

Smarter in the city? Lizards from urban and semi-natural habitats do not differ in a cognitive task in two syntopic species

Isabel Damas-Moreira^{a,*,**}, Birgit Szabo^{b,**,ID}, Georgios Drosopoulos^a, Carolin Stober^a, Duje Lisičić^c, and Barbara A. Caspers^{a,d}

^aDepartment of Behavioural Ecology, Bielefeld University, 33615, Germany

^bDivision of Behavioural Ecology, University of Bern, 3032, Switzerland

^cDepartment of Biology, University of Zagreb, 10000, Croatia

^dJoint Institute of Individualisation in a Changing Environment (JICE), University of Münster and Bielefeld University, 33615, Germany

*Address correspondence to Isabel Damas-Moreira. E-mail: isabeldamas.m@gmail.com.

**These authors contributed equally.

Handling editor: Vedrana Šlipogor

Abstract

Urbanization occurs at a global scale, imposing dramatic and abrupt environmental changes that lead to biodiversity loss. Yet, some animal species can handle these changes, and thrive in such artificial environments. One possible explanation is that urban individuals are equipped with better cognitive abilities, but most studies have focused on birds and mammals and yielded varied results. Reptiles have received much less attention, despite some lizard species being common city dwellers. The Italian wall lizard, *Podarcis siculus*, and the common wall lizard, *Podarcis muralis*, are two successful lizards in anthropogenic habitats that thrive in urban locations. To test for differences in a cognitive skill between urban and semi-natural environments, we investigated inhibitory control through a detour task in syntopic populations of the two species, across 249 lizards that were tested in partially artificial field settings. Sophisticated inhibitory control is considered essential for higher degrees of cognitive flexibility and other higher-level cognitive abilities. In this task, we confronted lizards with a transparent barrier, separating them from a desired shelter area that they could only reach by controlling their impulse to go straight and instead detour the barrier. We found no differences between lizards in urban and semi-natural environments, nor between species, but females overall performed better than males. Moreover, 48% of the lizards in our study did not perform a correct trial in any of the 5 trials, hinting at the difficulty of the task for these species. This study is among the first to address lizard cognition, through their inhibitory control, as a potential explanation for success in cities and highlights one should be careful with assuming that urban animals generally have enhanced cognitive performance, as it might be taxa, task, or condition dependent.

Key words: *Podarcis siculus*, *Podarcis muralis*, Behavior, Cognition, Detour task, Reptile.

Urbanization, one of the fastest forms of environmental change (Angel et al. 2011; Candolin and Wong 2012), has been steadily increasing (Ritchie 2019) and confronting animals with ever-new sets of challenges (Palumbi 2001; Sih et al. 2011; Sol et al. 2013; Griffin et al. 2017; Barrett et al. 2019). For most species, this anthropogenic environment with many abiotic and biotic changes has devastating consequences and severely reduces wildlife survival, and thus it is intriguing that some organisms can still survive or even thrive in cities (Lowry et al. 2013; Wong and Candolin 2015). Successful city dwellers need to deal with novel threats, different predator species and abundance, novel food sources and differences in food availability, drastic habitat changes, human disturbance, and many other urban stressors (Lowry et al. 2013; Johnson and Munshi-South 2017; Barrett et al. 2019; Elmqvist et al. 2021; Lee and Thornton 2021). Even if individuals only experience the same urban habitat throughout their lifetime, cities are challenging because they are a dynamic source of

unpredictable change, where ecological changes can take place more rapidly and frequently than in non-urban habitats (Shochat et al. 2006; Alberti et al. 2017). As we are facing a global biodiversity crisis (WWF 2020), it is essential to understand why some animals can cope with anthropogenic environments and thrive in cities. This knowledge is important for mitigating negative urban effects, helping more species utilize urban habitats, and counteracting species decline (Lowry et al. 2013; Sih 2013; Sol et al. 2013).

Animal cognition involves the mechanisms by which animals effectively obtain, retain, and process information from the environment through exploration, exploitation, or evasion, enabling animals to fulfill their survival needs and increase fitness (Shettleworth 2001; Lyon 2020). Accordingly, animal cognition likely plays a role in how individuals cope with urbanization, as cognitive processes have been linked to the ability to cope with abrupt and novel challenges (Griffin et al. 2017; Lee and Thornton 2021). Urban animals can be

Received 30 May 2023; accepted 22 March 2024

© The Author(s) 2024. Published by Oxford University Press on behalf of Editorial Office, Current Zoology.

This is an Open Access article distributed under the terms of the Creative Commons Attribution-NonCommercial License (<https://creativecommons.org/licenses/by-nc/4.0/>), which permits non-commercial re-use, distribution, and reproduction in any medium, provided the original work is properly cited.

For commercial re-use, please contact reprints@oup.com for reprints and translation rights for reprints. All other permissions can be obtained through our RightsLink service via the Permissions link on the article page on our site—for further information please contact journals.permissions@oup.com.

expected to perform better than non-urban animals at certain cognitive tasks, showing more flexibility, innovation, and problem-solving abilities (Sol et al. 2013, 2020; Lee and Thornton 2021). For example, sulfur-crested cockatoos (*Cacatua galerita*) living in residential areas improve their efficiency in opening trash bins in parallel with humans who increase the complexity of the bin locks (Klump et al. 2022). Indeed, avian species that inhabit urban hubs can show more feeding innovations than species from rural areas (Møller 2009). Furthermore, within the same species, there is a growing body of evidence showing that urban populations exhibit distinct behaviors compared to their non-urban counterparts (Sol et al. 2013). In some bird species, urban individuals can be faster problem-solvers than their rural counterparts, such as in Barbados bullfinches (*Loxigilla barbadensis*, Audet et al. 2016) and in great tits (*Parus major*, Preiszner et al. 2017). Similarly, urban striped field mice (*Apodemus agrarius*) have greater problem-solving ability in diverse novel tasks than rural mice (Mazza and Guenther 2021). Yet, urban house sparrows (*Passer domesticus*) only performed better than rural sparrows on one of 4 novel problem-solving tasks (Papp et al. 2015). Intriguingly, better performance in certain cognitive skills is not always found in populations that succeed in more urbanized environments; there are some exceptions to this trend (Kark et al. 2007). For instance, black-capped chickadees (*Poecile atricapillus*) do not differ in their spatial memory along an urban gradient (Thompson and Morand-Ferron 2019), and rural spotted hyenas (*Crocuta crocuta*) are more innovative than those in more urbanized and transitional areas (Johnson-Ulrich et al. 2021).

Studies addressing cognition in urban settings are heavily biased toward birds and mammals (highlighted in Lowry et al. 2013; Griffin et al. 2017; French et al. 2018; Sol et al. 2020; Lee and Thornton 2021), which can lead to overgeneralization. For example, honey bees (*Apis mellifera*) learning and memory are negatively affected by air pollution, a stressor highly associated with urban locations (Leonard et al. 2019). As a consequence, and contrary to most literature, this species could in fact show lower cognitive performance in cities. It is essential to expand studies on urban cognition beyond mammals and birds, given that different taxonomic groups perceive and obtain information from their surroundings differently, and therefore, may respond in various ways to anthropogenic disturbance (Ficetola et al. 2007; French et al. 2018). Reptiles, for example, are in global decline directly due to anthropogenic pressures, which can impact them in different ways than birds or mammals, due to drastic differences in ecology and behavior (French et al. 2018; Doherty et al. 2020). Nonetheless, little research has been conducted toward understanding how reptiles might cope with anthropogenic disturbance and urban challenges (e.g., reviewed in French et al. 2018; Doherty et al. 2020), and even less has been done on exploring if and how cognitive performance can play a role for urban reptiles. In fact, to the best of our knowledge, only 2 studies have addressed the impact of urbanization on reptile cognition (Kang et al. 2018; Batabyal & Thaker 2019), although by now we acknowledge that reptiles have better cognitive abilities than previously believed. Indeed, reptiles can use their cognitive abilities to solve novel tasks, adjust to changes and succeed in novel and unpredictable environments (Amiel et al. 2011; Szabo et al. 2020; de Meester and Baeckens 2021), also in urban environments (Batabyal and Thaker 2019). Kang and colleagues (2018)

found no link between urbanization and learning ability in the Delicate skink (*Lampropholis delicata*), while Batabyal and Thaker (2019) found a positive link in the Indian rock agama (*Psammodromus dorsalis*).

