Journal of Zoology

Journal of Zoology. Print ISSN 0952-8369

ORIGINAL RESEARCH

Do urban habitats induce physiological changes in Mediterranean lizards?

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Keywords
total evaporative water loss; metabolic rate; conservation physiology; reptiles; *Hemidactylus turcicus*; *Laudakia vulgaris*; urban ecology; lizards.

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Editor: Anthony Herrel

Received 4 January 2023; revised 7 May 2023; accepted 12 May 2023

doi:10.1111/jzo.13089

Abstract

Urban environments offer dramatically different habitats for wildlife compared with natural environments. They provide, for example, different levels of resource availability, anthropogenic night light, and microclimates (e.g., urban heat islands). For reptiles, increased temperatures in the city can lead to increased energetic demands and metabolic rates unless they change their morphology and physiology and adapt or acclimatize to the urban conditions. We explored differences in metabolic rate, evaporative water loss, and body size of two lizard species – rock agamas (*Laudakia vulgaris*) and Mediterranean house geckos (*Hemidactylus turcicus*), from urban habitats and nearby natural open areas. When tested in the lab, we expected to identify physiological adaptations resulting in decreased metabolism in urban individuals. Both species had similar body lengths and masses at both habitat types, suggesting any differences in costs and benefits between urban and natural environments do not affect their overall size or body condition. In the laboratory, metabolic rates were similar in individuals from both habitats for both species, indicating no long-term adaptations in this trait. However, urban geckos (but not agamas) had higher evaporative water loss than conspecifics from more natural habitats. This may suggest different compositions of epidermal lipids affecting the gecko skin's resistance to evaporation between the habitats. Overall, our results highlight different elements of the urban environment that might affect reptiles. However, the differences between species urge caution in interpreting the results to other species and locations. With increasing urbanization worldwide, understanding when and to what degree local adaptations can occur can help us predict reptile species distribution and survival in light of future anthropogenic changes.

Introduction

Urbanization has profound effects on wildlife. In addition to the direct habitat loss, processes such as construction and structural simplification of vegetation (removal of woody plants, leaf litter, and other microhabitats) often reduce the suitability of the remaining areas for wildlife (Marzluff, 2001; McKinney, 2008). Moreover, the urban environment offers different microclimates (e.g., urban heat islands), resource availability, anthropogenic night-light levels, exposure to pathogens, predation risk, and inter- and intraspecific interactions than the natural environment (Alberti, 2015; Bradley & Altizer, 2007; Foltz et al., 2015; Slabbekoorn & Ripmeester, 2008). Animal responses to urban environment characteristics involve behavioral, morphological, and physiological changes (Alberti, 2015). Most of our knowledge of such changes comes from birds and mammals (French et al., 2018). Despite more research in recent years, our understanding of reptile species' physiological responses to urban habitats is still in its infancy (French et al., 2018; Perry et al., 2008; Putman & Tippie, 2020).

As reptiles are ectotherms, temperature is among the most critical abiotic characteristics of their environment. In cities, the urban heat island effect can lead to up to 5°C higher temperatures in urban habitats than in the surrounding natural area (Thawley et al., 2019). Such thermal differences can drastically affect reptiles. Environmental temperature greatly influences ectotherm body temperature, metabolic rates, evaporative water loss, and activity seasons and hours (Meiri et al., 2013; Yue et al., 2012), which in turn affect life history traits and energy budgets. The urban heat island effect was shown to lead to physiological modifications including higher thermoregulatory effectiveness (Battles & Kolbe, 2019) and increased heat tolerance, linked to rapid evolutionary adaptations in urban environments (Campbell-Staton et al., 2020). Metabolic rates of

terrestrial ectotherms also increase in response to climate change (Seebacher et al., 2015). Thus, understanding the effects of increased environmental temperatures in cities can be of great importance for future reptile conservation both in and out of urban habitats.

Water availability can significantly restrict animal activity and distribution, at times, even more than temperatures (Carneiro et al., 2017; Kearney et al., 2018). Water availability in cities might increase due to year-round irrigation (Shochat et al., 2006), which might be especially significant in seasonally dry regions such as the Mediterranean. Stable water availability in the city was suggested to support a higher population density and lead to larger body size in urban *Lophognathus temporalis* compared with more natural habitats (Iglesias et al., 2012). However, increased moisture was also suggested as a mechanism enabling increased parasite infection in the city (Thawley et al., 2019).

