Volume 35 (July 2025), 226–237

Herpetological Journal

FULL PAPER

https://doi.org/10.33256/35.3.226237

Published by the British Herpetological Society

Urban areas as habitats for reptiles: the relative importance of environmental variables in predicting occurrence of common wall lizards *Podarcis muralis*

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Understanding how reptiles are affected by urban environments is important in predicting their occurrence and future use of these habitats, particularly as the degree of urbanisation increases. We investigated how temperature, solar heating, habitat quality, disturbance and predation risk predicted occurrence, and any age-related differences in the common wall lizard *Podarcis muralis* in Budapest, Hungary. Eleven line transects were carried out across diverse urban habitats, over 19 days in August 2023. Transects were repeated on average 5.3 times, and the presence of lizards was recorded along with measurements of environmental and confounding variables. Because of the high detectability of wall lizards when active, we assumed that multiple visits to the same place where no lizards were ever recorded were true negatives, and collected environmental data from a random sample of these absence points. Binomial, presence/absence General Linear Models showed that surface temperature was the most important predictor of lizard presence, but optimal surface temperature was lower for full sun exposure, confirming that solar heating increases the range of surface area at which habitats can be used. Lizards were present in moderately built-up areas across a broad range of surface temperatures, but less present in built-up environments under extreme temperatures, although they could be common there within a narrow temperature range. Humans and wind reduced lizard presence. Juvenile lizards were more sensitive to the presence of dogs and cats and were less present than expected in habitats with the best thermoregulatory properties, probably because of competition with adults. The results show the importance of urban structures that promote optimum temperatures and management of temperature by the lizards, as well as allowing avoidance of disturbance, although suboptimal areas are also important for juveniles. Access to sunlight and shelter should be considered when creating habitats for lizards in urban areas.

Keywords: conservation, thermoregulation, thermal ecology, habitat characteristics, disturbance, urban ecology

INTRODUCTION

Urbanisation is one of the most widespread and transformative processes affecting ecosystems worldwide. As cities expand and human populations grow, natural habitats are increasingly modified or replaced by urban landscapes creating a complex mosaic of challenges and opportunities (Alberti, 2005). The rapid growth of urbanised areas may pose significant challenges to reptiles because of ecosystem fragmentation and habitat loss (Grant et al., 2011; Delaney et al., 2021). Urban infrastructure developments, including roads and dams, intensify environmental damages through widespread habitat loss leading to population declines (Heigl et al., 2017; Hunt et al., 2013). The combined effect of these processes can significantly impact the distribution, physiology and behaviour of reptile species both in cities and natural habitats (Pattishall & Cundall, 2009; Bury & ZajĄc, 2020; Putman & Tippie, 2020). However, urban areas are increasingly recognised as important ecosystems which can be exploited for targeted conservation efforts and to study the interactions between humans and reptiles (Woolley et al., 2019). Some reptile species can use a variety of urban habitats, including green spaces like parks and artificial structures, underscoring the importance of urban design in supporting their populations. Habitat structure and connectivity between urban green spaces may be crucial for supporting urban lizard populations, indicating the need for urban planning that incorporates the requirements of both people and animals (Ryan et al., 2014; Taylor et al., 2016).

The environmental characteristics of urban areas may, however, also provide opportunities for reptiles. Urban environments function as heat islands through increased heat emission and radiation absorption, which provides potential for more efficient thermoregulation and extended activity for reptiles accustomed to living in such environments (e.g. Roth, 2002; Amadi et al., 2020;

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Mohanty et al., 2021). Lizards may also physiologically adapt to urban environments. In warmer climates, the excessive heat in cities can cause stress and disrupt life functions, but adaptations can occur such as heat-tolerant proteins (Battles & Kolbe, 2019; Campbell-Staton et al., 2020). Lizards can also display remarkable behavioural flexibility when facing disruptions in cities such as light pollution (e.g. Baxter-Gilbert et al., 2021). However, urban environments need to provide suitable conditions for reptiles such as lizards, and environmental variables and habitat characteristics will influence reptile behaviour and distribution in urban environments (Dékány et al., 2015).

The main environmental variable affecting lizard presence will be temperature. Increasing surface temperature will positively influence the presence of lizards with thigmothermic behaviour due to passive heat gain from warm surfaces, but urban sites with extreme heat will be avoided (Belliure & Carrascal, 2002; Ackley et al., 2015). The degree of urbanisation will then be important for lizard presence because of its influence on direct solar and passive heat gain and loss. Light intensity positively influences heliothermic lizard presence due to direct heat gain from solar radiation (Avery et al., 1982), so unshaded urban areas may be more favourable to lizards. Increased wind, however, may lead to reduced presence because it affects thermoregulatory efficiency of lizards through convective cooling and reduced prey availability (Ortega et al., 2017). Moderately built-up areas, with hard surfaces like concrete structures or brick fences, offer optimal conditions for basking and thermoregulation due to efficient heat absorption and retention (de Andrade, 2020). Conversely, highly built-up environments exhibit more impervious surfaces and homogeneity, offering consistent thermoregulation at the expense of decreased refuges and prey (Battles & Kolbe, 2019).

Habitat characteristics, however, will also be important in determining the presence or absence of lizards in urban environments, modifying the effect of temperature and solar radiation. Where there are basking spots, food resources and shelter available, lizards will be likely be more present independently of thermal conditions (Domínguez-Godoy et al., 2020). For example, less built-up areas often lack hard surfaces for basking but provide more vegetation and higher habitat diversity, leading to increased food and shelter availability, which may also decrease thermoregulatory stress (Garden et al., 2007). Similarly, increased perceived predation risk in the form of disturbance from passing humans and the presence of cats or dogs should directly reduce lizard presence, but they will also indirectly reduce site quality and so presence because of a negative effect on lizard energy budgets and ability to thermoregulate via basking (Martín & López, 1999).