Lacertidae, the most common lizard family in Europe, is among the reptile families that globally suffer the most due to anthropogenic habitat modification (Doherty et al. 2020). However, different lacertid species can vary in their tolerance to anthropogenic environments, even when living in sympatry (Speybroeck et al. 2016). The Italian wall lizard (*Podarcis siculus*) and the common wall lizard (*Podarcis muralis*) are very successful in urbanized habitats, both along their invasive and native range (e.g., Ferner et al. 2004; CABI 2016; Speybroeck et al. 2016; Williams 2019). These are medium-sized lizards with similar ecological requirements that can reach abundant densities and might overlap in their native distributions, along much of Italy and Croatia (Speybroeck et al. 2016). Some populations can even occur in syntopy, in both urban and non-urban areas. Thus, studying these lizards is a great opportunity to understand 1) the differences in cognitive abilities between urban and semi-natural lizard populations, and 2) if two species that are successful in anthropogenic environments will show a similar cognitive performance along an urban gradient.

Our main aim was to understand if lizards from 2 species living in urban or semi-natural environments differ in their cognitive performance. Given individuals need to face a range of challenges in urbanized environments, we tested the lizards' motor response inhibition, the ability to inhibit a prepotent motor response of directly reaching a goal. Motor response inhibition is part of inhibitory control, a general cognitive domain that is suggested to be essential for cognitive flexibility and other higher-level cognitive abilities (Diamond 2013). Inhibitory control likely provides an advantage in urban areas in daily crucial tasks, such as when dealing with traffic and human disturbance, or even finding the best food (e.g., Coomes et al. 2022). To this end, we used the detour task (previously validated in lizards; Szabo, Noble, et al. 2019; Storks and Leal 2020), in which we confronted wild caught Italian wall lizards and common wall lizards with a transparent barrier separating individuals from a desired goal (i.e., the familiar area). To reach this goal an individual has to control their impulse to keep going straight, and detour the transparent obstacle to the side (e.g., Kabadayi et al. 2016; Juszczak and Bobrowska 2020). We expected to find differences in motor response inhibition across urban and non-urban habitats in both *P. siculus* and *P. muralis* lizards. Grounded on the prediction that urban lizards are equipped with better motor response inhibition, we expected that urban individuals of both species would detour without interacting with the barrier more often compared to lizards from semi-natural areas. We also predicted animals to learn to detour across successive trials, and expected to find no differences in behavior between the 2 tested species, as they have similar ecological requirements, live in syntopy, and are urban dwellers.

Materials and Methods

Collection

Data were collected from 249 adult *P. siculus* and *P. muralis* in two urban and two semi-natural populations (as in e.g., Preiszner et al. 2017) in Croatia. These two lizard species can occupy a wide range of habitat types, having similar activity

patterns when in sympatry and highly overlapping in their food niche and consumption intake; both are predominantly insectivorous, but able to expand their diet to even eat fruits or plant matter (Avery 1978; Capula et al. 1993; Speybroeck et al. 2016). They can differ in their microhabitat use, with *P. siculus* making more usage of vegetation and drier habitats and *P. muralis* using more rocky and humid habitats (e.g., Capula et al. 1993; Speybroeck et al. 2016). Nevertheless, in all the 4 locations in our study, the 2 species can be found living in syntopy and often sharing the exact same habitat. We tested 56 *P. siculus* from urban habitats (29 males and 27 females); 53 from semi-natural habitats (28 males and 25 females); 76 *P. muralis* from urban habitats (38 males and 38 females); and 64 from semi-natural habitats (27 males and 37 females; Table S1). As urban locations we used the cities of Zagreb (Zagreb county, “A_U1”) and Rovinj (Istria county, “A_U2”), and as semi-natural locations we used the forests in Park Zlatni Rt (Istria county, “B_S1”) and near Vrlika (Split-Dalmatia county, “B_S2”); see the ESM for more information. The colonization history of the urban populations is unknown, except for *P. siculus* in Zagreb, for which molecular analysis predictably confirmed its origin from the Adriatic region (Oskeyko et al. 2022). In both urban environments lizards can be found in the town center, surrounded by high levels of habitat modification, artificial structures, and anthropogenic disturbance. The semi-natural environments consist of 2 forest areas predominantly composed of natural substrate, with a low amount of artificial structures and impermeable surfaces, and with some degree of human presence during the daytime (due to nearby human settlements). All experiments took place in the field between May and August of 2021 and were conducted in partially artificial settings (lizards were caught from the wild, transferred and

tested in tubs outdoors, and released on the same day). This allowed us to test a larger number of individuals increasing our ability to obtain a better estimate of natural behaviors (Bueno-Guerra and Amici 2018), as the transfer from wild to laboratory conditions can overshadow behavioral differences (e.g., for boldness and exploration in an open field test, with urban and wild *Microtus arvalis* voles, Mazza et al. 2020).

Testing procedure and set-up

On any given experimental day, we collected a maximum of 8 lizards by noose during the early morning. We placed each lizard in an individual numbered breathable linen bag until the start of the experiments. We also collected a portion of the substrate from the location the lizard was captured with gloves, to use as substrate in the experimental tub to promote acclimation. Until use, the soil was stored in a plastic bag to preserve the original scents as much as possible. All experiments took place outside, under an opaque gazebo (to avoid direct sunlight during the experiments and even out the amount of light across the tubs), near the collection sites with no human disturbance.

Prior to the experiments, we cleaned all experimental tubs and materials with 96% ethanol. Each tub was made of dark plastic and measured 650L × 340W × 320H mm (at the base). In each tub, we placed a small ceramic bowl with water, 2 brick shelters, and the respective lizards' soil samples obtained during collection. We then opened the linen bag inside each tub and gently released the lizard. We placed a hand warmer (Firebag™; warms up to 50 °C) inside the same linen bag and put it in the shelter area to allow lizards to thermoregulate (see Figure 1A). We left the lizards to acclimate in the experimental tub for 40 min without disturbance. Once this period was over, we started the first trial. We repeated

