
Urbanization, Metabolic Rate, and Body Size Variation of a Common Urban Lizard

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ABSTRACT

Human-induced rapid environmental change is intensifying globally. Urbanization, a major form of human-induced rapid environmental change, alters ecosystems and exposes wildlife to environmental changes, including pollution, altered ambient temperatures, changes in habitat structure, and resource shifts. These alterations can benefit particular species while imposing challenges to others, influencing their behavior, physiology, and morphology. Changes in resource availability and ambient temperature are particularly relevant for ectotherms, which are less independent of environmental conditions than endotherms for thermoregulatory behavior and physical activity. To date, physiological and morphological responses have been less well studied than behavioral responses to urban environments in ectotherms. In this study, we measured standard metabolic rate ($N = 38$) of common wall lizards (*Podarcis muralis*) inhabiting habitats that differ in the degree of urbanization (as measured by impervious surface area). Over a period of 4 yr, we also recorded body size (mass and snout-vent length) of lizards from urban ($N = 123$) and nonurban ($N = 125$) habitats. Standard metabolic rate did not differ between urban and nonurban habitats or with degree of urbanization. While females showed no habitat-associated differences in any trait, males from urban habitats exhibit a reduced body mass and shorter snout-vent length than their nonurban counterparts. Despite these differences, body condition did not vary between the two habitat types. These findings indicate that

although sex-specific patterns in body mass and length occur, standard metabolic rate does not vary with urbanization. This underlines the importance of studying physiological and morphological traits of both sexes to better understand the impact of urbanization on wildlife.

Keywords: ectotherm, energy expenditure, human-induced rapid environmental change, metabolism, *Podarcis muralis*, scaled mass index, urbanization.

Introduction

Urbanization represents one of the most prominent human-induced rapid environmental changes to the natural environment (McKinney 2002; Sih et al. 2011). It simultaneously alters several ecological conditions, exposing wildlife to different types of stressors, such as pollution (e.g., light, noise, and air), altered resource availability and quality, and novel and altered biotic interactions with pathogens, competitors, and predators (Alberti et al. 2020; Isaksson and Bonier 2020; Sanders et al. 2021). Furthermore, urban structures and human activities lead to the urban heat island effect, in which urban areas experience higher temperatures than surrounding rural areas, changing the microclimatic conditions (Imhoff et al. 2010). As urban environments continue to expand worldwide, it is imperative to study the species that can live in urban areas and the extent to which they are affected by altered environmental conditions in these habitats. The first adjustment to cope with altered environments is often behavioral (Tuomainen and Candolin 2011). Many urban populations exhibit distinct behaviors compared to their nonurban counterparts (Sih et al. 2011; Lowry et al. 2013; Sol et al. 2013; Gaynor et al. 2018), including endotherms (Thompson et al. 2018; Ritzel and Gallo 2020) and ectotherms (Sparkman et al. 2018). The additive effects of intrinsic (e.g., behavioral) and extrinsic (e.g., environmental) changes can have profound impacts on physiology, morphology, and, ultimately, fitness consequences. For example, changes in metabolic rates in response to urban conditions may have implications for organisms by impacting survival and reproduction, directly influencing their fitness (Pettersen et al. 2018; Norin and Metcalfe 2019). Although an increasing body of literature has examined how urban environments drive physiological and morphological shifts (Alberti 2015) in both endotherms (Bonier 2012; Thompson et al. 2022, 2025) and ectotherms (Winchell et al. 2016, 2018; Diamond et al. 2018;

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French et al. 2018; Sparkman et al. 2018; Campbell-Staton et al. 2020; Putman and Tippie 2020; Yilmaz et al. 2022), these aspects have received less attention than behavioral responses to urbanization.

Maintenance metabolism represents the minimal cost of living and is a major functional trait because it constrains the allocation of energy to survival, growth, and reproduction (Glazier 2015). Maintenance metabolism refers to the minimal energetic cost of sustaining basic physiological functions in a resting postabsorptive animal. In endotherms, this minimum is quantified as basal metabolic rate (BMR), which is measured under strict conditions, in postabsorptive, inactive, normothermic, nonreproductive, adult individuals during their inactive period and in their thermoneutral zone (McNab 1997). Because these conditions are difficult to achieve outside the laboratory, many ecological and field studies instead measure resting metabolic rate (RMR), which relaxes some constraints (e.g., animals may not be fully postabsorptive) but is still assessed during rest and within the thermoneutral zone (Speakman et al. 2004). In ectotherms, the equivalent measure is standard metabolic rate (SMR). Across taxa, environmental changes associated with urbanization and global warming have been found to alter metabolic rates. For instance, urban populations of Eurasian red squirrels (*Sciurus vulgaris*) show weaker metabolic responses to ambient temperature variation than rural squirrels (Wist et al. 2023). Urban greater white-toothed shrews (*Crocidura russula*) and great tits (*Parus major*) exhibit lower RMRs and BMRs, respectively, than their rural counterparts (Andersson et al. 2018; Oliveira et al. 2020). While traffic noise decreases the RMR of house sparrow (*Passer domesticus*) nestlings (Brischoux et al. 2017), human presence at night does not alter the RMR of house finches (*Haemorhous mexicanus*) from urban and rural habitats (Hutton et al. 2018). These examples illustrate that metabolic responses to urbanization-related environmental changes can be complex, species specific, or dependent on the type of environmental stressor. The variability in results highlights the need for additional studies across diverse taxa before more general conclusions can be drawn.