Adult and juvenile lizards should, however, have different responses to the environmental factors we consider above because of competition, and therefore have different thresholds determining presence at a site. While adults can optimise, juveniles may be excluded by the larger and more dominant adults and forced to use suboptimal conditions and habitats (Delaney & Warner, 2017). Juveniles may then use sites with greater degree of solar heating whereas adults can select consistently warmer sites that provide reliable passive heat gain. Additionally, adults should be more tolerant of perceived predation risk and less susceptible to fluctuations in environmental temperature through the day (Martín & López, 2003) because of their greater energy reserves resulting from higher body mass (interrupted foraging).

The common wall lizard *Podarcis muralis* is a species native to Europe, with a widespread distribution across the continent. Budapest, the capital of Hungary, is a large city with varied levels of urbanisation situated at the periphery of the native range of this lizard. Wall lizards show high abundance across some habitats of the city, making it an excellent model organism for investigating the responses of reptiles to urbanisation. We conducted extensive field observations across diverse urban habitats to determine what predicted lizard's presence or absence. Although detectability of wall lizards is high when they are active (Falaschi, 2021), we carried out a repeated transect design to deal with problems of confounding true absences with false absences that arise simply because the lizard is inactive and undetectable. We assumed that sites that were visited repeatedly (up to eight times), where we never saw a lizard, represented true absences with which to compare sites where we saw a lizard on any visit. Detectability in lizards is, however, always confounded by activity which is fundamentally dependent on time of day (House et al., 1979) and time of year (Falaschi, 2021), and some sites where lizards were not recorded on any visit, may have had lizards present. We therefore considered these confounding effects when predicting site occupancy in wall lizards. We also considered differences between adults and juveniles. Here we considered only sites where lizards were present, testing how the probability of an adult or juvenile being present depended on environmental and habitat variables. These tests were not affected by any confounding effects of detectability because whether or not the lizard recorded was an adult or juvenile is not affected by the occurrence of false absences.

Our hypotheses and predictions were based on theoretical expectations and previous research suggesting that environmental variables and habitat characteristics influence reptile distribution in urban environments (Dékány et al., 2015) as introduced above. Our study aimed to identify which of these variables were most important to predict occurrence for wall lizards in Budapest. We predicted that the major environmental determinants of lizard presence or absence would be surface temperature, shown by an optimum temperature (quadratic relationship with temperature) for maximum probability of presence at a site. However, this optimum or the degree variation in this optimum (i.e. the degree of peak in the quadratic relationship) would depend on the degree of urbanisation and light

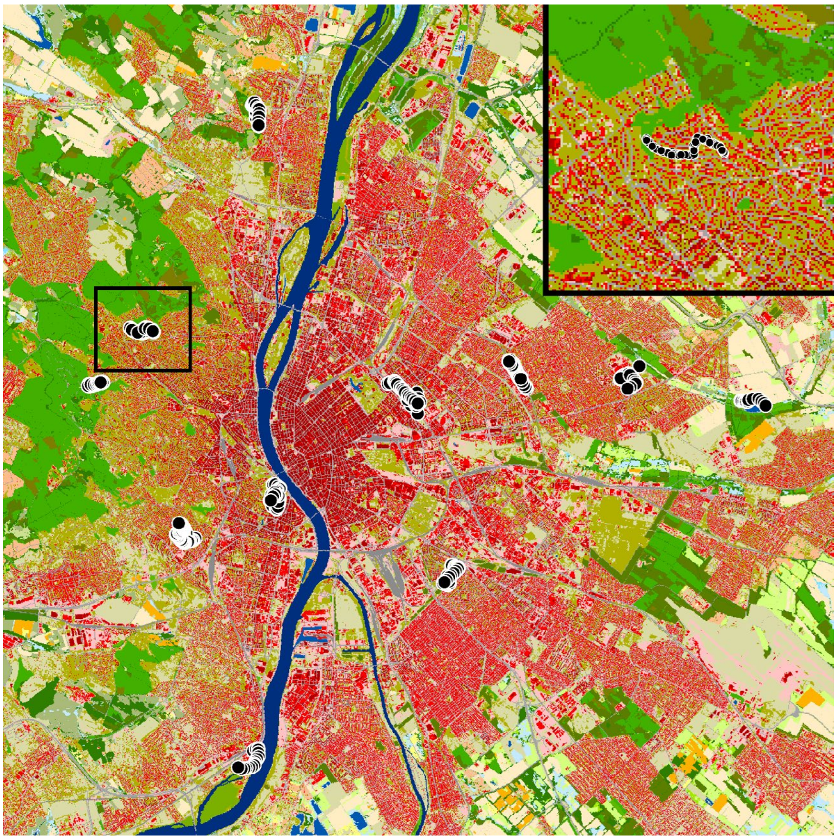

Figure 1. Map showing the data collection localities in several urban, suburban and semi-natural areas. The map is integrated from the Ecosystem Map of Hungary, with the collected data points (black circles) overlaid in QGIS (Agrárminisztérium, 2019). Red are built up areas, green are green spaces, grey are roads and rails, and blue is water. A closer view of one transect is highlighted and shown in the top right corner.

intensity (degree of solar radiation) that would modify the constraints imposed by low and high ambient temperatures at a site, controlling for the effects of time of day. We also predicted lower lizard presence in windier and more disturbed sites, particularly if sites had disturbance from both humans and cats and dogs, and higher lizard presence with better local habitat suitability in terms of foraging and shelter. Finally, we predicted that variables determining the presence of adult and juvenile lizards would be different. For sites where lizards occur, we predicted that juveniles would occur more commonly in risky sites than adults, and be recorded where they were present over a longer period of the day.