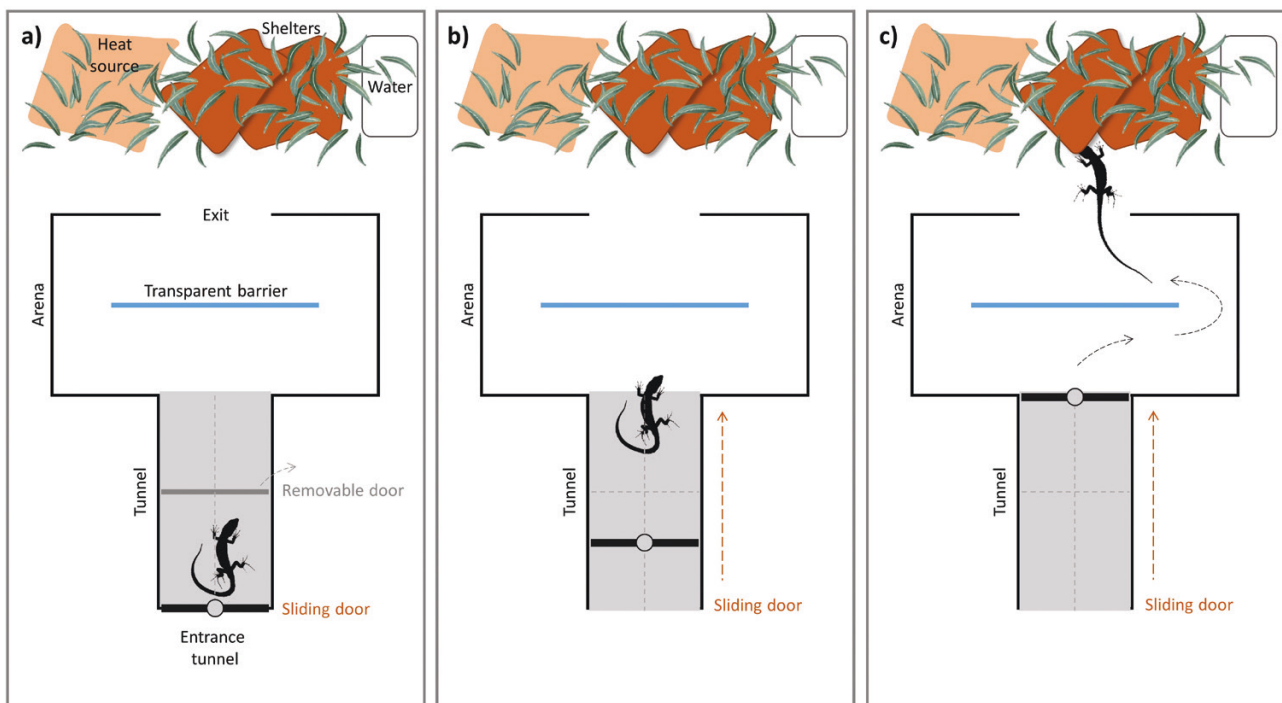


Figure 1. The sequence of a lizard performing the cognitive task (A–C). After 5 min inside the dark tunnel, we lifted the removable door (A) and slowly chased the lizard with a sliding door through the tunnel (B) to ensure that all individuals would reach the arena with the transparent barrier. Afterwards the lizards had 10 min to detour the barrier (in this figure, through the right side) and go back to their familiar area in the tub (C).

each trial 5 times on the same day, with an inter-trial interval of 1 h. On average, experiments took place between 11:45 h and 17:00 h. All hand warmers were boiled each evening for 20 min to reset and clean them from scent residue.

The test apparatus was built in a *t*-shape (Figure 1). The base was a dark tunnel from which lizards emerged (after handling) into an open area (closed off with a transparent lid) that included the transparent barrier that they had to detour to reach the familiar area containing their shelter, water, soil, and the hand warmer (Figure 1A). The transparent barrier was positioned in the middle of the open area, 80 mm from the long and 55 mm from the short walls. The entire apparatus was made of 10 mm thick dark gray polyvinyl chloride (PVC). The transparent lid and barrier were made of 5 mm thick transparent Plexiglas®.

At the beginning of a trial, we first captured the lizard from its tub, placed the task apparatus inside the tub, then gently released the lizard inside the tunnel of the test apparatus and closed the tunnel from behind. While the individual stayed inside the tunnel for 5 min, we replaced the hand warmer. We then started the trial by softly lifting the removable door that was holding the lizard inside the dark tunnel (Figure 1A). Then, we slowly moved the sliding door from the back of the tunnel behind the lizard forward, thereby forcing the lizard to emerge from the tunnel (Figure 1B). This procedure also prevented the lizard from going back into the tunnel. Each lizard was given 10 min to detour the barrier either to the left or right (Figure 1C), starting from the moment it entered the open arena. All trials were filmed from above with portable cameras (LAMAX X8.1 Sirius) attached to power banks. After completing 5 trials, we measured the size (snout-vent length; SVL) and weight of each lizard and took photographs. Thereafter, lizards were released back at their capture site, on the same day. No lizards were kept overnight, nor were hurt or died during this study.

Data collection

For each trial, we scored 4 response variables from the videos (Table 1): 1) if lizards interacted with (touched) the transparent barrier before detouring it, 2) the time spent interacting with the transparent barrier, 3) latency to detour the transparent barrier, and 4) which side (left or right) the lizard used to detour the transparent barrier. Videos were recorded at half speed, therefore, continuous variables were scored

with values between 0 and 1200 (twice 600 s, or 10 min). We decided to use these values to avoid manipulating and rounding the measurements we used. More information on how we scored and used these variables in the analysis can be found in Table 1. A trial was considered successful if the individual inhibited its response of going straight to the exit and detoured the transparent barrier without touching it, and unsuccessful if the individual touched the barrier before detouring. Furthermore, we initially tested a higher number of lizards (304 individuals) but we removed all lizards that did not participate in trials (i.e., did not move during the whole trial or did not cross the barrier to exit the apparatus) from the analysis, to ensure, to the best of our capabilities, that all tested individuals were motivated to perform the task.

Video scoring and inter-observer reliability

Video scoring and data extraction were performed by GD and CS using the software BORIS (Friard and Gamba 2016). Both scorers were unaware of the lizards' capture location, species, or sex. They scored different videos, but initially, both scored the same 25% of trials (83 lizards, thus 415 trials out of a total of 1,520 trials). We calculated inter-observer reliability using Cohen's Kappa for the 2 observers (interaction with the barrier: kappa = 0.851, *P* value < 0.001; side bias: kappa = 0.973, *P* value < 0.001) and Single Score Intraclass Correlation, ICC (3,1), with type "consistency" (time interacting with the barrier: ICC = 0.966 with 95% confidence interval = 0.959–0.972; latency to detour the barrier: ICC = 0.988 with 95% confidence interval = 0.985–0.990), and found extremely high agreement between the 2 observers (all above 0.85).

Statistical analyses

We performed all statistical analyses in R (version 4.2.2) (R Core Team 2022). We first explored our data following Zuur et al. (2010) to ensure our data fitted model assumptions. We also analyzed variation in SVL and body condition between species and sex in urban and semi-natural habitats (Supplementary Table S2). Overall, we found significant differences in the SVL between species and sexes (LM, $\beta = 4.584 \pm 1.769$, $t = 2.591$, $P = 0.010$), with *P. muralis* being smaller than *P. siculus*, for both males and females, and with *P. siculus* females being significantly smaller than males. We further calculated animals' body condition through the scaled

Table 1. Response variables were scored from the experimental videos, with respective descriptions and values. Each trial lasted for 10 min (600 s), but we filmed videos at half speed, so continuous response variables have values up to 1,200. We indicate also which data frame subset was used to study each variable in the analysis

Variable	Description	Scoring	Used dataset
1) Interaction with the barrier	Lizards were scored as having interacted with the transparent barrier before detouring if they touched it, either with their snout or front legs.	1 = did not interact with the barrier; 0 = interacted with the barrier	<i>detour</i> dataset: included all trials.
2) Time interacting with the barrier	The time lizards spent interacting with the transparent barrier (with snout or front legs) before detouring it.	0–1,200	<i>interacted_with_barrier</i> dataset: included only trials in which individuals interacted with the barrier before detouring; that is, were not successful in the task.
3) Latency to detour the barrier	Lizards' latency to detour the transparent barrier. Scored regardless of if individuals interacted with the barrier before detouring or not.	1–1,200	<i>detour</i> dataset: included all trials.
4) Side bias	Side through which Lizards detoured the transparent barrier.	R = right = 1 L = left = 0	<i>detour</i> Dataset: included all trials.

mass index (SMI; Peig and Green 2009) and found that females exhibited lower SMI than males (LM, $\beta = 0.669 \pm 0.141$, $t = 4.748$, $P < 0.001$). All results are in [Supplementary Table S2](#). Thus, we excluded SVL and SMI from further analyses to ensure no collinearity between variables (species and sex). To assess the variation of SMI across habitats, we subset the data for each species and sex and found SMI not to vary between urban and semi-natural habitats (for all 4 LM models, $P > 0.05$) for each species and sex ([Supplementary Table S3](#)).