Ectotherms are expected to respond differently to urbanization than endotherms because their body temperatures track environmental conditions more closely, making them especially sensitive to habitat structure and thermal variation, which can have profound consequences for behavior and physiology (Stevenson 1985; Angilletta 2009). Understanding how ectotherms adjust their metabolic rates in response to environmental change is therefore crucial for predicting population persistence and species resilience under urbanization and global warming (Nowakowski et al. 2018). However, research on the effects of urbanization on metabolic changes in ectotherms has been limited to date, and studies report mixed results. Some ectotherms exhibit higher metabolic rates in urban environments, for example, acorn-dwelling ants (*Temnothorax curvispinosus*) and common toads (*Bufo bufo*; Touzot et al. 2019; Chick et al. 2021). In contrast, other ectotherms, including rock agamas (*Laudakia vulgaris*) and Mediterranean house geckos (*Hemidactylus turcicus*), show no metabolic differences between urban and natural habitats (Vardi et al. 2023). These inconsistent findings highlight a key unresolved question: Why do some ectotherms increase metabolic rates in urban environ-

ments, while others show no change or even reductions (French et al. 2018; Doherty et al. 2020; Putman and Tippie 2020)?

One potential explanation lies in broader biogeographic patterns. Comparative biogeographic studies report that ectotherms from warmer climates often have lower metabolic rates than those from cooler climates (Addo-Bediako et al. 2002; Gaston et al. 2009; DeLong et al. 2018). This countergradient pattern has been interpreted as an adaptation to cold climates characterized by short growing seasons. Recently, this view has also been applied to climate-warming contexts, where reduced metabolic rates may mitigate the negative effects of heat stress (Pilakouta et al. 2020). Similar mechanisms may operate in urban environments experiencing the urban heat island effect (Imhoff et al. 2010), potentially explaining why some urban populations exhibit reduced metabolic rates. As an alternative explanation, it has been suggested that individuals living in urban environments may exhibit lower metabolic rates than those living in nonurban habitats. This could be a result of energy-conserving physiological strategies in response to reduced resource availability, habitat fragmentation, and anthropogenic stressors (Amdekar et al. 2018).

Body size, a trait closely linked to metabolism, also shows heterogeneous responses to urbanization. A global meta-analysis found that lizards tend to have larger body sizes and a similar body condition in urban habitats (Putman and Tippie 2020). However, these findings are based on a geographically and taxonomically biased dataset (e.g., *Anolis* lizards provided 75% of effect sizes), limiting their generalizability across clades. Notably, both no change (e.g., rock agamas [*L. vulgaris*], house geckos [*H. turcicus*], and side-blotched lizards [*Uta stansburiana*]) and reductions in body size and limb length (e.g., Western fence lizards [*Sceloporus occidentalis*] and Australian water dragons [*Intellagama lesueurii*]) in urban populations have been reported (Sparkman et al. 2018; Baxter-Gilbert et al. 2021; Vardi et al. 2023; Putman et al. 2024). Together, these mixed metabolic and morphological responses show that more research is needed to better understand the observed patterns across lizard species.

Urban environments can pose both unique challenges and novel opportunities for lizards. Human-made surfaces, for instance, may provide suitable perches or shelters for lizards inhabiting cities (French et al. 2018). The prevalence of artificial light at night (ALAN) can have mixed effects on reptiles (Maurer et al. 2019). ALAN can interfere with natural circadian rhythms, potentially altering hormone levels and thereby influencing metabolism, body condition, and energy use (Ouyang et al. 2018; Seebacher 2022). Extended light periods may enable diurnal reptiles to remain active for longer durations (Perry and Fisher 2006) and attract insects, increasing prey availability. However, this abundance may also intensify competition, introduce novel interspecific interactions, and elevate the risk of predation (Perry et al. 2008). Altogether, urbanization introduces a complex array of ecological pressures and resources that can influence reptile populations in multifaceted ways.

Lacertidae lizards in Europe are globally among the most affected reptile families because of anthropogenic habitat modification (Doherty et al. 2020). Yet this family also includes a few species with a remarkable ability to thrive in anthropogenic

habitats, such as the common wall lizard (*Podarcis muralis*). This species is highly successful in urbanized habitats, within both its native and invasive range (Ferner 2004; Williams 2019), and often found in city centers, exposed to high levels of habitat modification, artificial structures, and anthropogenic disturbance. Urban populations are more gregarious than nonurban conspecifics (Maune et al. 2025). Urban common wall lizards can exhibit a lower scaled mass index (SMI), a proxy for body condition (Lazić et al. 2017), especially when exposed to elevated nocturnal temperatures (Perry et al. 2025). In some locations, urban common wall lizards show higher developmental instability than rural conspecifics, measured by fluctuating asymmetry in morphological traits (Lazić et al. 2013), though these patterns are not reported at other locations (Sacchi et al. 2018). To better understand the physiological and morphological adjustments of ectotherms to urbanization, the goals of this study were to assess variation in (i) metabolic rate (measured as SMR), (ii) body length and mass, and (iii) body condition between common wall lizards from urban and nonurban habitats and with the degree of urbanization (determined via impervious surface area [ISA]). Urbanization may alter the metabolic rates of ectotherms in multiple ways. One hypothesis predicts that urban ectotherms exhibit higher metabolic rates because of elevated ambient temperatures associated with the urban heat island effect and increased physiological demands linked to disturbance and pollution (Seebacher et al. 2015; Diamond et al. 2017; Touzot et al. 2019; Chick et al. 2021). Alternatively, urban individuals may exhibit lower metabolic rates than those from nonurban habitats, reflecting energy-conserving physiological strategies in response to reduced resource availability, habitat fragmentation, and anthropogenic stressors. Given the available, albeit biased, meta-analysis on urbanization-related changes in reptile body size (Putman and Tippie 2020), we predicted that urban individuals would be larger than lizards from nonurban areas. If urban habitats are detrimental to common wall lizards, we expect them to have a lower body condition than individuals living in nonurban habitats.