Urban habitats may present further challenges and opportunities for reptiles. Artificial substrates can serve as preferable perching sites or refuges for urban lizards (French et al., 2018). Increased night light in the city can affect reptiles positively and negatively (Maurer et al., 2019). It can disrupt natural day–night cycles, which can modify hormone secretion affecting metabolism, body mass, and energy expenditure (Ouyang et al., 2018). It can affect activity patterns, allowing diurnal species to prolong their activity time (Perry & Fisher, 2006). Night light may also attract invertebrates – increasing food availability for reptiles. However, the great attraction may also lead to increased competition, novel interspecific interactions, and greater predation risk (Perry et al., 2008). Indeed, reptiles in urban habitats were shown to experience increased predation pressure from domestic pets, invasive species, and native predators (French et al., 2018; Purger et al., 2022). They also face novel diseases and increased parasite loads in more human-dominated habitats (Bradley & Altizer, 2007; Lazić et al., 2017). Thus, urbanization represents a net of complex factors that may affect wildlife in various ways.

Persisting under different environmental conditions may lead to changes in animal physiology and morphology (McDonnell & Hahs, 2015). As reptiles' metabolic rate is linked to environmental temperatures, increased temperatures in the city may lead to increased metabolism and evaporative water loss (Chejanovski & Kolbe, 2019; Nowakowski et al., 2018). However, constant exposure to urban conditions may induce long-term physiological or morphological changes leading to shifts in individuals' thermal performance curves (Campbell-Staton et al., 2020; Nowakowski et al., 2018). Local adaptation to urban conditions could result in decreased metabolic rates at high temperatures, which can be favorable in cases of limited food availability due to reduced arthropod abundance (Fenoglio et al., 2020) or increased conspecific competition (Battles et al., 2013). Urban conditions can also lead to behavioral changes, for example, changing activity times, which could dampen the need for physiological and morphological changes (Buckley et al., 2015).

We tested the physiology of reptiles by comparing the metabolic rate and evaporative water loss of of two lizard species, *Hemidactylus turcicus* and *Laudakia vulgaris*, from both urban and nearby natural environments, under laboratory conditions. We further compared body length and mass. The Mediterranean house gecko, *H. turcicus*, is an insectivorous nocturnal species (Bar et al., 2021) known to be attracted to artificial light sources for feeding (Punzo, 2001). Their home range is very small, with distinct genetic differences found between populations only 100 m apart (Trout & Schwaner, 1994). The rock agama, *L. vulgaris*, is a sedentary, diurnal, omnivorous lizard (Bar et al., 2021). Males' and females' home ranges rarely reach 500 m^2 (Loman et al., 2013). Both species are common and abundant throughout Israel (Bar et al., 2021). Geckos are extremely common in cities (Bar et al., 2021), perhaps since biblical times (Proverbs 30: 28), and agamas are known to be living in human settlements in Israel for more than 40 years (authors' personal observations) and potentially much earlier (Biton et al., 2021). Living under urban conditions, these species may have developed physiological and morphological changes for more efficient metabolism. Thus, if local physiological changes to the urban environment occurred, we expected to find reduced metabolic and water loss rates compared with conspecifics from natural habitats when tested under similar conditions. Similar rates would indicate no local adaptations to traits measured (the most parsimonious explanation). Alternatively, it could suggest that any potential physiological differences between the habitats are either temporal and plastic (rely on physiological plasticity) and cease under similar (lab) conditions, or that individuals behave differently in urban and natural habitats, thus compensating behaviorally for the different conditions without the need to change their physiology.