We ran four different models separately to analyze the 1) interaction with the barrier, 2) time interacting with the barrier, 3) latency to detour the barrier, and 4) side bias (side chosen to detour). See [Table 1](#) for details. In all models, we integrated the fixed effects of species (*P. siculus* or *P. muralis*), habitat (urban or semi-natural), sex (male or female), and trial number (1–5); we also included the random effects of lizard's identity (to account for repeated measures), the experimental day (1–42) and the collection site (urban U1, U2, and semi-natural S1, S2). For all 4 models, we also tested for an interaction between the fixed effects species and habitat. For the response variables 1) interaction with the barrier and 4) side bias, we initially used generalized linear mixed effects models (GLMM) with a binomial distribution (using the function *glmer* from the lme4 R package; [Bates et al. 2015](#)). Because our binomial model 4) regarding the side bias was singular and over dispersed, and given the random effects explained nearly zero of the remaining variance, we decided to use the number of right side choices per individual as a response variable in a GLM model with Poisson distribution instead (not including thus the random effect of animal identity). To further investigate laterality in detour behavior, we determined the percentage of individuals with a clear side preference when detouring (turned 5 times to the left/right during the trials). Additionally, we calculated a laterality index (LI) using the formula $(N_{right} - N_{left}) / (N_{right} + N_{left})$, in which -1 indicates a bias to the left and 1 a bias to the right. Moreover, to gain a measure of the strength of lateralization we also calculated the absolute value of LI (0–1 values). For the models investigating 2) time interacting with the barrier and 3) latency to detour the barrier, we used GLMMs (also using the function *glmer*) with Gamma distribution (log-link), due to the right-skewedness of our data (from the same lme4 package). Mixed models were fitted by maximum likelihood with adaptive Gauss–Hermite quadrature = 0, to allow convergence of the models ([Bates et al. 2015](#)). We investigated the results of interactions using least-square means post hoc tests with the *emmeans* function of the package *emmeans* (LSM, [Lenth 2023](#)). For all models, α was set at 0.05.

Our code and dataset can be assessed at OSF: <https://doi.org/10.17605/OSF.IO/N9J85>.

Results

Contrary to our predictions, we found no differences between lizards from urban and semi-natural habitats, in any of the investigated response variables ($P > 0.05$, [Table 2](#)). This pattern was similar for both species ($P > 0.05$, [Table 2](#)). We found no difference in the lizards' ability to detour the barrier without touching, between lizards from different habitats (GLMM, $\beta = -0.413 \pm 0.442$, $t = -0.933$, $P = 0.351$; [Table 2](#)). We also found no differences between species, but males overall made less correct detours than females ($\beta = -0.512 \pm 0.218$, $t = -2.345$, $P = 0.019$; [Figure 2C](#)). We

did not find lizards to improve their performance over the 5 trials ($\beta = 0.072 \pm 0.053$, $t = 1.365$, $P = 0.172$; [Figure 2A](#)). To further understand if the sex difference was associated with differences in performance over trials, we ran another similar model, which additionally included an interaction between sex and trial number. We found no significant interaction (GLMM, $\beta = 0.008 \pm 0.106$, $t = 0.074$, $P = 0.941$), indicating that, despite females performed better than males, both sexes performed in the same way across the 5 trials ([Figure 2B](#)). In the first trial, 82.7% (206 out of 249) of the lizards interacted with the barrier before detouring; particularly, 81.1% (107 out of 132) of the urban lizards and 84.6% (99 out of 117) of the semi-natural populations. Furthermore, 48% of the lizards (109 out of 249) did not perform a correct trial in any of the 5 trials.

When considering only those trials in which lizards interacted with the barrier before detouring (i.e., made an incorrect choice), we found that lizards spent more time interacting with the barrier as trials progressed (GLMM, $\beta = 0.090 \pm 0.026$, $t = 3.449$, $P = 0.001$), but there were no differences among habitat, species, or sex ([Table 2](#)). Moreover, we found no differences among habitat, species, or sex in the latency taken to detour the barrier ([Table 2](#)) or the side bias ([Table 2](#)). Nonetheless, despite the majority of animals showing no clear bias when detouring the barrier, a few individuals were showing a distinct side bias, turning 5 times to the left/right during the trials. Specifically, in *P. siculus*, 11.1% of females and 3.5% of males in urban habitats, and 4% of females and 25% of males in semi-natural habitats, showed a clear side bias ([Supplementary Table S4](#)). In *P. muralis*, 7.9% of females and 13.2% of males in urban habitats, and 13.5% of females and 25.9% of males in semi-natural habitats, showed a clear side bias ([Supplementary Table S4](#)). For both species, the percentage of males with a clear side bias was nearly twice as high as that of females, and the percentage of males exhibiting a clear side bias was also higher in semi-natural than urban habitats. Among all animals exhibiting a distinct side bias, we found a preference for the left side in all groups. Interestingly, not a single lizard in urban habitats displayed a clear bias to detour the barrier to the right side. Overall, we found a low LI across groups (average ranging from -0.244 to 0.103), and only females from semi-natural environments (of both species) showed a LI more biased to the right ([Supplementary Table S4](#); [Supplementary Figure S2](#)). The strength of laterality was also weak, reaching a maximum average of 0.5 ([Supplementary Table S4](#); [Supplementary Figure S3](#)).