Methods

Study Sites and Animals

We studied 38 adult common wall lizards (*Podarcis muralis*) living in the city of Rovinj, Croatia (45.082639, 13.636167), a popular tourist destination, and a less disturbed forested area (45.065344, 13.652087) located 3 km from the city center (fig. 1). In June 2024, we captured 19 individuals (8 females, 11 males) at two sites (630 m apart; fig. 1) inside the city, where the level of habitat modification, artificial structures, and anthropogenic disturbance is high. We captured an additional 19 individuals (7 females, 12 males) at three sites (390–555 m apart) in the nonurban area (Cuvri Beach; fig. 1). This site is a coastal area of forest and natural rocky outcrops, with relatively low human disturbance and minimal infrastructure (Maune et al. 2025).

We quantified the percentage of ISA surrounding each individual's capture site using the Copernicus 10-m imperviousness raster (<https://land.copernicus.eu>; 10-m resolution, EU coverage). Copernicus data at 10-m resolution are widely used in ecological studies (Gervais et al. 2025; Sexton et al. 2025) and provide stan-

dardized high-quality land cover information. Site coordinates were first projected to the raster's coordinate reference system (ETRS89/LAEA Europe, EPSG:3035). Home ranges of common wall lizards are small and range between 15 and 25 m² (Brown et al. 2015; Abalos et al. 2020). A previous study conducted on the same populations did not observe individuals moving between the urban and nonurban sites (Maune et al. 2025). Thus, we generated circular buffers, with a radius of 25 m around each capture site and extracted raster values within each buffer using the function `extract` in the R package `terra` (Hijmans 2025). For each buffer, we calculated the mean ISA to represent the degree of urbanization. Nonurban sites had an average ($\pm$ SD) ISA of $0.03\% \pm 0.11\%$ (range: 0.0%–0.48%) and urban sites had an average ($\pm$ SD) ISA of $31.2\% \pm 23.7\%$ (range: 1.2%–74.4%). Although we did not collect temperature data at the collection sites, the urban heat island effect has been documented in other Croatian coastal cities (e.g., Dubrovnik; Boras et al. 2022). Given that Rovinj exhibits similar patterns of urban development, impervious surface cover, and coastal morphology, comparable processes are expected to occur (Salvati et al. 2017).

We captured animals with a noose and transported lizards in an individually numbered breathable linen bag. We kept lizards individually for 2 d in small terraria (18 cm $\times$ 33 cm, with a height of 13 cm), at a 16L:8D cycle, at a room temperature of 25°C, and without providing any food to ensure that they were in a post-absorptive state during metabolic rate measurements (Žagar et al. 2015; Mell et al. 2016). Each terrarium was equipped with a shelter and a small ceramic bowl with *ad lib.* water. Daily, we placed a hand warmer (Firebag) next to the shelter area to allow lizards to thermoregulate (Damas-Moreira et al. 2024). One individual had a regenerating tail (female from a nonurban habitat). Three females, all from urban sites, were classified as gravid because they exhibited a distended abdomen and/or the presence of eggs was confirmed by gentle abdominal palpation.

Measurements of Standard Metabolic Rate

We measured SMR using an open-circuit system with a field metabolic system (FMS; Sable Systems, Las Vegas, NV). Similar to a previous study on the metabolism of *P. muralis* (Žagar et al. 2015), we conducted measurements between 6:50 a.m. and 2:15 p.m., which falls within the activity hours of these lizards. We weighed individuals using a digital scale (± 0.1 g) and then placed one individual in an air-tight metabolic glass chamber (55-mm diameter, 680-mL nominal volume). An empty chamber of the same size was used as a reference baseline, and the air temperature was measured inside the baseline chamber using a thermocouple from the FMS (Sable Systems). Outside air was used as incurrent air. Subsequently, we initiated measurements and video recordings of the behavior of individuals in the metabolic chambers using an action camera (CU-SPC06, COOAU, Shenzhen, China). We measured SMR in a climate-controlled room maintained at a constant temperature of 25°C ($\pm 0.61^\circ\text{C}$), using an air conditioning system; 25°C corresponds to the mean shaded ambient temperature during wall lizard activity hours in July, reflecting a realistic temperature regime, falling between two temperature regimes used in the study species previously (Žagar et al. 2015).