MATERIALS & METHODS

The study took place in the capital of Hungary, Budapest, a large city with varied levels of urbanisation, good accessibility and abundant reptile populations. A species-specific sighting map from the National Herpetological Mapping Program was used to gauge the initial presence and distribution of wall lizards (MME, 2024). Based on this information and prior knowledge of the ecology and behaviour of the lizards 11 x 1 km transect lines were established with the aim of covering a wide range of habitats (Fig. 1). The surveyed habitat encompassed areas adjacent to flowing and stagnant water bodies, alongside railways, on natural hillsides, within semi-natural forests, in suburban regions and in locations experiencing significant human activity. Data collection was done on 17 days between 31 July and 18 August in 2023: no surveys were done on rainy days. Line transect walks were conducted 58 times aiming for a similar number of repetitions across the 11 locations. Each day, data were collected at various parts of the day between 08:00 h and 20:00 h, grouped into 2-hour groups. This meant seven time slots in a day, although data was only collected from the 20:00 h timeslot a few times towards the beginning of the data collection period, as sunset became earlier later in the study.

Every time a lizard was seen along a transect, it was recorded along with its age (using differences in body size and morphology, with additional identifying characteristics, such as many juveniles having blue tails). Environmental variables were logged on the exact spot where the lizard was first sighted, and the other variables were recorded within a 2-metre radius of the initial detection location. We used a homemade device that was constructed by soldering sensors that measure light intensity and ambient temperature to an Arduino board and a small display; which were put in a protective enclosure box. A digital infrared thermometer (AXIOMET AX-7510) was also used to record surface temperature. The recorded hypothesis variables were surface temperature, light intensity, air temperature, the

Table 1. The effect of variables on lizard presence probability; relative importance is shown by the change in R^2 and AIC when they are removed from the model. Overall pseudo R^2 = 65%.

Variable	Estimate	SE	P value	%R^2	AIC
(Intercept)	-82.4	18.54	<0.0001		
Surface temperature	3.27	1.02	0.0014	20.1	409
Quadratic of surface temperature	-0.039	0.015	0.011	6.7	131.7
Light intensity	0.00037	0.00013	0.76	3.1	61.4
Ambient temperature	0.15	0.049	<0.0001	1	18.5
Quadratic of ambient temperature	0.013	0.09	0.88	0	-2
Degree of urbanisation 2	-9.38	5.35	0.079	3.2	56.4
Degree of urbanisation 3	-55.71	18.88	0.003		
Presence of passersby	-3.08	0.59	<0.0001	2	39.6
Number of dogs	0.072	0.13	0.57	0.2	0.2
Time of day	0.12	0.032	0.00024	2.6	44.8
Quadratic of time of day	-0.00053	0.000017	0.0023	1	17.8
Date	1.31	0.13	<0.0001	6.8	141.3
Quadratic of date	-0.064	0.0069	<0.0001	5.1	108.4
Habitat suitability 1	1.46	0.48	0.0022	3.4	66.5
Habitat suitability 2	2.53	0.46	<0.0001		
Habitat suitability 3	3.57	0.56	<0.0001		
Presence of wind	-0.95	0.3	0.0014	0.5	8.4
Number of cats	0.37	0.16	0.019	0.3	3.4
Surface temperature * light intensity	0.0000049	0.0000085	0.56	1.1	20.4
Quadratic of surface temperature * light intensity	-0.00000016	0.00000014	0.24		
Surface temperature * degree of urbanisation 2	0.65	0.35	0.066	1.1	16.1
Surface temperature * degree of urbanisation 3	3.52	1.13	0.0019		
Quadratic of surface temperature* degree of urbanisation 2	-0.0088	0.0056	0.12		
Quadratic of surface temperature* degree of urbanisation 3	-0.054	0.017	0.0014		
Surface temperature * time of day	-0.0044	0.0013	0.001	0.8	11
Surface temperature * quadratic of time of day	0.0000012	0.00000059	0.036		
Quadratic of surface temperature * time of day	0.000042	0.000015	0.0045		
Presence of passersby * number of dogs	0.6	0.34	0.079	0.1	1

presence or absence of wind, the degree of urbanisation (33% or less vegetated habitat, 33–67% and 67% or more), the presence or absence human passersby in a 20 m radius, and the number of cats and dogs in total along the transect. The recorded confounding variables were time and date. Habitat suitability was also recorded on a scale of 0–3 calculated based on how many conditions were met within two metres from the following: good basking spots (abundance of hard surfaces), food resources (any vegetation as a proxy for insect abundance (Mata et al., 2017)) and shelter availability (any structural complexity and refuge). In sections where no lizard was sighted for 25–50 metres on any transect, and therefore areas which we assume to represent true absences, random locations were selected. These locations represented absence points, and the same variables as above were recorded.