Discussion

Contrary to our predictions, Italian wall lizards and common wall lizards living in urban and semi-natural areas did not differ in their motor response inhibition and did not improve their performance over trials. Nevertheless, females were more likely to detour the barrier without interacting with it (correct trial), but we found no differences between the sexes in their performance across trials. Almost half of the lizards in the study failed to complete a single correct trial. This could indicate the difficulty of the task for these 2 species, either due to the nature of the task requirements or to the lizards' unfamiliarity with transparent surfaces ([Kabadayi et al. 2016](#)). When looking at trials in which lizards touched the barrier, we found that the time interacting with the barrier increased over trials, but did not differ based on habitat (urban versus

Table 2. Outcomes of the models for each response variable. We included the fixed effects of species (PS: *P. siculus* or PM: *P. muralis*), habitat (Ur: urban or Sn: semi-natural), and sex (M: male or F: female), with an interaction between species and habitat. For the first 3 models, we also included the fixed effect trial number (1–5), and the random effects lizard identification (a code assigned to each individual), day (1–42), and site (urban 1 and 2 or semi-natural 1 and 2). All significant results are highlighted in bold

1) Interaction with the barrier $N_{obs} = 1,245$				
Fixed effects	β	SE	z	P
Intercept (PM, F, Ur)	−1.138	0.357	−3.193	0.001
Species (PS)	0.017	0.316	0.053	0.958
Habitat (Sn)	−0.413	0.442	−0.933	0.351
Sex (M)	−0.512	0.218	−2.345	0.019
Trial number	0.072	0.053	1.365	0.172
Species (PS): Habitat (Sn)	−0.455	0.470	−0.968	0.333
Random effects	σ^2	SE		
Lizard ID	1.204	1.097		
Day	0.361	0.600		
Site	0.073	0.269		
2) Time interacting with the barrier $N_{obs} = 968$				
Fixed effects	β	SE	z	P
Intercept (PM, F, Ur)	1.706	0.399	4.274	<0.001
Species (PS)	0.157	0.255	0.615	0.539
Habitat (Sn)	0.528	0.543	0.972	0.331
Sex (M)	0.088	0.181	0.486	0.627
Trial number	0.090	0.026	3.449	0.001
Species (PS): Habitat (Sn)	−0.325	0.366	−0.887	0.375
Random effects	σ^2	SE		
Lizard ID	1.591	1.261		
Day	0.015	0.123		
Site	0.233	0.483		
Residuals	1.305	1.142		
3) Latency to detour the barrier $N_{obs} = 1,245$				
Fixed effects	β	SE	z	P
Intercept (PM, F, Ur)	3.370	0.360	9.348	<0.001
Species (PS)	0.402	0.318	1.263	0.207
Habitat (Sn)	0.049	0.482	0.101	0.920
Sex (M)	0.021	0.223	0.095	0.925
Trial number	0.029	0.026	1.117	0.264
Species (PS): Habitat (Sn)	0.042	0.459	0.092	0.926
Random effects	σ^2	SE		
Lizard ID	2.660	1.631		
Day	0.113	0.336		
Site	0.130	0.361		
Residuals	1.622	1.273		
4) Side bias $N_{obs} = 1,245$				
Fixed effects	β	SE	z	P
Intercept (PM, F, Ur)	0.801	0.089	9.038	<0.001
Species (PS)	−0.101	0.125	−0.812	0.417
Habitat (Sn)	0.145	0.112	1.293	0.196
Sex (M)	−0.103	0.086	−1.210	0.226
Species (PS): Habitat (Sn)	0.090	0.173	0.524	0.600

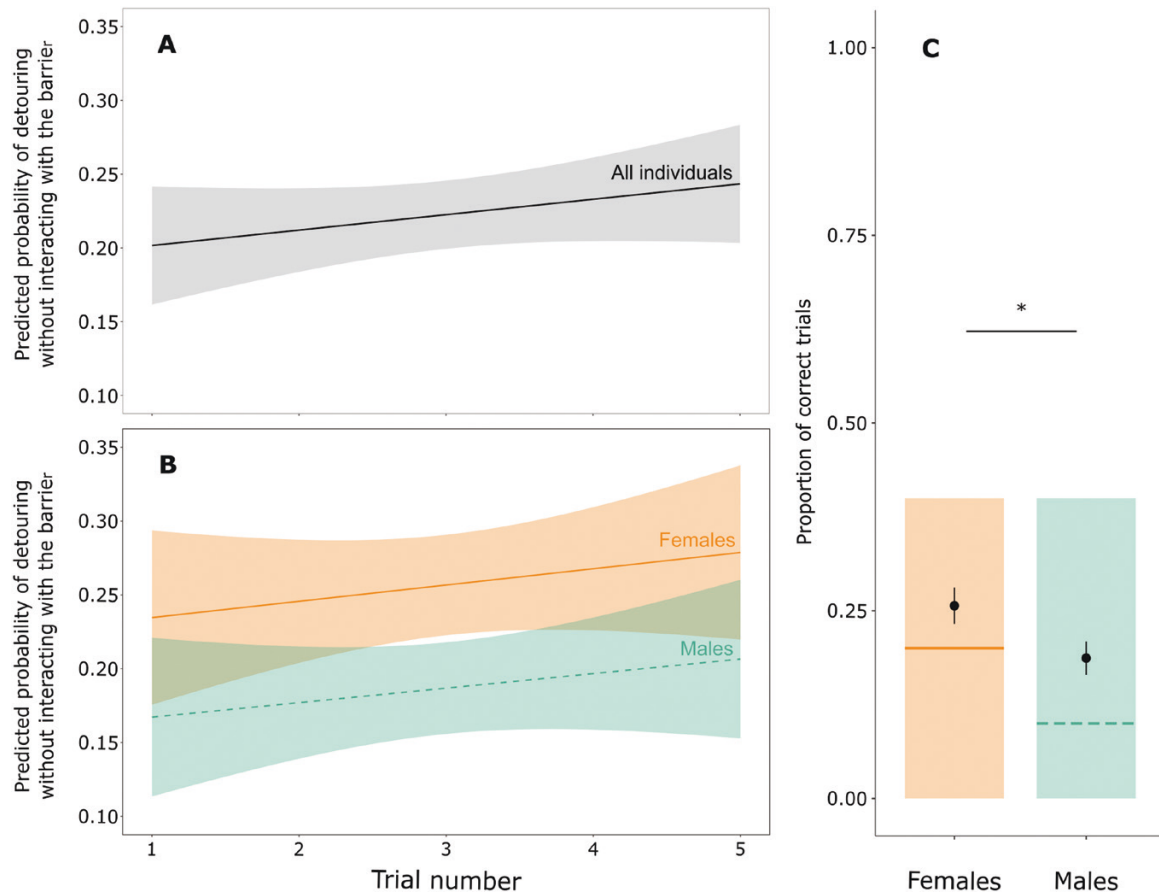


Figure 2. The predicted probability of detouring the barrier without interacting with it (= correct trial) over the 5 trials (A) for all individuals in the study and (B) for each sex; and (C) the proportion of correct trials overall between females (in orange with solid line) and males (in green with dashed line). In (A) and (B), we plotted the data with a linear model fit and 95% confidence intervals (shaded area), and in (C), we plotted the ranges from raw data, with the corresponding mean indicated with black dots, and the median indicated with horizontal lines. The asterisk indicates $P < 0.05$. Artwork and image assembly performed with Inkscape.

semi-natural), species, or sex. There were also no differences between any variables regarding the time taken to detour the barrier, or the side to which individuals detoured.

Our results show no differences in motor response inhibition across urban and semi-natural populations regardless of the species tested. Although most previous studies across taxa found populations in cities exhibiting enhanced cognitive abilities (Lowry et al. 2013; Sol et al. 2013; Griffin et al. 2017; Barrett et al. 2019; Lee and Thornton 2021), some also demonstrated no link (e.g., Kang et al. 2018; Thompson and Morand-Ferron 2019). There are multiple possible non-mutually exclusive explanations for our findings. First, the urban environment might not pose a more challenging environment in regard to motor response inhibition to the lizard species in our study, and consequently, no selection occurred on higher performance in these urban habitats (Sih et al. 2011). Adjusting to urban environments might not always require refined cognitive abilities but instead demand other modifications (Sol et al. 2013) such as in habitat usage, morphology, or locomotor performance (e.g., in urban *Anolis* lizard species; Winchell, Carlen, et al. 2018; Winchell, Maayan, et al. 2018). It is possible that selection in urban habitats acts on cognition in mammals and birds but not, or less so, in lizards because they face different challenges. The impact of urbanization can be highly dependent on the organism's ecology, size, and habitat requirements, but it could also depend

on the level of human–wildlife conflict with preventive measures often targeting certain species (Barrett et al. 2019; Klump et al. 2022). Thus, this could potentially select for better innovation, flexibility, and problem-solving skills in those species that must overcome such preventive measures to survive in urban environments. This stands in contrast to lizards, which are generally not considered nuisance species for humans. Moreover, the microhabitat features between urban and semi-natural environments might not be divergent enough to require higher inhibitory control for these lizards to live in urban environments (as also suggested in Kang et al. 2018 for cognitive abilities).