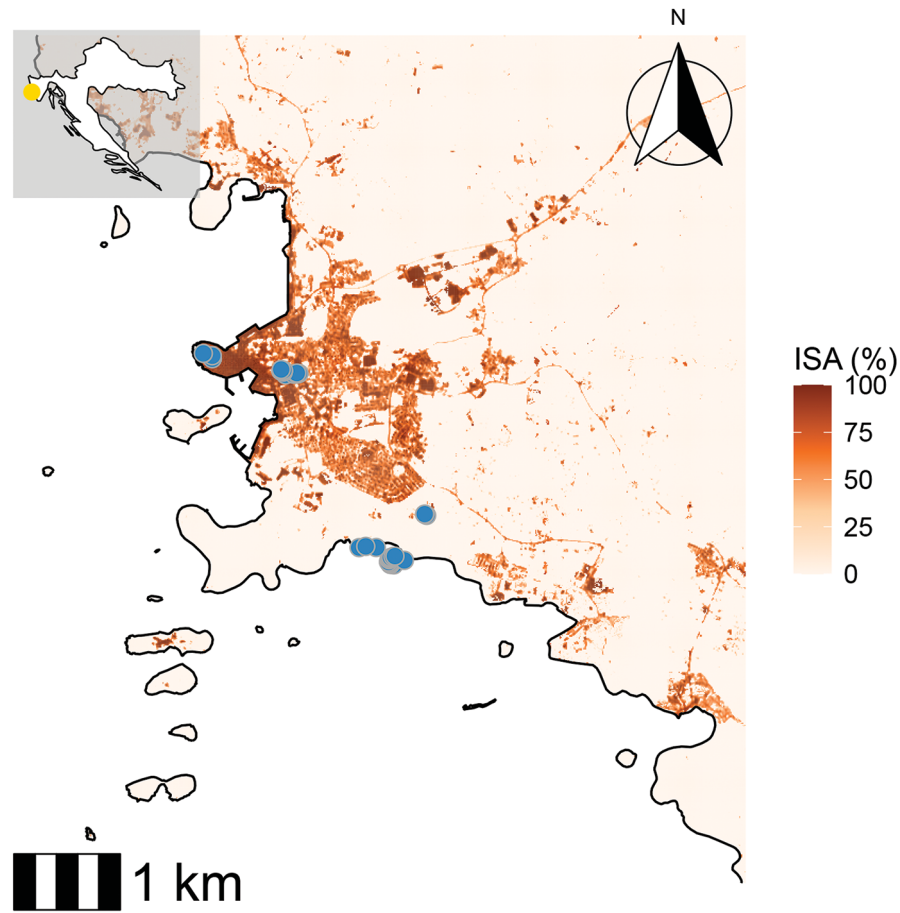


Figure 1. Locations of captures sites in Croatia. The map shows the spatial distribution of impervious surface areas (ISAs; percentage of cover, light orange indicates rural areas, dark orange indicates urban areas with very high impervious surface cover, and white indicates bodies of water) within a 3-km buffer area around Rovinj, Croatia. Capture sites are marked with blue points. The inset map of Croatia shows the relative location of Rovinj (yellow point). Impervious surface raster data are from the Copernicus 10-m imperviousness layer (<https://land.copernicus.eu>; 2021). Coastline and land boundaries are based on OpenStreetMap data (<https://osmdata.openstreetmap.de/>; accessed April 2026).

O₂ and CO₂ sensors (fuel cell sensor and dual wavelength nondispersive infrared sensor, respectively) took readings of O₂ and CO₂ every second for 10 min four times during a total measurement period of 1 h. Before each 10-min window, an empty baseline chamber was referenced for 5 min. Air was pulled through the system at a rate of 100 mL/min using the diaphragm pump integrated in the FMS. Six or seven animals were measured per day; the order of individuals on any given day was chosen randomly. After taking the measurements, we weighed individuals again and used the average body mass for analysis to account for mass changes during the measurements (e.g., because of waste excretion). We processed metabolic records using a macro program recorded in ExpeData (Sable Systems). All gas concentrations (O₂ and CO₂) and flow rates were mathematically corrected to dry conditions using barometric pressure (BP) and water vapor pressure (WVP), following standard equations: O₂(dry) = O₂ × BP/(BP – WVP), CO₂(dry) = CO₂ × BP/(BP – WVP), and flow(dry) = flow × (BP – WVP)/BP. We calculated whole-animal SMR from the lowest level of O₂

consumption recorded for 300 consecutive readings (i.e., 5 min). We confirmed the resting state of individuals by visual inspection of oxygen consumption rates and video recordings of lizards inside the chamber. All data were corrected for drift in O₂, CO₂, and H₂O baselines using the drift correction function in ExpeData.

Morphometric Measurements

After metabolic rate measurements, we measured each lizard's snout-vent length (SVL) to the nearest 0.1 mm using a digital caliper. All measurements of SVL were conducted by a single researcher (A. L. Maune). We classified all lizards as adults, based on their SVL (>47 mm) and the occurrence of femoral pores in males (Sacchi et al. 2012; Vacheva and Naumov 2024). Subsequently, we released individuals at the site of capture. To increase the statistical power regarding morphological measurements, we supplemented the 38 individuals measured for this study with an existing dataset of 210 common wall lizards (80 females, 130 males). These additional animals were captured and measured during

previous studies conducted in the same urban and nonurban habitats in 2021, 2022, and 2023 (June–July each year). Measurements from 2021 have been published previously (Damas-Moreira et al. 2024). Body mass and SVL of these additional animals were determined by two researchers (I. Damas-Moreira and A. L. Maune), using the same methods as described above. This resulted in a total sample size of 248 lizards, 125 from nonurban habitats (46 females, 79 males) and 123 from urban habitats (49 females, 74 males), for which we measured body mass and SVL. Given that the species exhibits sexual dimorphism and that females could be in different reproductive states, we analyzed morphological data separately for males and females. We also calculated the SMI from the standardized major axis regression of log-transformed SVL and log-transformed body mass for males and females separately. SMI accounts for the allometric relationship between body mass and body length (Peig and Green 2009).

Statistical Analysis

We conducted all analyses using R (ver. 4.4.1; R Core Team 2024). To assess variation in SMR ($N = 38$) between urban and rural habitats, we used a linear model (LM) to assess the effect of habitat type (urban/nonurban), sex, average body mass, and time of measurement on log-transformed SMR using the lme4 package (Bates et al. 2015). We analyzed whole-animal SMR with body mass included as a covariate, rather than using mass-specific values, as ratio-based approaches can introduce statistical artefacts and are no longer recommended (Tschöp et al. 2012; Wu et al. 2024). To assess whether SMR varies with the degree of urbanization, we also fitted a LM including ISA, sex, average body mass, and time of measurement as fixed effects. Metabolic rate can be elevated in gravid females compared to in nongravid females (Angilletta and Sears 2000). To assess whether our results were influenced by the three gravid females in the dataset, we refitted the models excluding these individuals. The results were qualitatively unchanged, and we therefore report the full dataset analysis. Results from models excluding gravid females are provided in the supplemental material (table S1; fig. S1 [available online]).