Data analysis

Analysis was carried out using R (R Core Team, 2021, version 4.1.1). Generalised Linear Models with a binomial error distribution were used to test the hypotheses. The variables were individually assessed based on biological relevance, statistical significance and contribution to model AICc and pseudo R^2 calculated from null and residual deviance. The importance of individual terms in any model were evaluated by removing the individual variable from the model and examining the subsequent change in model AIC and pseudo R^2. The best mathematical function (linear or quadratic) was selected to describe the relationship for each variable based on minimising AIC. Biologically relevant potential interactions between variables were explored to create two final global models.

A single, global multivariate GLM was constructed to test predictors of lizard presence or absence:
Presence/absence of lizards ~ the quadratic of surface temperature + light intensity + the quadratic of air temperature + air temperature + degree of urbanisation + presence/absence of humans + total transect number of cats + total transect number of dogs + the quadratic of time of day + the quadratic of date + habitat suitability + presence/absence of wind + the quadratic of surface

Table 2. The effect of variables on probability that a lizard was a juvenile; relative importance is shown by change in R^2 and AIC when they are removed from the model. Overall pseudo R^2 = 8%.

Variable	Estimate	SE	P value	%R^2	AIC
(Intercept)	27.7	25.29	0.27		
Surface temperature	-2.4	1.53	0.12	2.8	16.9
Quadratic of surface temperature	0.056	0.025	0.023	2.1	19.7
Light intensity	-0.00034	0.00017	0.052	0.6	3
Ambient temperature	-0.78	0.43	0.071	1	10.6
Quadratic of ambient temperature	0.016	0.008	0.037	0.3	2.5
Degree of urbanisation 2	-0.5	12.04	0.97	0.4	-6.8
Degree of urbanisation 3	7.79	22.03	0.72		
Presence of passersby	-1.47	0.87	0.091	0.7	5.6
Number of dogs	-0.22	0.1	0.026	0.8	7.1
Time of day	0.048	0.033	0.14	2.8	29.6
Quadratic of time of day	-0.000042	0.000018	0.025	0.5	3.2
Date	0.27	0.089	0.0027	0.8	7
Quadratic of date	-0.012	0.0046	0.007	0.5	5.5
Habitat suitability 1	-0.7	0.7	0.32	0.4	-0.1
Habitat suitability 2	-0.92	0.69	0.18		
Habitat suitability 3	-0.54	0.7	0.44		
Presence of wind	-0.23	0.2	0.25	0.1	-0.7
Number of cats	0.36	0.16	0.024	0.4	3.3
Surface temperature * light intensity	0.000022	0.000011	0.039	0.3	0.9
Quadratic of surface temperature * light intensity	-0.00000036	0.00000017	0.035		
Surface temperature * degree of urbanisation 2	0.2	0.82	0.81	0.4	-2.8
Surface temperature * degree of urbanisation 3	-0.33	1.39	0.81		
Quadratic of surface temperature* degree of urbanisation 2	-0.0059	0.014	0.67		
Quadratic of surface temperature* degree of urbanisation 3	0.0022	0.022	0.92		
Surface temperature * time of day	-0.00053	0.0014	0.7	0.6	2.8
Surface temperature * quadratic of time of day	0.0000011	0.00000059	0.051		
Quadratic of surface temperature * time of day	-0.000025	0.00002	0.2		
Presence of passersby * number of dogs	1.6	0.61	0.0091	0.5	5.2

temperature * light intensity + the quadratic of surface temperature * degree of urbanisation + the quadratic of surface temperature * time of day + presence/absence of humans * total transect dogs (see Table 1).

Repeat sampling due to multiple repeated transects was reasonably even, and varied randomly by transect. An even sampling program was intended, and variation only arose randomly from logistical difficulties unrelated to whether the survey could have been carried out on a particular day. Sampling design also precluded a sensible mixed model (to account for repeated measures) because data from absence points (random points) were collected on a single final transect, whereas presence points accumulated from multiple visits, with data being collected during the transect that the presence was recorded. Furthermore ignoring random effects led to a robust model and allowed predicted values to be calculated and plotted for illustration. In any case, when we considered transect as a random effect in a mixed model (R Libraries nlme4, and MuMIn) to attempt to fully account for any reduced independence between points within a transect and between points in different transects, rescaling light, date, temperature and time to between 0 and 1 (so that the model would converge), the random effect only accounted for 7.5% of overall variation accounted for by the model. Individual presence and absence points were therefore almost entirely independent regardless of any overall differences due to transect. Consequently, parameter estimates from a binomial model identical in structure to the model in Table 1, except with a random effect of transect and rescaled predictors (as above), were biologically more or less identical in effect to the estimates presented in Table 1, and statistical significance was very similar (Supplementary material Table S1). We therefore ignored the effects of point sampling clustered within transects in the models presented here.

The second part of the analysis focused on how the variables have a differential influence on lizard age groups, consequently, the dataset was truncated to include lizard presence data only. A second single,

