving a dynamic of increased juvenile survivorship that is proportional to declines in adult numbers (e.g. Žagar & Carretero, 2012; Ineich et al., 2022). Moreover, the twice-per-year reproductive effort found here and in other French populations (Barbault & Mou, 1988) increases the capacity of *P. muralis* for population recovery. Unfortunately, hatchlings and juveniles were more difficult to detect and identify, especially in the hedgerow, which presented greater plant cover and hence limited accurate measurements of numbers present. The general trends indicated most hatchling/juvenile sightings occurred during the latter part of the year, which suggests the hatchlings sighted at this time were from the second clutch and slightly larger individuals were from the first clutches from spring matings. Mortality is likely high in these smaller classes not only from predators that include the sympatric *L. bilineata* but also adult wall lizards (Simović & Markov, 2013; Žagar & Carretero 2012; Ineich et al., 2022).

One of the key findings of our study is the importance of urban gardens and hedgerow systems for lizards, especially *P. muralis*, in anthropogenic modified environments. However, expansion of agriculture and urban areas are now a feature of large areas of Europe, and can potentially negatively impact on reptile population persistence. Hedgerows, for example, are not just corridors for many species to access prime habitat, they represent year-round habitat for many species that include *P. muralis*. In addition, snakes *Hierophis viridiflavus*, *Natrix helvetica* and *Vipera aspis* are frequent visitors along with various mammals and bird species. Hedgerows therefore play a crucial part in population persistence, whether to serve as permanent habitat or pathways between prime habitat. However, hedgerows have experienced declines during the last 100 years due to changes to intensive crop farming (Robinson & Sutherland, 2002; Guiller et al.,

2022) and are disappearing rapidly (Guiller et al., 2022). Their loss could impact on metapopulation persistence not just for reptile populations but other animal species, emphasising that legislation and conservation measures are needed to conserve these systems (e.g. Simberloff & Cox, 1987). Habitat protection is difficult to achieve, but along with raising the awareness of local authorities and public awareness of their importance, other possible avenues are possible. For example herpetological or other environmental organisations should be encouraged to purchase natural areas not just pristine habitats but also hedgerow systems, which if securely preserved maintain a future for habitat connectivity. An example of land purchase policy is that operated by the British Herpetological Society in the UK who in partnership with other organisations, for example the Royal Society for the Protection of Birds (RSPB), regularly purchase prime habitat. This ensures habitat continuity and thus increases the community of conservationists and ecologists stake in the future of habitat for reptiles and other life forms.

In summary, our study showed that both populations were active from February–March until October–December. We observed a mid-summer gap of very low or zero numbers during approximately from June to September including in the garden population despite the presence of ponds as a water source. Two batches of hatchling lizards were seen, the first around June and a further batch during autumn indicating females deposit two clutches annually. Regression analysis indicated male lizards with high presence were more likely to be seen with females than males that were seen less frequently. Diversity and equality analysis indicated stable populations in both study localities with a wide range of individuals and their frequency of presence.

Author Contributions

Conceptualisation: R.M. and L.L.; methodology, R.M. and L.L.; formal analysis, R.M.; field work/data collection, R.M.; writing original draft preparation, R.M., L.L. and RAA; writing, review and editing, R.M. and L.L. All authors have read and agreed to the published version of the manuscript.

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