Materials and methods

Capture sites

We captured a total of 23 Mediterranean house geckos, *H. turcicus*, and 19 rock agamas, *L. vulgaris*, by hand in an urban habitat and a nearby natural habitat in two regions in central Israel: Tel-Aviv and Rosh Ha'Ain. Both are Mediterranean climates, characterized by a dry summer (June–October) with no rainfall and a short, cooler, rainy winter. We captured animals between October 27 and November 25, 2021 and on December 21, 2022, in Tel Aviv, and between June 1 and August 9, 2022, in Rosh Ha'Ain. The urban site in Tel Aviv was in and around the Zoological Garden of Tel-Aviv University (32.112N, 34.808E), and the natural site was an open area 2 km to the north (32.130N, 34.802E). In Rosh Ha'Ain, the urban sites were two small urban parks and playgrounds (32.092N, 34.961E, and 32.099N, 34.963E) for agamas and a small urban park (32.095N, 34.966E) for geckos. Open areas were in Rosh Ha'Ain Forest 2.3 km south of the urban site (32.077N, 34.973E) for geckos and a forest 2 km east of the urban site (32.097N, 34.984E) for agamas. Given the species' small home ranges, we assume that we sampled different populations with limited gene flow between them. We captured individuals under permit #42875 from the Israel Nature and Parks Authority and brought them to the Zoological Garden at

Tel-Aviv University. They were kept in individual terraria (302 × 196 × 147 mm and 460 × 302 × 165 mm for geckos and agamas, respectively) at a 12–12 light–dark cycle and a constant temperature of 28°C (± 1°C) for 6–24 days (median: 9 days) before being measured (except one gecko that was measured after 33 days). Individuals were fed crickets up to three times a week and had free access to water. All applicable institutional guidelines for the care and use of animals were followed. Protocols for animal maintenance and experimental treatments were conducted following the ethical guidelines for animal research established and approved by the Tel Aviv University Committee for the Ethical Care and Use of Animals in Experiments (Authorization Number IL-04-21-071 and 18 616). All animals were released unharmed within meters of their places of capture (using GPS locations) within days after experiments ended.

Metabolic rate and evaporative water loss

Before entering the metabolic chamber, individuals were weighed using an analytic scale (Sartorius, Goettingen, Germany) to the nearest 1 mg and measured (snout-to-vent length; SVL) using a Mitutoyo ABSOLUTE Digimatic calliper. Individuals were deprived of food for 4 days before experiments to allow standard measurements in a postabsorptive state. We measured resting metabolic rates (RMRs) and total evaporative water loss (TEWL) of all individuals. Each individual was measured for 24 h in a dark, isolated metabolic chamber (50 and 1400 mL for geckos and agamas, respectively) connected to a constant flow of CO_2-free dry air at a flow rate of 100 mL/min (FB8-flow bar, Sable Systems, Las Vegas, NV, USA). The chamber was placed inside an incubator (Thermo Fisher Scientific, Waltham, MA, USA) at 30°C and monitored by an IR camera. An empty chamber of the same size (50 or 1400 mL), with a constant air flow of 100 mL/min, was used as a reference baseline. Air exiting the chambers flowed through a multiplexer (RM-8, Sable Systems) into a LICOR LI-7000 CO_2/H_2O analyzer (LICOR, Lincoln, NE, USA). Baseline was measured every 30 min for 7 min. For recording the data and analysis, we used Sable Systems Expedata version 1.9.20 and the equations (11.4) of Lighton (2008). We calculated the mean rate of carbon dioxide production (mL/min) and the mean rate of water loss during 30 min when the animal was resting between 2:15–4:00 and 5:00–8:20 for agamas and geckos, respectively. Carbon dioxide production was calculated based on a respiratory quotient of 0.8, estimated for a postabsorptive state, and then log-transformed. EWL was calibrated using a linear calibration curve created by injecting microliter amounts of water into a stream of CO_2-free dry air passing through the empty metabolic chamber under the same experimental temperature and integrating the area under the resulting H_2O trace. During the measurement, evaporative water loss and CO_2 were simultaneously recorded by Expedata, and EWL was later corrected following the calibration to μL/min, then log-transformed.