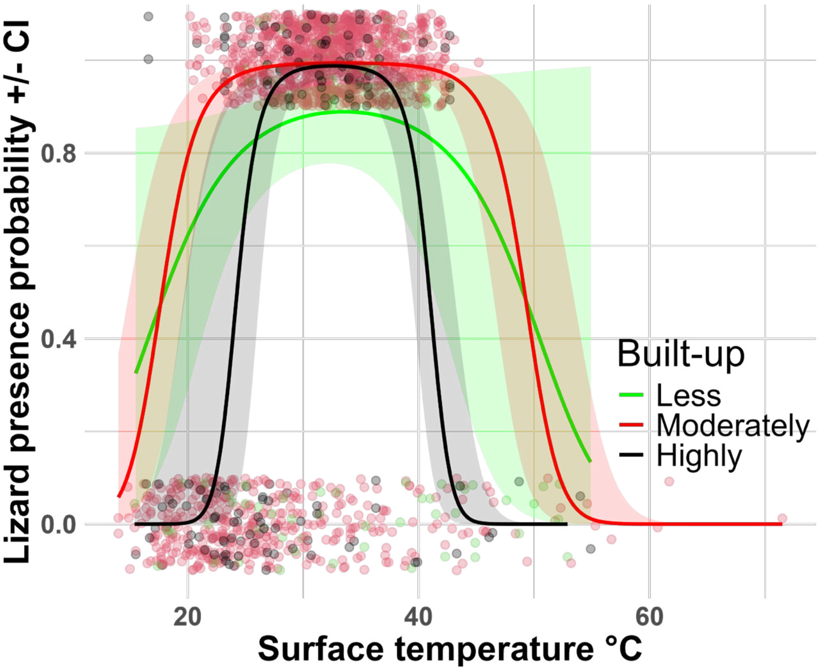

Figure 2. The effect of surface temperature (°C) on lizard presence probability (±CI) under different levels of built-up habitat. Continuous variables are set to their mean values, while 'habitat suitability' is set to 2, 'wind' is set to yes and 'passersby' is set to no.

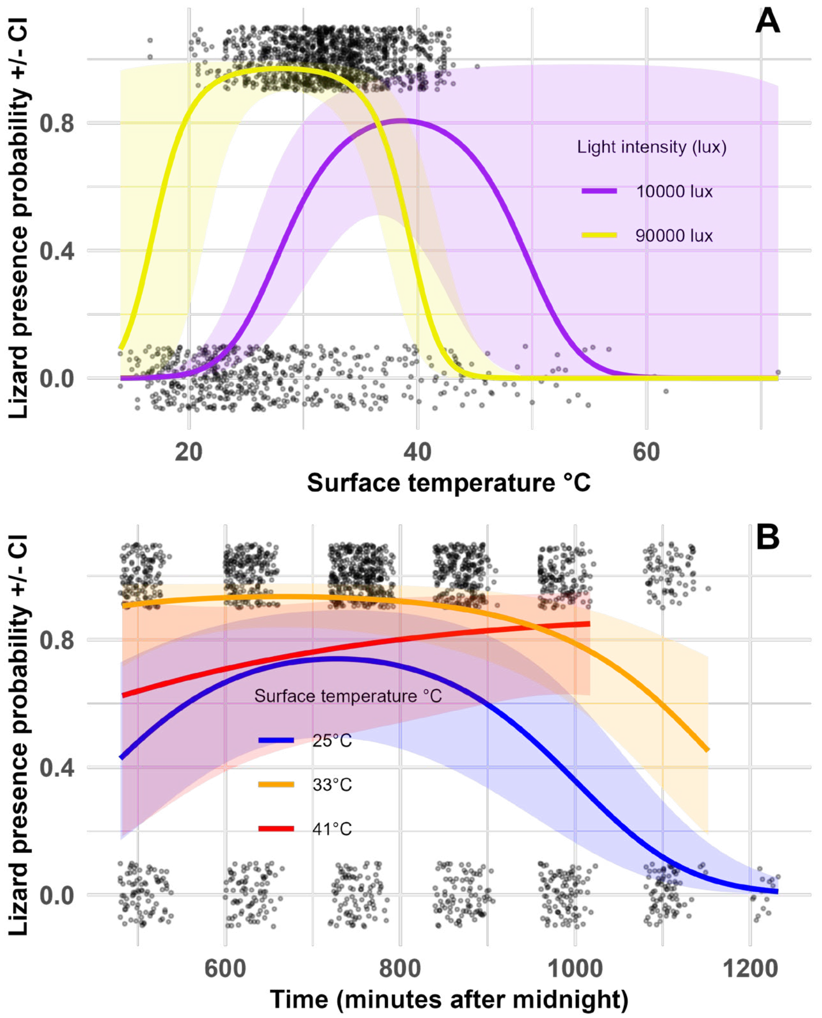

Figure 3. **A.** The effect of surface temperature (°C) on lizard presence probability (±CI) under different levels of light intensity (lux). Continuous variables are set to their mean values, while 'habitat suitability' is set to 2, 'built-up' is set to 2, 'wind' is set to yes and 'passersby' is set to yes. **B.** The effect of time of day (minutes after midnight) on lizard presence probability (±CI) under different surface temperatures (°C). Continuous variables are set to their mean values, while 'habitat suitability' is set to 1, 'built-up' is set to 2, 'wind' is set to yes and 'passerby' is set to yes.

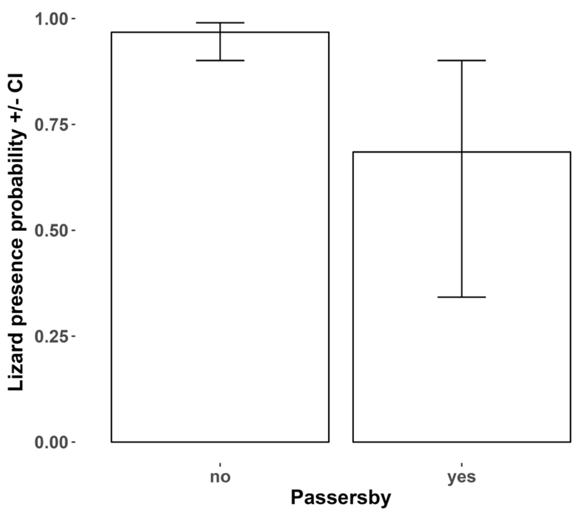

Figure 4. The effect of passersby on lizard presence probability (±CI). Continuous variables are set to their mean values, while 'habitat suitability' is set to 1, 'built-up' is set to 3, 'wind' is set to yes and 'passersby' is set to yes.