As this species exhibits sexual dimorphism (Sacchi et al. 2015), we analyzed morphological data separately for females ($N = 95$) and males ($N = 153$). For the body mass analysis, linear mixed effects models (LMMs) including year as a random factor resulted in a single fit. Thus, we used one LM per sex to assess habitat differences in body mass, including year as a fixed factor. We used one LMM per sex to assess habitat differences in SVL and SMI and included habitat type (urban vs. nonurban) as fixed effects and year as a random factor.

For all models, we tested for one-way interactions between the fixed effects and determined the contribution of interaction terms using likelihood ratio tests by comparing the model with the interaction term to the model without. We excluded all interaction terms because the explanatory power of the model was not improved by the inclusion of the interaction based on the likelihood ratio test (Pinheiro and Bates 2000). For all models, we verified that assumptions of linearity, homoscedasticity, and normality of residuals were met and, for LMMs, that random

effects were normally distributed and not overparameterized by inspecting residuals and using the functions `check_model`, `check_singularity`, and `check_normality` in the performance package (Lüdtke et al. 2021). We plotted predictor effects plots using the effects package (Fox and Weisberg 2018, 2019) and the ggplot2 package (Wickham 2016).

Results

Standard Metabolic Rate

Whole-animal SMR did not differ between lizards from urban (untransformed raw data: mean $\pm$ SD = 3.03 ± 1.14 mL O_2 /h) and nonurban (3.84 ± 1.78 mL O_2 /h) habitats ($\beta \pm$ SE = -0.12 ± 0.14 , $t = -0.83$, 95% confidence interval [CI] = -0.40 to 0.17 , $P = 0.41$, $R^2 = 0.24$, R^2 adjusted = 0.15 ; fig. 2A). In the LM with habitat type, sex ($\beta \pm$ SE = 0.06 ± 0.18 , $t = 0.36$, 95% CI = -0.30 to 0.43 , $P = 0.72$), body mass ($\beta \pm$ SE = 0.13 ± 0.07 , $t = 1.81$, 95% CI = -0.02 to 0.27 , $P = 0.08$), and time of measurement ($\beta \pm$ SE = -0.02 ± 0.03 , $t = -0.52$, 95% CI = -0.08 to 0.04 , $P = 0.61$) were not significant predictors of SMR. The model with ISA, instead of using the dichotomous variable habitat type, showed that SMR did not vary with ISA ($\beta \pm$ SE = -0.001 ± 0.003 , $t = -0.32$, 95% CI = -0.01 to 0.01 , $P = 0.75$, $R^2 = 0.23$, R^2 adjusted = 0.14 ; fig. 2B). Body mass had a positive effect on SMR ($\beta \pm$ SE = 0.14 ± 0.07 , $t = 2.05$, 95% CI = 0.00 to 0.28 , $P = 0.048$), indicating that heavier individuals exhibited higher metabolic rates. SMR did not differ between males and females ($\beta \pm$ SE = 0.04 ± 0.18 , $t = 0.26$, 95% CI = -0.32 to 0.41 , $P = 0.80$), and time of measurement ($\beta \pm$ SE = -0.01 ± 0.03 , $t = -0.39$, 95% CI = -0.07 to 0.05 , $P = 0.70$) was not a significant predictor of SMR.

Morphometrics and Body Condition

Females from urban (3.88 ± 0.91 g, $N = 49$) and nonurban (3.98 ± 0.81 g, $N = 46$) habitats did not differ in body mass (LM: $\beta \pm$ SE = -0.09 ± 0.18 , $t = -0.52$, 95% CI = -0.44 to 0.26 , $P = 0.60$, $R^2 = 0.025$; fig. 3A). Males from urban habitats (5.00 ± 1.18 g, $N = 74$) were lighter than males from nonurban locations (5.40 ± 1.15 g, $N = 79$; LM: $\beta \pm$ SE = -0.40 ± 0.19 , $t = -2.10$, 95% CI = -0.77 to -0.02 , $P = 0.037$, $R^2 = 0.047$; fig. 3B). Year did not significantly influence body mass in either sex (all $P > 0.15$). Females from urban (59.3 ± 4.8 mm, $N = 49$) and nonurban (60.5 ± 4.3 mm, $N = 46$) habitats did not differ in SVL (LMM: $\beta \pm$ SE = -1.21 ± 0.91 , $df = 90.6$, $t = -1.32$, $P = 0.19$, R^2 marginal = 0.017 , R^2 conditional = 0.121 ; fig. 3C). Males from urban habitats (61.1 ± 5.3 mm, $N = 74$) had a shorter SVL than males from nonurban habitats (62.8 ± 4.8 mm, $N = 79$; LMM: $\beta \pm$ SE = -1.77 ± 0.82 , $df = 148.2$, $t = -2.16$, $P = 0.033$, R^2 marginal = 0.030 , R^2 conditional = 0.037 ; fig. 3D). Female SMI did not differ between habitat types (urban: 3.94 ± 0.41 g, $N = 49$; nonurban: 3.84 ± 0.46 g, $N = 46$; LMM: $\beta \pm$ SE = 0.10 ± 0.088 , $df = 90.46$, $t = 1.17$, $P = 0.25$, R^2 marginal = 0.013 , R^2 conditional = 0.088 ; fig. 3E). Male SMI also did not differ between habitats (urban: 5.15 ± 0.50 , $N = 74$;