Differences in RMR [log CO_2 production (in mL/min)] and evaporative water loss [log H_2O (μL/min)] among individuals were tested using linear mixed models for each species. The fixed effects in these models were habitat type (urban or natural) and log-transformed body mass (both metabolic rate and total evaporative water loss scale allometrically with body mass; Le Galliard et al., 2021). The random factor was the region (Tel Aviv or Rosh HaAin). Preliminary analysis (linear mixed models including sex as a fixed factor) showed no significant differences between males and females in the measured parameters. We therefore excluded sex from the models reported here. SVL and body mass (both log-transformed) differences between urban and natural sites were tested using linear mixed models for each species. The fixed effects in these models were habitat type (urban or natural) and sex, and for body mass, also log SVL to account for size differences. The random factor was the region (Tel Aviv or Rosh HaAin).

Results

We did not find any significant differences between habitat types in body length or mass. Agamas from both habitats had similar lengths ($t = -1.53$, $P = 0.145$; see Table 1 for mean ± SE) with no significant differences between males and females ($t = 1.53$, $P = 0.145$). Log-transformed body mass increased significantly with (log) SVL ($t = 5.88$, $P < 0.001$). Male agamas were significantly heavier than females relative to their SVL ($t = 2.29$, $P = 0.037$). However, no significant difference in mass was found between agamas from the city and nearby natural habitat after SVL was controlled for ($t = -1.97$, $P = 0.067$). Urban and natural geckos also had similar body lengths ($t = 1.44$, $P = 0.17$; Table 1) and masses corrected for SVL ($t = -1.47$, $P = 0.16$) in both habitats. Male geckos had similar body lengths as females ($t = -3.16$, $P = 0.06$) and similar body masses ($t = 1.73$, $P = 0.1$). Masses (log-transformed) increased significantly with (log) SVL ($t = 5.26$, $P < 0.001$).

Resting metabolic rates, measured by (log) CO_2 production rates, significantly increased with (log) body mass ($t = 6.74$, $P < 0.001$ and $t = 3.4$, $P = 0.003$ for agamas and geckos, respectively) but did not differ between habitat types in either species ($t = 0.68$, $P = 0.51$ and $t = 0.47$, $P = 0.65$ for agamas and geckos, respectively; see Table 1). Total evaporative water loss significantly increased with (log) body mass in agamas but not in geckos ($t = 3.54$, $P = 0.003$ and $t = 2.02$, $P = 0.06$ for agamas and geckos, respectively; Fig. 1). However, water loss was significantly higher for urban geckos than for individuals from a nearby natural area ($t = 2.8$, $P = 0.01$; Table 1 & Fig. 1). Agamas showed no significant difference in evaporative water loss between urban and natural sites ($t = 1.36$, $P = 0.2$; Table 1 & Fig. 1).

Discussion

For the most part, we found no significant differences between individuals from urban and natural habitats in the parameters measured in agamas and geckos. Both agamas and geckos had similar body lengths and body masses [and thus also similar body condition, which is often evaluated based on body mass and length (Sion et al., 2021)] and metabolic rates in both habitat types. However, urban geckos, but not agamas, lost

Table 1 Results (means ± SE) for body mass (g), SVL (mm), metabolic rate (CO_2 production, μL/min), and water loss (μL/min) for agamas and geckos from the natural and urban sites, and for males and females

	Sample size	Body mass (g)	SVL (mm)	CO_2 production rates (mL/min)	Water loss (μL/min)
(A) Agamas					
Natural	10	64.2 (±6.5)	107.2 (±4.0)	0.04 (±0.005)	0.19 (±0.02)
Urban	9	49.4 (±3.9)	100.3 (±2.8)	0.034 (±0.002)	0.18 (±0.02)
Male	14	61.6 (±4.9)	106.0 (±3.1)	0.039 (±0.003)	0.20 (±0.02)
Female	5	44.6 (±4.5)	98.3 (±3.1)	0.032 (±0.001)	0.13 (±0.01)
(B) Geckos					
Natural	9	2.5 (±0.12)	46.1 (±0.84)	0.0033 (±0.0002)	0.027 (±0.003)
Urban	14	2.5 (±0.18)	46.7 (±0.94)	0.0034 (±0.0002)	0.038 (±0.003)
Male	12	2.3 (±0.15)	44.9 (±0.89)	0.0034 (±0.0002)	0.033 (±0.003)
Female	11	2.7 (±0.17)	48.2 (±0.64)	0.0033 (±0.0002)	0.034 (±0.004)

Significant differences were found between male and female agamas' body mass, and between natural and urban geckos' water loss.