global multivariate GLM was constructed using the same principles described in the first part of the analysis but tested the predictors of whether a lizard that was present was an adult (1) or a juvenile (0). The model structure of the predictor variables was the same as detailed above. Again we ignored the repeated transects in the analysis, adopting a more robust and straightforward General Linear Model approach. When we considered transect as a random effect in a mixed model, rescaling as above so that the model would converge, the random effect accounted for only 24% of overall variation accounted for by the model. Parameter estimates from a binomial model identical in structure to the model in Table 2, except with a random effect of transect and rescaled predictors, were again biologically and statistically similar in effect to the estimates presented in Table 2 (Supplementary material Table S2).

Predicted values from models were illustrated using the R library ggplot2. For variables in the model not illustrated in the figures, continuous variables were set to their mean values, and factors were set to values which best differentiated the effects of the illustrated variables (as detailed in the Figure legends).

RESULTS

Overall, we recorded 1,213 lizard presence datapoints and 531 absence datapoints. Most variables had a statistically significant effect on lizard presence (Table 1). Surface temperature as a quadratic function accounted for most of the variation in the dataset (pseudo R^2 = 0.27) followed by date (pseudo R^2 = 0.12), with a peak presence at about 33 °C. But the relationship between presence and surface temperature was significantly dependent on both degree of built-up habitat and light intensity (Table 1). The range of peak presence depended on the degree of built-up habitat. Lizards were almost always present in moderately built-up areas over a temperature range of 20 to 42 °C, but were almost always present in highly built-up areas over a range of temperatures from 27 to about 36 °C; in less built-up areas, there were fewer lizards and presence was less dependent on surface temperature (Fig. 2). At high light intensities (direct sun exposure 90,000 lux) lizards were almost always present, and were present at lower surface temperatures, from about 20 to 34 °C, whereas at normal light intensities (10,000 lux), lizards were less present (about 80% presence) with a peak presence between 36 and 42 °C (Fig. 3A). There was a strong relationship between time of day and lizard presence that depended on surface temperature (pseudo R^2 = 0.13, Table 1). At low surface temperatures (e.g. 25 °C) there was a clear peak in presence at midday, whereas at 33 °C, lizard presence was always very high, except late in the day, and at 41 °C activity peaked later in the day (Fig. 3B).

Lizard presence significantly increased with increasing habitat suitability (Table 1), but lizard presence was significantly lower in the presence of wind, but with trivial biological effect (Table 1). Lizard presence was also significantly lower when there were humans within 20 m of the site (Fig. 4) and more cats, but there was no additional effect on presence caused by the number of dogs, or the simultaneous presence of humans and dogs (Table 1).

Whether a lizard that was present was an adult or a juvenile depended significantly on surface temperature, light intensity, date, ambient temperature, time of day and number of dogs and cats (Table 2). Similarly to Model 1, surface temperature accounted for most of the variation in the dataset (pseudo R^2 = 0.05), followed by time of day (pseudo R^2 = 0.03). Ambient temperature, date, presence of dogs and passersby and light accounted for less variation (pseudo R^2 = 0.01 for each). In normal daylight conditions (10,000 lux), juveniles tend to avoid extreme cold or hot surface temperatures, with their probability of presence peaking at about 32 °C; conversely, under direct sun exposure (90,000 lux), the ratio of juveniles to adults remained consistent across surface temperatures (Fig. 5A). The proportion of juvenile lizard presence was highest at 24 °C ambient temperature and decreased in colder and warmer conditions (Table 2). An increase in the number of dogs and cats correlated with a decrease in the probability of juvenile lizards being present at a site (Fig. 5B).

DISCUSSION

This study found that surface temperature was the primary factor affecting lizard presence, with the most optimal temperature of around 33 °C, consistent across different urbanisation levels. Moderate urbanisation was shown to be the most favourable habitat condition for lizards, but less built-up areas had higher presence of lizards than in extreme temperatures, while highly built-up areas only had a high peak lizard probability over a