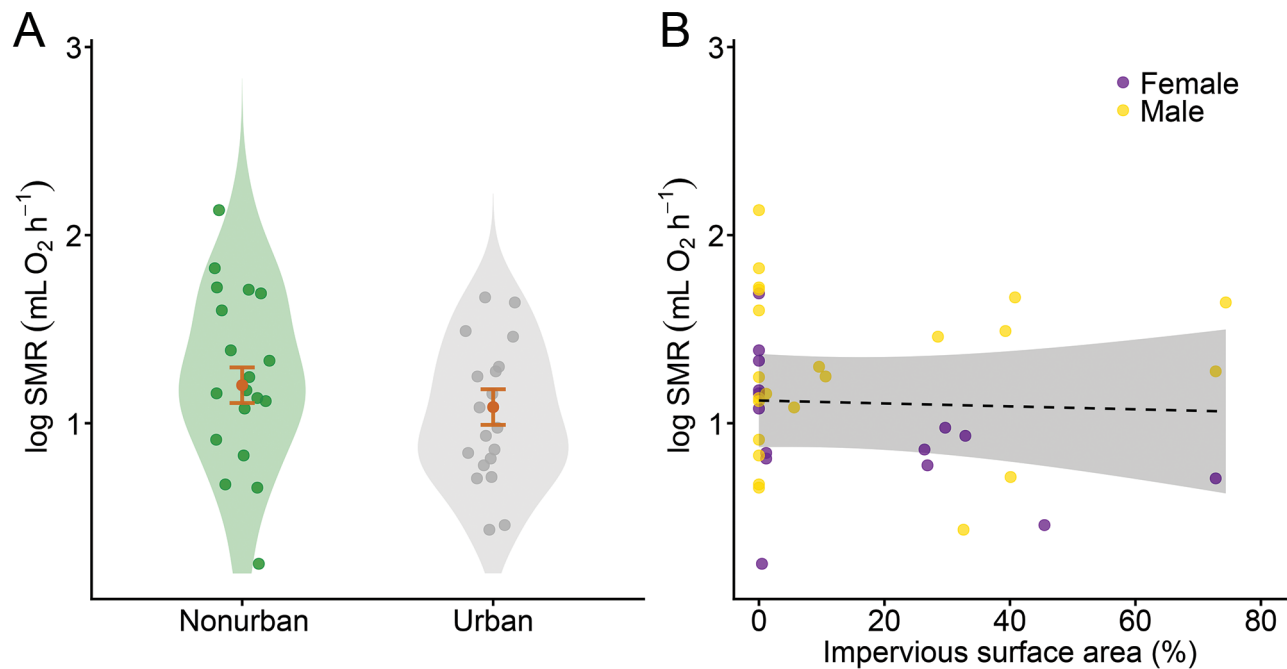


Figure 2. Standard metabolic rate (SMR) of common wall lizards (*Podarcis muralis*) does not vary between urban and nonurban habitats (A) or with changes in impervious surface area (B). In A, green and gray points represent raw data for nonurban ($N = 19$) and urban ($N = 19$) lizards, respectively, and orange points and error bars indicate the model-predicted means and their standard errors. The shaded areas represent kernel density plots, generated using a Gaussian kernel with automatically selected bandwidths ($\text{bw} = \text{"nrd0"}$ in `ggplot2`), showing the distribution of the raw data for each habitat type. In B, purple and gold points show raw data for females and males, respectively. The dashed line represents the model-predicted relationship between impervious surface area and log-transformed whole-animal SMR, holding average body mass and sex at the reference level. The shaded area indicates the 95% confidence interval for the model predictions.

nonurban: 5.14 ± 0.55 , $N = 79$; LMM: $\beta \pm \text{SE} = 0.01 \pm 0.08$, $\text{df} = 147.9$, $t = 0.11$, $P = 0.915$, $R^2 \text{ marginal} = 0.00$, $R^2 \text{ conditional} = 0.281$; fig. 3F). Although some annual variation in SVL and SMI was detected (table S1, available online), inclusion of year as a fixed effect did not alter the effect of habitat type on morphological traits.

Discussion

Our study investigated variation in physiological and morphological traits of common wall lizards inhabiting urban and nonurban habitats. We found that male, but not female, lizards from urban habitats had smaller body length and mass than males from nonurban habitats. We did not detect statistically significant differences in body condition between habitat types in either sex. Urban and nonurban lizards exhibited similar SMRs, suggesting that the observed differences in male body length and mass are not accompanied by detectable differences in metabolism. These findings contribute to our understanding of how ectotherms might adjust to anthropogenic habitat modification.

Our results show no statistically significant habitat-specific differences in SMR. Similarly, rock agamas (*Laudakia vulgaris*) and Mediterranean house geckos (*Hemidactylus turcicus*) from urban and natural habitats do not differ in metabolic rate (Vardi et al. 2023). Our results suggest that urbanization has not led to detectable shifts in baseline energy expenditure in the studied

population of common wall lizards. This result contrasts with studies reporting elevated or suppressed metabolic rates in urban-dwelling endotherms, such as mammals (Oliveira et al. 2020; Wist et al. 2023) and birds (Brischoux et al. 2017; Andersson et al. 2018), and ectotherms, such as amphibians (Touzot et al. 2019) and insects (Chick et al. 2021), potentially reflecting taxa- or species-specific responses. SMR represents the energetic costs of basic maintenance, which may be, to some extent, buffered against environmental variation or compensated through behavior (Clark et al. 2016). In that case, it may be that metabolic responses to urbanization occur primarily in other components of the energy budget. For example, field metabolic rates, but not maintenance metabolism, may diverge, as reported in Florida scrub jays (*Aphelocoma coerulescens*; Ellis and Bowman 2020; Ellis et al. 2022), if urban individuals experience different foraging demands, altered predator regimes, or distinct movement and escape behaviors. Such differences could allow individuals to maintain similar SMRs while still exhibiting energetic adjustments to urban environments. In the present study, acclimation to shared laboratory conditions before metabolic measurements may have reduced habitat-related differences in metabolic rate. Although internal body temperatures were not recorded, the 48-h exposure to constant ambient conditions before measurement likely ensured thermal equilibration among individuals. However, without direct measurements, small deviations from ambient temperature cannot be fully excluded. Common wall lizard males exhibit ventral color polymorphism