Second, as both Italian and common wall lizards have successfully existed near anthropogenic environments for a long time, lizards from urban and semi-natural habitats might not differ because they could have common adaptations to human-altered environments (Papp et al. 2015). Despite the proportion of successes in this one cognitive task not being very high for both of our species (similarly to another study on inhibitory control in different lizard species; Szabo, Noble, et al. 2019), and 48% of the lizards having failed to perform a single correct trial, it is unknown whether sympatric species that are unable to live in cities would perform even less proficiently at this task. The house mouse (*Mus musculus*), for example, has been sharing a habitat with humans for millennia, and its problem-solving skills increased across tasks

in subspecies that have coexisted with humans for longer (Vrbanec et al. 2021). Furthermore, it is well documented that Italian and common wall lizards from different native source populations can establish invasive populations in many novel locations (e.g., Ferner 2004; Podnar et al. 2005; Silva-Rocha et al. 2014; Speybroeck et al. 2016), which might point to an overall quick adjustability of these 2 species. To disentangle the relationship between urbanization and general cognitive flexibility, one would need to include further sympatric species that cannot cope well with anthropogenic environments and are noninvasive in future studies.

Finally, cognitive abilities might vary across an urban gradient, but we were unable to capture this variation with the detour task. For example, the house sparrow (*P. domesticus*) is commonly associated with anthropogenic environments and still urban individuals do not show better cognitive performance overall compared to rural birds (Papp et al. 2015). Instead, differences could only be detected in the hardest of 4 novel foraging tasks and the best problem solvers were urban birds with larger body mass (Papp et al. 2015). Moreover, Eurasian red squirrels (*Sciurus vulgaris*) show differences in solving a novel food-extraction task across an urban gradient, but their performance also depends on other factors, such as human disturbance and squirrel population size (Chow et al. 2021). Our semi-natural locations were located close to human settlements, which might have enough human disturbance to mask differences between urban and semi-natural lizard populations when compared to more remote wild populations (Baxter-Gilbert et al. 2019). Furthermore, it could be worth investigating locations that experienced recent dynamic urban change. Indian rock agamas (*P. dorsalis*) from suburban areas that had gone through extensive recent construction and buildup learned the location of a safe shelter faster compared to rural conspecifics (Batabyal and Thaker 2019). Thus, in future studies, it might be possible to unravel cognitive differences across an urban gradient if taking task difficulty and task variety into account and including other environmental variables or populations (Papp et al. 2015; Chow et al. 2021; Mazza and Guenther 2021).

Although we found no effect of urbanization on task performance, we found an effect of sex. In most studies on lizard cognition, sex is either not considered or only males are tested (e.g., Szabo, Whiting, et al. 2019), even in the context of urbanization (Kang et al. 2018; Batabyal and Thaker 2019). When sex is taken into account, cognitive studies yield different conclusions (e.g., Carazo et al. 2014; Szabo, Whiting, et al. 2019). The 2 studies that previously tested a detour task in lizards reported no sex differences (Szabo, Noble et al. 2019; Storks and Leal 2020), but their sample sizes were much smaller than in our study. Evidence for a sex difference in the context of urbanization was, however, found in a study with birds (common myna, *Acridotheres tristis*) in which rural females learned a task quicker than rural males (testing was limited to females in urban populations; Federspiel et al. 2017). It is possible that females differed from males in our task due to differences in their body condition and personality, especially because experiments took place during the breeding season. Females might be more cautious than males and performed better because they were more motivated to find their shelter or because they discovered the gap on the side of the barrier more efficiently. Nevertheless, given both sexes face similar challenges in their environment, and there are no studies directly testing differences in personality across

males and females in these species, further investigation is needed to better understand the sex difference we found.

Our results do not show lizards significantly improving with trial numbers, despite estimates hinting at this trend. The absence of improvement across trials may suggest that our experiment genuinely assessed motor self-regulation rather than individuals' learning speed (Kabadayi et al. 2017). Alternatively, the low number of repetitions of the task (only 5), could be insufficient to detect improvement. Those individuals who were unable to detour successfully without touching the barrier across trials showed an increase in the time they interacted with the barrier over trials. Striped field mice (*A. agrarius*) that failed to solve a cognitive test were also more persistent and interacted longer with the apparatus (Mazza and Guenther 2021). The increase in time spent interacting with the barrier might reflect lizards being more persistent when trying to leave the testing area as they had experienced escape in previous trials. Alternatively, this behavioural change might be related to an increase in frustration across trials due to their inability to perceive the transparent barrier. From our experiment, we are unable to determine why lizards that failed to detour increasingly interacted with the transparent barrier.

Both the time taken to detour and the side detoured were not related to sex, habitat, or species. This might indicate that neither morphological differences nor laterality were important for solving our task. In both species, fewer females displayed a clear side bias compared to males; and more males in semi-natural habitats, as opposed to urban males, exhibited a clear side bias. Overall, we found more individuals to prefer to detour the barrier to the left side, except for females living in semi-natural areas who showed a higher preference for the right. However, our LI and its strength were weak, likely because we tested individuals only 5 times, as we did not explicitly focus on laterality. Previous studies on common wall lizards found lizards to prefer to detour a mesh barrier to the left (Csermely et al. 2010), or to be instead more heavily biased to the right (Bonati et al. 2010), but both studies tested the lizards 10 times. To better understand these lateralized preferences, further studies would need to be conducted focusing on lateralized behavior in these lizard species.

In conclusion, we found no evidence for differences in motor response inhibition across lizards from urban and semi-natural populations. This can indicate that these urban lizards do not require enhanced inhibitory control to thrive in cities, that these species already have sufficiently high motor response inhibition to cope with anthropogenic environments, or that our task could not detect potential differences. To the best of our knowledge, our study is only the third to assess the impact of urbanization on cognitive performance in a reptile species (after Kang et al. 2018; Batabyal and Thaker 2019; both with lizards), and the first performed with wild-caught lizards in the field. We are, therefore, only just beginning to understand how urban lizards can cognitively cope with urban challenges. It is worth highlighting that when conducting studies involving immediately captured wild animals, essential information concerning their reproductive condition, dietary status, and overall health remains unavailable. Despite our efforts to minimize and account for these factors, it is important to recognize their potential influence on our results. We further suggest that future studies should also include non-urban sympatric species, a wider array of tasks

testing a range of cognitive abilities with increasing difficulty, or other ecological variables and environments, to better assess cognitive differences across an urban gradient. As we are currently facing a global biodiversity crisis (WWF 2020), with lizards also experiencing a decline worldwide (French et al. 2018; Doherty et al. 2020), it is encouraging that at least some species are able to cope and thrive in human-dominated landscapes, and it is promising what future research might unveil regarding the role of cognition in the success of urban animals.