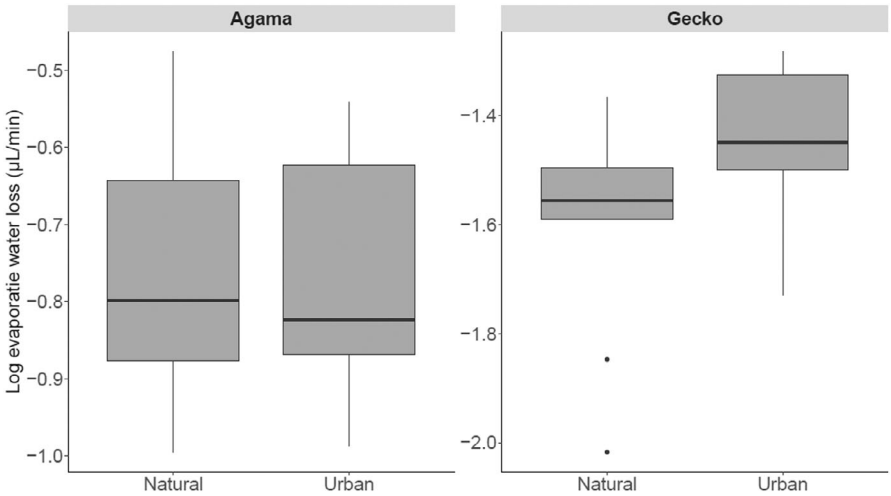

Figure 1 Log total evaporative water loss rate of agamas (19) and geckos (23) from the natural sites compared with the urban sites. Lines are medians, boxes cover 25th–75th percentiles ±1.5 interquartile range and outliers. Water loss was significantly higher for urban geckos than natural ones. No significant difference was found for the agamas.

significantly more water than their conspecifics from outside the city. The different responses of the two species that are phylogenetically distinct and differ from one another in many ways including size, activity times, and diets, call for caution when generalizing urbanization effects on reptiles. These could vary not only between species but also across different locations and cities.

Urbanization effects on body condition in reptiles seem to vary, with some species showing better body condition (Chejanovski et al., 2017), some similar (Thawley et al., 2019), and others worse body condition (Lazić et al., 2017) in urban compared to natural habitats. Foraging success and food availability in the city depend on various factors such as arthropod abundance and inter- and intraspecific competition (Battles et al., 2013; Fenoglio et al., 2020). It may further be affected by attributes such as the presence of invasive species (Suarez et al., 2000), urban parks management, vegetation (Philpott et al., 2014), or different predation pressures (Amo et al., 2007). Our results suggest that, all things considered, foraging success appears to be similar in both habitats for both species.

Metabolic rates increased significantly with (log) body mass but did not vary between individuals from the two habitat types in either species. These results can have several explanations involving internal and external factors. First, environmental conditions in urban habitats may not be different enough to induce local adaptations in metabolic rates. Many studies found that reptiles belonging to different populations or species, inhabiting different habitats, nonetheless, possess similar temperature-related traits (e.g., Angilletta et al., 2013; Cruz et al., 2009; Van Damme et al., 1990). For example, metabolic rates in Sinai fan-fingered geckos (*Ptyodactylus guttatus*) were similar in individuals from the north- and south-facing slopes, differing in their microclimate conditions (Schwarz et al., 2022) or between populations from arid and Mediterranean habitats (Schwarz, 2023). The fact that we found no differences in metabolic rates under similar conditions in the lab may suggest that no physiological or morphological

adaptations had occurred in this trait in response to urbanization. Instead, these species may rely on plasticity to adjust their metabolism to their environment. Better understanding of when local adaptations do occur can help predict what species can thrive in human-dominated habitats (Winchell et al., 2020).