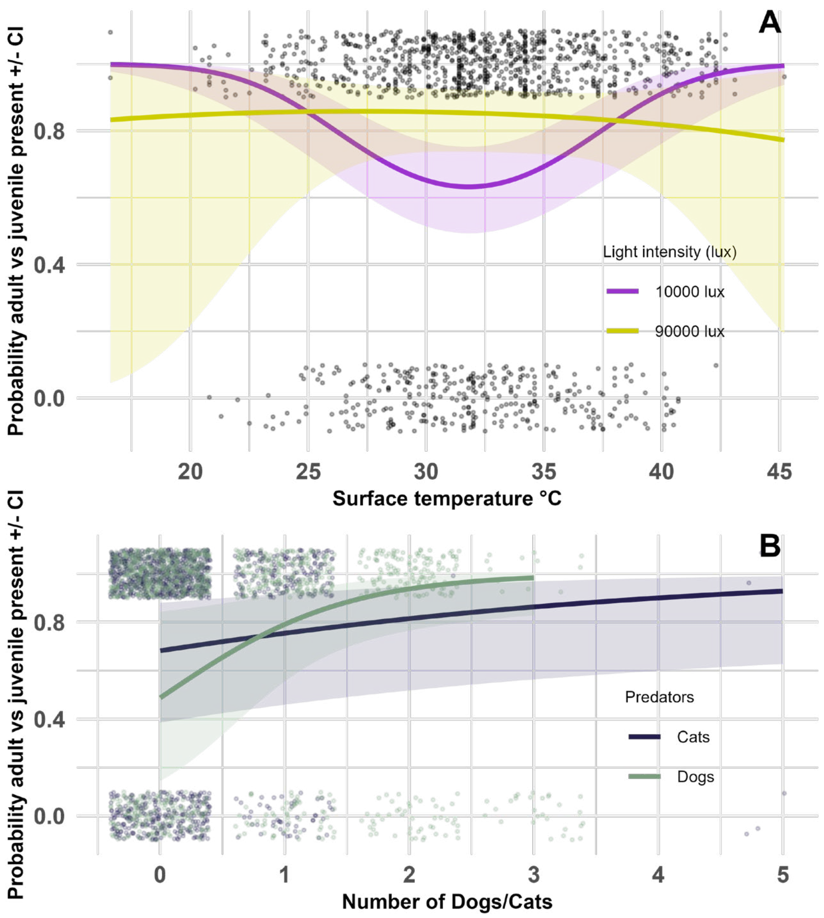

Figure 5. **A.** The effect of surface temperature (°C) on the probability of a lizard being 0 juvenile or 1 adult (±CI) under different levels of light intensity (lux). Continuous variables are set to their mean values, while 'passersby' is set to no. **B.** The effect of the number of dogs and cats on the probability of a lizard being a juvenile or an adult (±CI) given the presence of passersby. Continuous variables are set to their mean values, while 'habitat suitability' is set to 1, 'built-up' is set to 2, 'wind' is set to yes and 'passersby' is set to no.

narrow temperature range. Lizard presence probability peaked around midday and lizards were present at lower temperatures when solar heating was available through basking. Disturbance, such as the presence of passersby or predators like dogs, reduced the presence of lizards. Juvenile lizards were likely excluded from the most optimal environmental conditions through competition with adults and were likely more sensitive to predation pressure or disturbance from dogs and cats.

Lizard presence peaked in moderately built-up areas at 80%, decreased to 69% in highly built-up areas, and dropped to 31% in less urbanised settings. These findings align with a study by Germaine & Wakeling (2001) conducted in the United States on how lizard species abundance, richness and evenness change along the urban gradient. They note an initial increase in these measures with low to moderate urbanisation, followed by a significant decline at higher levels. However, their results diverge by highlighting a considerably lower lizard presence in highly urbanised areas compared to less developed ones, a potential result of different climates. A study on Peters's lava lizard *Tropidurus hispidus*, a species thriving in tropical urban settings, reported a clear preference for peri-urban and medium urbanisation levels, with significantly higher densities in highly urbanised areas than in rural settings (de Andrade, 2020). This mirrors our observations that high urbanisation, when accompanied by structural complexity and connectivity to suitable habitats, can sustain healthy reptile populations. The ideal body temperature for *P. muralis* was identified by Florentino (1991) at approximately 33.8 °C closely aligning with our findings of an optimal surface temperature around 33 °C. Furthermore, studies have shown that artificial structures in urban areas can mimic natural rocky outcrops, suggesting that the thermal qualities of these habitats are comparable (Bády & Vági, 2012; de Andrade, 2020). If artificial substrates can replicate natural thermal characteristics, they can support urban lizard populations and enhance annual survival rates (Adolph & Porter, 1993). These results suggest urbanisation's impact on lizard populations varies depending on how factors like presence of suitable surfaces and habitat complexity in urban areas allow lizards to optimise their temperature.

At full sun exposure, lizards were present at lower surface temperatures, with peak presence averaging around 28 °C. In comparison, in normal daylight conditions, the peak presence temperature rose to 39 °C, with a 16% decrease in peak lizard probability. This aligns with previous studies stating that the optimal range of body temperatures for viviparous lizard *Zootoca vivipara* is 30–36 °C, enhancing prey capture and handling efficiency (Avery et al., 1982). The thermoregulatory strategies of lizards involve a complex interplay between direct solar radiation and conductive heat transfer from the substrate, and this may be species dependent (e.g. Gontijo et al., 2018). Optimal basking sites provide both heat sources, allowing lizards to use behavioural adjustments to regulate their body temperature. The passive heat gain from hard surfaces can be especially important in environments where sunlight is variable. Solar exposure can be a crucial heat source under less favourable conditions, highlighted by a study showing *P. muralis* basking in urban settings in winter conditions, when they would usually hibernate (Sakelarieva et al., 2023). This provides evidence that urban areas could extend the yearly activity period of lizards allowing their occupation of otherwise marginally suitable habitats.

There was a unimodal pattern in lizard daily activity across a range of surface temperatures. This finding contradicts previous studies reporting a bimodal activity pattern for *P. muralis* during the summer months (Florentino, 1991). We hypothesise that daily activity patterns within the same species and season could differ based on variables like maximum daily environmental temperature. For example, warm urban surface temperatures allow the presence of lizards across a greater range of habitat quality sites because activity can occur throughout the day.

Our study showed, unsurprisingly, that habitat suitability positively correlated with lizard abundance. The three main components of habitat suitability were the presence of surfaces providing optimal thermoregulation, structural complexity for overnight refuge and presence of appropriate vegetation facilitating both predation and short-term refuge. The importance of thermoregulation to maintain optimal physiological function has been emphasised by several studies (Avery et al., 1982; Florentino, 1991). Habitat structural complexity, in the form of beneficial habitat modifications, that increase rock coverage, like brick and stone fences are also associated with higher lizard abundance (Rurik et al., 2022).