Acknowledgements

We thank Sergio Luna for his assistance in the field and throughout the whole season. We also thank, for their input on protocols and general framework of the study, the Department of Behavioural Ecology from Bielefeld University, and those involved in the project CRC-TRR 212 “A novel synthesis on individualisation across Behaviour, Ecology and Evolution (NC³).” We also thank the 3 reviewers of our manuscript for their insightful comments. Finally, we thank all the lizards that participated in the study.

Funding

This study was funded by a “Bielefeld Young Researchers’ Fund” grant awarded by Bielefeld University (Germany) to I.D.M. under the code BYRF2021-DamasMoreira.

Conflict of Interest

None declared.

Authors’ Contributions

I.D.M., B.S., D.L., and B.A.C.—Conceptualization; I.D.M. and B.A.C.—Funding acquisition; I.D.M.—Protocol implementation; G.D., C.S.—Video scoring; I.D.M., B.S., G.D., and C.S.—Data analysis; I.D.M. and B.S.—Formal analysis and visualization; I.D.M.—Project administration; I.D.M., B.S., G.D., C.S., D.L., and B.A.C.—Writing, review & editing.

Ethical Statement

All the individuals tested in this study were free-living. All were caught from the wild, tested 5 times for a detour task in 1 single day, and released back at their exact capture site. Besides other reasons mentioned in the “Methods” section, one important motivation for conducting the experiment in the field was to maximize ethical considerations. By collecting and releasing the lizards on the same day, instead of transporting them to laboratory conditions for an extended period of time, we aimed to minimize stress and potential long-term reproductive impacts. Lizard captures and all experimental procedures were approved by the Department for Environmental and Nature Protection of the Croatian Ministry of Economy and Sustainable Development, under the permit number 517-10-l-1-21-3 of the class AP/I-612-07/21-48/83.

Supplementary Material

Supplementary material can be found at <https://academic.oup.com/cz>.

References

- Alberti M, Marzluff J, Hunt VM, 2017. Urban driven phenotypic changes: Empirical observations and theoretical implications for eco-evolutionary feedback. *Philos Trans R Soc B Biol Sci* 372:20160029.
- Amiel JJ, Tingley R, Shine R, 2011. Smart moves: Effects of relative brain size on establishment success of invasive amphibians and reptiles. *PLoS One* 6(4):e18277.
- Angel S, Parent J, Civco DL, Blei A, Potere D, 2011. The dimensions of global urban expansion: Estimates and projections for all countries, 2000-2050. *Progr Plan* 75(2):53–107.
- Audet JN, Ducatez S, Lefebvre L, 2016. The town bird and the country bird: Problem solving and immunocompetence vary with urbanization. *Behav Ecol* 27(2):637–644.
- Avery RA, 1978. Activity patterns, thermoregulation and food consumption in two sympatric lizard species (*Podarcis muralis* and *P. sicula*) from central Italy. *J Anim Ecol* 47(1):143–158.
- Barrett LP, Stanton LA, Benson-Amram S, 2019. The cognition of ‘nuisance’ species. *Anim Behav* 147:167–177.
- Batabyal A, Thaker M, 2019. Lizards from suburban areas learn faster to stay safe. *Biol Lett* 15(2):20190009.
- Bates D, Mächler M, Bolker BM, Walker SC, 2015. Fitting linear mixed-effects models using lme4. *J Stat Softw* 67(1):1–48.
- Baxter-Gilbert J, Riley JL, Whiting MJ, 2019. Bold New World: Urbanization promotes an innate behavioral trait in a lizard. *Behav Ecol Sociobiol* 73(8):105.
- Bonati B, Csermely D, López P, Martín J, 2010. Lateralization in the escape behaviour of the common wall lizard (*Podarcis muralis*). *Behav Brain Res* 207(1):1–6.
- Bueno-Guerra N, Amici F eds, 2018. *Field and Laboratory Methods in Animal Cognition: A Comparative Guide*. Cambridge: Cambridge University Press.
- CABI, 2016. *Podarcis sicula* (Italian wall lizard) [original text by Silva-Rocha IJ]. In: *Invasive Species Compendium*. Wallingford: CAB International. www.cabi.org/isc
- Candolin U, Wong B, 2012. *Behavioural Responses to a Changing World*. Oxford: Oxford University Press.
- Capula M, Luiselli L, Rugiero L, 1993. Comparative ecology in sympatric *Podarcis muralis* and *P. sicula* (Reptilia: Lacertidae) from the historical centre of Rome: What about competition and niche segregation in an urban habitat? *Ital J Zool* 60(3):287–291.
- Carazo P, Noble DWA, Chandrasoma D, Whiting MJ, 2014. Sex and boldness explain individual differences in spatial learning in a lizard. *Proc Royal Soc B* 281(1782):20133275.
- Chow PKY, Uchida K, Von Bayern AMP, Koizumi I, 2021. Characteristics of urban environments and novel problem-solving performance in Eurasian red squirrels. *Proc Royal Soc B* 288(1947):1–9.
- Coomes JR, Davidson GL, Reichert MS, Kulahci IG, Troisi CA et al., 2022. Inhibitory control, exploration behaviour and manipulated ecological context are associated with foraging flexibility in the great tit. *J Anim Ecol* 91(2):320–333.
- Csermely D, Bonati B, Romani R, 2010. Lateralisation in a detour test in the common wall lizard (*Podarcis muralis*). *Lateralality* 15(5):535–547.
- de Meester G, Baeckens S, 2021. Reinstating reptiles: From clueless creatures to esteemed models of cognitive biology. *Behaviour* 158:1057–1076.
- Diamond A, 2013. Executive functions. *Annu Rev Psychol* 64:135–168.
- Doherty TS, Balouch S, Bell K, Burns TJ, Feldman A et al., 2020. Reptile responses to anthropogenic habitat modification: A global meta-analysis. *Glob Ecol Biogeogr* 29(7):1265–1279.
- Elmqvist T, Andersson E, McPhearson T, Bai X, Bettencourt L et al., 2021. Urbanization in and for the Anthropocene. *Npj Urban Sustain* 1(1):1–6.
- Federspiel IG, Garland A, Guez D, Bugnyar T, Healy SD et al., 2017. Adjusting foraging strategies: A comparison of rural and urban common mynas (*Acridotheres tristis*). *Anim Cogn* 20(1):65–74.