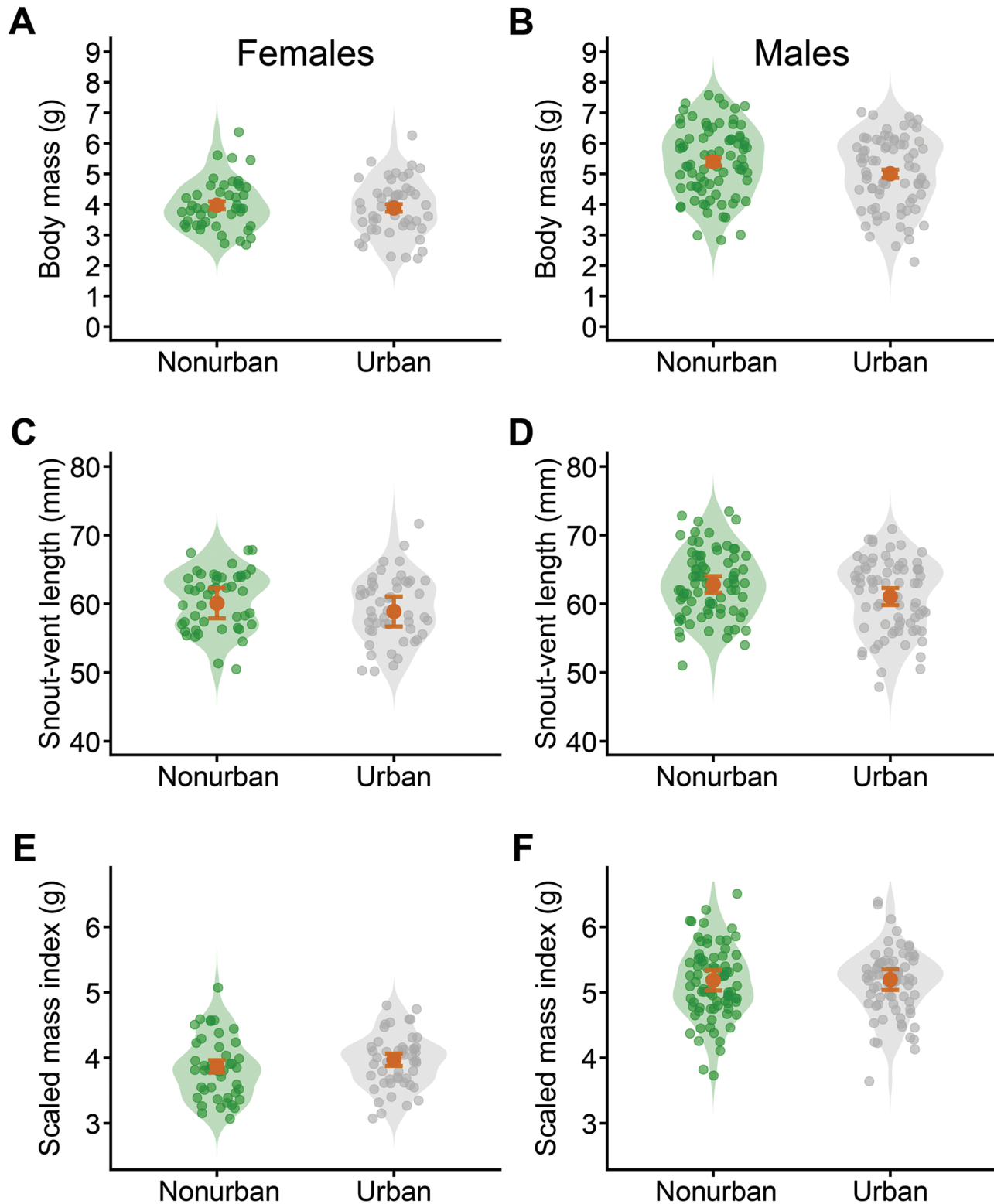


Figure 3. Sex-specific habitat-related variation in body mass, snout-vent length, and body condition (scaled mass index) in common wall lizards (*Podarcis muralis*). Females (nonurban: $N = 46$; urban: $N = 49$) showed no habitat-associated differences in any trait (A, C, E). Males from urban habitats ($N = 74$) exhibited lower body mass (B) and shorter snout-vent length (D) than males from nonurban habitats ($N = 79$), whereas body condition did not differ between habitats (F). Green and gray points represent raw data for nonurban and urban lizards, respectively, and orange points and error bars represent the model-predicted means and their standard errors. The shaded areas represent kernel density plots, generated using a Gaussian kernel with automatically selected bandwidths ($bw = "nrd0"$ in `ggplot2`), showing the distribution of the raw data for each habitat type.

(Sacchi et al. 2007; Calsbeek et al. 2010), with color morphs differing in physiological traits (Amer et al. 2024) that may extend to metabolic rates. We recommend that future studies explicitly incorporate color morph identity to better understand its role in shaping metabolic variation. Further studies incorporating field-based measurements, stronger contrasts in urbanization intensity, or common garden experiments may help clarify whether and how urban environments are associated with variation in metabolic traits, such as SMRs and field metabolic rates.