Wind reduced lizard presence probability by 17%. Wind can have a negative impact on lizard thermoregulation (e.g. Ortega et al., 2017), because ectothermic organisms rely on basking to elevate their body temperature to optimal levels to maintain physiological processes and activities such as foraging and reproduction (Ortega et al., 2017).

Disturbance or perceived predation risk in the form of close proximity to humans reduced lizard presence by around 22%. This reduction is supported by other studies showing that constant disturbance causes lizards to spend more time in refuges, reducing lizard mass and presence (Martín & López, 1999). Increased time in refuge reduces body temperature and physiological function and results in decreased foraging time. However, urban lizards can adapt to non-lethal disturbance from humans by utilising more complex environments which reduces the necessity for risk aversion behaviours (Batabyal et al., 2017). Consequently, further research should collect higher resolution data on *P. muralis* predators, including cats and dogs, and predatory birds such as most corvids (Martín & López, 1990).

Adult and juvenile lizards' spatial distribution was affected differently by the interplay between temperature, light and body size. The apparent competitive exclusion of juveniles by the larger and more dominant adults from basking spots with the best thermal properties may have forced juveniles to adapt by utilising warm surfaces under daylight conditions (e.g. Fig. 5A). Adult *P. muralis* typically weigh between 4–10 grams, suggesting that the smaller juveniles experience faster heating and cooling rates than adults (Herczeg et al., 2007). This may lead juveniles to prefer more varied microhabitats offering both shade and sunlight for quicker thermoregulation. San-Jose et al. (2016) found that higher densities of adult viviparous lizards reduce pre-hibernation survival rates of juveniles and negatively impact their growth, body size and overall performance. This inter-class competition therefore affects the development, survival and reproductive success of juvenile lizards, forcing them into locations with suboptimal thermoregulatory properties, as reflected by our results.

The effects of disturbance and predation pressure from dogs and cats on wall lizards, particularly across age groups, remain understudied. We hypothesised that adult lizards, with their larger energy reserves, might be less impacted by these pressures, enabling them to better adapt to areas with frequent human and dog activity. Our study found that an increase in either the number of dogs or cats resulted in a lower proportion of juveniles, which supports our hypothesis. Just one dog decreased juvenile presence significantly and two or three dogs almost resulted in their disappearance. In contrast, an increase in the number of cats resulted in a more gradual decrease of juveniles between one and five cats. These results show that even at low levels predation pressure and disturbance can have profound effects on juvenile lizards. However, our analysis of dog- and cat-related disturbances or predation relies on transect-level data, so conclusions are more limited. Further studies with higher resolution data that incorporate predatory birds are also necessary to uncover the differential effects of predation and disturbance on lizards across age groups.

Our study revealed a surprising significant effect of date on predicting lizard presence and age in a quadratic function (Tables 1 & 2). Furthermore, date was a major contributor to model AIC and R^2 values, indicating notable variations in lizard observations over the 19 days of data collection, with fewer lizards and a relatively higher proportion of juveniles found at the beginning and end of the study. Given the quadratic nature of the relationship identified in the models, we conclude that these results are not due to improved detection efficiency, and detection does not, in any case, confound the adult/juvenile analysis. A 19-day period during the summer, characterised by relatively stable weather conditions, seems too brief to record significant differences in seasonal behaviours, life cycle events or habitat structure changes, nevertheless this strong effect suggests that this might have been the case.

Overall, this study highlights the importance of factors such as temperature, habitat quality, solar heating, disturbance, predation and competition on the presence of wall lizards in urban environments. The most crucial finding of our study was that sites that allow appropriate thermoregulation determine *P. muralis* presence and that an increased level of urbanisation probably provides additional niches that support body temperature regulation. This aligns with the broader context of reptile urban ecology, suggesting that urban environments can support reptile populations if conditions mimic natural thermal and structural habitats while minimising stressors, like human disturbance. Cities may then provide new and enhanced habitats for reptiles, but perhaps more significantly, they have the potential to become conservation hotspots through public engagement and education, potentially resulting in a shift in how people perceive biodiversity and their connection to nature (Woolley et al., 2019). Green spaces and innovative environmental architecture, like green roofs and walls may increase habitable space for some lizard species in cities, helping to connect fragmented populations of lizards but also connecting people with wildlife. Understanding how to promote lizards occurrence in urban areas may then be both of direct conservation benefit to the species targeted but also of indirect benefit to conservation generally by changing attitudes to biodiversity among the increasing proportion of humans that live in urban areas.

ACKNOWLEDGEMENTS

We thank Dr Gergely Babocsay for his advice on *P. muralis* ecology in Budapest. Special thanks to Gábor Simon for assisting with soldering sensors and to David De Angelis for proofreading and advice.

Author contributions

The authors confirm contribution to the paper as follows: study conception and design: Á. Simon, W. Cresswell; data collection: Á. Simon; analysis and interpretation of results: Á. Simon, W. Cresswell; draft manuscript preparation: Á. Simon, W. Cresswell. All authors reviewed the results and approved the final version of the manuscript.

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Accepted: 12 February 2025

Please note that the Supplementary Material for this article is available online via the Herpetological Journal website: https://thebhs.org/publications/the-herpetological-journal/volume-35-number-3-july-2025