- Ferner JW, 2004. The introduction of European and Italian wall lizards (*Podarcis muralis* and *P. sicula*; Reptilia, Lacertidae) into the United States. *J Ky Acad Sci* 65(1):1–4.
- Ficetola GF, Sacchi R, Scali S, Gentili A, De Bernardi F et al., 2007. Vertebrates respond differently to human disturbance: Implications for the use of a focal species approach. *Acta Oecol* 31(1):109–118.
- French SS, Webb AC, Hudson SB, Virgin EE, 2018. Town and country reptiles: A review of reptilian responses to urbanization. *Integr Comp Biol* 58(5):948–966.
- Friard O, Gamba M, 2016. BORIS: A free, versatile open-source event-logging software for video/audio coding and live observations. *Methods Ecol Evol* 7(11):1325–1330.
- Griffin AS, Tebbich S, Bugnyar T, 2017. Animal cognition in a human-dominated world. *Anim Cogn* 20(1):1–6.
- Johnson MTJ, Munshi-South J, 2017. Evolution of life in urban environments. *Science* 358(6363):eaam8327.
- Johnson-Ulrich L, Yirga G, Strong RL, Holekamp KE, 2021. The effect of urbanization on innovation in spotted hyenas. *Anim Cogn* 24(5):1027–1038.
- Juszcak GR, Bobrowska A, 2020. Assessment of problem-solving skills and inhibitory control in mice using water escape detour test. *Curr Protoc Mouse Biol* 10(3):1–19.
- Kabadayi C, Krashenninnikova A, O'Neill L, van de Weijer J, Osvath M et al., 2017. Are parrots poor at motor self-regulation or is the cylinder task poor at measuring it? *Anim Cogn* 20: 1137–1146.
- Kabadayi C, Taylor LA, von Bayern AM, Osvath M, 2016. Ravens, New Caledonian crows and jackdaws parallel great apes in motor self-regulation despite smaller brains. *R Soc Open Sci* 3:160104.
- Kang F, Goulet CT, Chapple DG, 2018. The impact of urbanization on learning ability in an invasive lizard. *Biol J Linn Soc* 123(1):55–62.
- Kark S, Iwaniuk A, Schalintzek A, Banker E, 2007. Living in the city: Can anyone become an “urban exploiter?”. *J Biogeogr* 34(4):638–651.
- Klump BC, Major RE, Farine DR, Martin JM, Aplin LM, 2022. Is bin-opening in cockatoos leading to an innovation arms race with humans? *Curr Biol* 32(17):R910–R911.
- Lee VE, Thornton A, 2021. Animal cognition in an urbanised world. *Front Ecol Evol* 9:1–20.
- Lenth RV, 2023. *emmeans: Estimated Marginal Means, aka Least-Squares Means (R package version 1.8.5)*.
- Leonard RJ, Pettit TJ, Irga P, McArthur C, Hochuli DF, 2019. Acute exposure to urban air pollution impairs olfactory learning and memory in honeybees. *Ecotoxicology* 28(9):1056–1062.
- Lowry H, Lill A, Wong BBM, 2013. Behavioural responses of wildlife to urban environments. *Biol Rev Camb Philos Soc* 88(3):537–549.
- Lyon P, 2020. Of what is “minimal cognition” the half-baked version? *Adaptive Behav* 28(6):407–424.
- Mazza V, Dammhahn M, Lösche E, Eccard JA, 2020. Small mammals in the big city: Behavioural adjustments of non-commensal rodents to urban environments. *Glob Chang Biol* 26(11):6326–6337.
- Mazza V, Guenther A, 2021. City mice and country mice: Innovative problem-solving in rural and urban non-commensal rodents. *Anim Behav* 172:197–210.
- Møller AP, 2009. Successful city dwellers: A comparative study of the ecological characteristics of urban birds in the Western Palearctic. *Oecologia* 159(4):849–858.
- Oskyrko O, Sreelatha LB, Silva-Rocha I, Sos T, Vlad SE et al., 2022. Molecular analysis of recently introduced populations of the Italian wall lizard (*Podarcis siculus*). *Acta Herpetol* 17(2):147–157.
- Palumbi SR, 2001. Humans as the world's greatest evolutionary force. *Science* 293(5536):1786–1790.
- Papp S, Vincze E, Preiszner B, Liker A, Bókony V, 2015. A comparison of problem-solving success between urban and rural house sparrows. *Behav Ecol Sociobiol* 69(3):471–480.
- Peig J, Green AJ, 2009. New perspectives for estimating body condition from mass/length data: The scaled mass index as an alternative method. *Oikos* 118(12):1883–1891.
- Podnar M, Mayer W, Tvrtković N, 2005. Phylogeography of the Italian wall lizard, *Podarcis sicula*, as revealed by mitochondrial DNA sequences. *Mol Ecol* 14(2):575–588.
- Preiszner B, Papp S, Pipoly I, Seress G, Vincze E et al., 2017. Problem-solving performance and reproductive success of great tits in urban and forest habitats. *Anim Cogn* 20(1):53–63.
- R Core Team, 2022. R: A Language and Environment for Statistical Computing. *R Foundation for Statistical Computing*, Vienna. <https://www.R-project.org>
- Ritchie H, 2019. *Urbanization*. Available from: <https://ourworldindata.org/urbanization>
- Shettleworth SJ, 2001. Animal cognition and animal behaviour. *Anim Behav* 61(2):277–286.
- Shochat E, Warren PS, Faeth SH, McIntyre NE, Hope D, 2006. From patterns to emerging processes in mechanistic urban ecology. *Trends Ecol Evol* 21:186–191.
- Sih A, 2013. Understanding variation in behavioural responses to human-induced rapid environmental change: A conceptual overview. *Anim Behav* 85(5):1077–1088.
- Sih A, Ferrari MCO, Harris DJ, 2011. Evolution and behavioural responses to human-induced rapid environmental change. *Evol Appl* 4(2):367–387.
- Silva-Rocha I, Salvi D, Harris DJ, Freitas S, Davis C et al., 2014. Molecular assessment of *Podarcis sicula* populations in Britain, Greece and Turkey reinforces a multiple-origin invasion pattern in this species. *Acta Herpetol* 9(2):253–258.
- Sol D, Lapiedra O, Ducatez S, 2020. Cognition and adaptation to urban environments. In: Szulkin M, Munshi-South J, Charmantier A editors. *Urban Evolutionary Biology*. Oxford: Oxford University Press, 253–267.
- Sol D, Lapiedra O, González-Lagos C, 2013. Behavioural adjustments for a life in the city. *Anim Behav* 85(5):1101–1112.
- Speybroeck J, Beukema W, Bok B, Van Der Voort J, 2016. *Field Guide to the Amphibians and Reptiles of Britain and Europe*. UK: Bloomsbury Publishing.
- Storks L, Leal M, 2020. Thinking outside the box: Problem-solving in free-living lizards. *Behav Ecol Sociobiol* 74:1–9.
- Szabo B, Noble DWA, Whiting MJ, 2019. Context-specific response inhibition and differential impact of a learning bias in a lizard. *Anim Cogn* 22(3):317–329.
- Szabo B, Noble DWA, Whiting MJ, 2020. Learning in non-avian reptiles 40 years on: Advances and promising new directions. *Biol Rev* 96(2):331–356.
- Szabo B, Whiting MJ, Noble DWA, 2019. Sex-dependent discrimination learning in lizards: A meta-analysis. *Behav Processes* 164:10–16.
- Thompson MJ, Morand-Ferron J, 2019. Food caching in city birds: Urbanization and exploration do not predict spatial memory in scatter hoarders. *Anim Cogn* 22(5):743–756.
- Vrbanc L, Matijević V, Guenther A, 2021. Enhanced problem-solving ability as an adaptation to urban environments in house mice. *Proc Royal Soc B* 288(1945):20202504.
- Williams RJ, 2019. *The Invasion Ecology of Common Wall Lizard (Podarcis muralis): Population Dynamics, Interactions and Adaptations*, PhD thesis. University of Leeds, UK.
- Winchell KM, Carlen EJ, Liam ARP, 2018a. Divergent habitat use of two urban lizard species. *Ecol Evol* 8:25–35.
- Winchell KM, Maayan I, Fredette JR, Revell LJ, 2018b. Linking locomotor performance to morphological shifts in urban lizards. *Proc Royal Soc B* 285:20180229.
- Wong BBM, Candolin U, 2015. Behavioral responses to changing environments. *Behav Ecol* 26(3):665–673.
- WWF. 2020. Living Planet Report 2020—Bending the curve of biodiversity loss. World Wildlife Fund.
- Zuur AF, Ieno EN, Elphick CS, 2010. A protocol for data exploration to avoid common statistical problems. *Methods Ecol Evol* 1(1):3–14.