Contrary to our predictions, we observed smaller body length and mass in urban lizards than in lizards from nonurban habitats. This pattern was restricted to males, suggesting that urban-associated effects may disproportionately affect the larger sexually dimorphic sex. Similar patterns have also been reported in Australian water dragons (*Intellagama lesueurii*), with males from urban habitats in Sydney exhibiting a reduced body length (Baxter-Gilbert et al. 2021). In contrast, water dragons were found to show more pronounced sexual size dimorphism in urban habitats in Brisbane than in natural habitats, a pattern mediated by population density (Littleford-Colquhoun et al. 2019). In the area of our study, population densities of common wall lizards do not appear to differ detectably between urban and nonurban habitats (Maune et al. 2025), suggesting that other mechanisms may contribute to the observed patterns in male morphological traits. Our results of reduced mass and body length contrast with previous studies that found larger body sizes in urban reptiles (Putman and Tippie 2020). However, Australian water dragon (*I. lesueurii*) hatchlings from urban populations exhibit shorter body lengths than conspecifics from natural habitats, suggesting that differences in size can be established early in life rather than being the result of postnatal environmental effects (Baxter-Gilbert et al. 2021). If urban *Podarcis* hatchlings are similarly smaller, differences in adult body size might partly reflect early ontogenetic influences. These size differences may result from multiple factors, including altered resource availability or quality, increased exposure to pollutants, or differences in thermal resources, such as access to radiant heat (Sinervo and Adolph 1989; Mugabo et al. 2010). Urban individuals may also exhibit phenotypic plasticity, adjusting growth trajectories in response to developmental stressors, as demonstrated in zebra finches, where stressful conditions alter growth and reduce body size and condition (Kraft et al. 2019). Elevated temperatures accelerate juvenile growth in multiocellated racerunners (*Eremias multiocellata*), but do not affect adult body mass and length, while also inducing oxidative stress and telomere shortening during early life stages (Hao et al. 2021; Zhang et al. 2023). Altered body sizes could further reflect evolutionary pressures favoring faster life histories in urban environments (Brans and De Meester 2018). Another possible explanation is that the increased social tolerance observed in this species in the same urban environment (Maune et al. 2025) could reduce the selective pressure for territorial defense, potentially relaxing selection for larger body size in males. Additionally, if urban habitats consist of smaller anthropogenic crevices, smaller body sizes could be favored in cities, especially in the larger sex, allowing lizards to shelter and fit into tighter spaces. The differences in body mass and length we observed in this study were relatively small, and additional studies are needed to assess im-

plications for other fitness-related traits, such as locomotor performance, predator escape, or reproductive success (Tatu et al. 2024).

An alternative explanation for the observed pattern of smaller male body size in urban populations may simply be age differences. Urban environments could impose an elevated predation pressure that reduce lifespan, potentially leading to a younger average age distribution in urban populations than in nonurban ones. In *Podarcis* lizards, there is clear sexual dimorphism (Speybroeck et al. 2016), males are usually more conspicuous than females (Marshall and Stevens 2014), and dorsal coloration varies chromatically with sex in some species (Abalos et al. 2025). Moreover, male-colored models of *Podarcis* are more conspicuous to avian predators and suffer higher attack rates than female-colored models, suggesting that conspicuous male phenotypes may be selectively disadvantaged in environments with high predator densities (Marshall et al. 2015). Such sex-biased detectability could translate into disproportionate male mortality where visual predators are abundant. *Anolis* lizards from areas with domestic cats have a high incidence of tail regeneration, and adult males exhibit a significantly higher incidence than females and juveniles, indicating a higher exposure to predation attempts (Bateman and Fleming 2011). This pattern aligns with the idea that adult males are at greater risk of predator attacks, which could skew age distributions, especially in urban areas where cat densities are high. Additional work is needed to clarify whether the observed pattern reflects plasticity, selection on growth, or demographic bias introduced by differential mortality.

Despite differences in male body length and mass, we found no statistically significant difference in body condition between urban and nonurban lizards, suggesting that body condition is maintained across habitats. This may indicate that urban lizards are capable of adjusting their behavior and/or physiology and morphology to optimize energy intake and expenditure in urban environments. For instance, urban lizards could adjust their daily activity patterns to minimize energy expenditure or exploit food sources available around anthropogenic structures, such as insects attracted by ALAN. Interestingly, Indian rock agamas (*Psammophilus dorsalis*) also exhibit no difference in body condition between urban and rural habitats but urbanization-triggered physiological coping responses, including lower heterophil-to-lymphocyte ratios and lower testosterone levels (Amdekar et al. 2018). Our findings contribute to the growing evidence that ectotherms exhibit diverse and context-dependent responses to urbanization. While smaller body sizes were observed in males, the long-term consequences for fitness and population dynamics remain unclear. For instance, reduced body size could potentially influence reproductive output. Future studies, including temporal replication and larger sample sizes, will help clarify how urbanization affects the physiology and morphology of lizards and other ectotherms.

The variation in responses to urbanization observed among reptile species highlights the need for more taxonomically and geographically diverse studies. The similarity in SMR and the differences in male body size between urban and nonurban common wall lizards underscore the importance of studying physiological and morphological traits together to better understand how organisms adjust to urbanization. Further research could investigate the potential genetic basis of these changes, the role of developmental

plasticity, and the interaction between urban stressors such as pollution, habitat structure, and temperature.

Conclusions and Future Directions

Overall, our results demonstrate that common wall lizards exhibit sex- and habitat-specific morphological variation to urbanization. Urban male lizards had smaller body sizes than males from nonurban habitats, potentially reflecting responses to altered environmental conditions in urban areas. These findings highlight the importance of studying both physiological and morphological traits in both sexes to better understand the effects of urbanization on wildlife. As urbanization continues to expand globally, further research on the mechanisms underlying these responses, such as plasticity or evolutionary change, will be crucial for predicting species resilience and informing conservation strategies.

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