In addition to physiological changes (plastic or adaptive), animals can change their behavior to thermoregulate (Clusella-Trullas & Chown, 2014; Kapsalas et al., 2016). Many lizard species shift their activity times or change microhabitats and substrates to thermoregulate (Clusella-Trullas & Chown, 2014). For example, Southern tree agamas (*Acanthocercus atricollis*) often use anthropogenic substrates for basking and sheltering, changing their orientation throughout the day and over seasons to regulate their body temperature (Singh et al., 2021). Urban reptiles may also change their activity times to thermoregulate or to seize new opportunities (Amadi et al., 2021; Perry et al., 2008). For example, the diurnal red-headed rock agama (*Agama agama*) was reported to show nocturnal activity in a city in Gabon around neon lights (Pauwels et al., 2004), and in suburban areas in Nigeria (Amadi et al., 2021), to thermoregulate and forage. Activity time shifts in response to urbanization are known from other taxa as well. Many urban mammal species, for example, were found to switch to more nocturnal activity to avoid human interferences (Gaynor et al., 2018). Further, urban European robins (*Erithacus rubecula*), for instance, were shown to sing at night to avoid noise pollution during the day (Fuller et al., 2007).

Other explanations for the lack of urban/natural differences in metabolic rates may relate to our experimental setup. First, individuals were measured after being kept in captivity for several days (6–24 days) under similar conditions. Physiological changes in urban habitats might be flexible and easily reversible under different conditions (McDonnell & Hahs, 2015). Such plasticity in metabolic rates, as well as other traits, can limit the need for local adaptations. Second, despite the small home ranges known for both agamas and geckos, the individuals we sampled may belong to populations with substantial gene flow between them (Schwarz et al., 2022). Future studies examining populations at greater distances can shed light on this issue. Third, had we tested animals at a temperature higher than 30°C, which may be more frequently experienced in the city, we may have revealed differences in temperature-dependent traits between the habitats (see Bodensteiner et al., 2021). We refrained from testing the animals at higher temperatures so as not to put them at greater discomfort.

We found that urban geckos (but not agamas) lost significantly more water than their counterparts from natural areas (Fig. 1) when tested at 30°C. This can suggest adaptation to urban habitats. Alternatively, plastic changes in epidermal lipid contents (see below) that may be induced by the environment but only reversible after multiple moulting cycles could cause such differences with no adaptive changes occurring. Water availability is higher in cities thanks to artificial watering (Parris & Hazell, 2005). Thus, water is less of a limiting factor in urban habitats, and animals can afford increased water loss. Urban habitats are also more stable and predictable than nearby natural environments (Shochat et al., 2006; Vardi & Berger-Tal, 2022). Indeed, Sannolo et al. (2020) suggested that exposure to extreme and unpredictable climate conditions may drive decreases in water loss more than mean environmental temperature or humidity. Thus, urban geckos' increased water loss might be in response to long-term stable conditions rather than simply the increased temperatures and water availability. Agamas, however, as diurnal heliotherms, might be more susceptible to water loss than nocturnal species such as house geckos (Lahav & Dmi'el, 1996) and did not show significant differences in water loss between habitat types. This may indicate that urban habitats present different challenges and opportunities to different reptile species, which may lead to different responses and adaptations.

Epidermal lipid content can greatly affect the skin's permeability and resistance to water evaporation (Roberts & Lillywhite, 1980). If the production or maintenance of high epidermic lipid content is costly, limiting it in areas with greater water availability, such as urban habitats, may be beneficial. We thus suggest that reduced selection pressure for water retention in urban habitats allows individuals to invest less in synthesizing epidermal lipids, leading to decreased lipid content that underlies urban geckos' propensity to increased water loss. Western fence lizards (*Sceloporus occidentalis*), acclimated to humid conditions, showed higher cutaneous evaporative water loss (water loss across the skin) than ones acclimated to dry conditions (Weaver et al., 2022). Kattan and Lillywhite (1989) found similar trends in green anoles (*Anolis carolinensis*) and showed that anoles acclimated to dry conditions lost less water even 10 days after experiencing humid air. The authors suggested that the acclimation could be reversed after skin-shedding but presented contradicting results for this claim. One of our urban geckos shed its skin (Vardi et al., 2023) and was measured a few weeks later. This individual still had increased evaporative water loss compared to geckos from the natural sites (0.052 μL/min compared with an average of 0.027 for all geckos from the natural sites). This suggests that a single molt event may not be sufficient to alter skin permeability, and such potential plastic changes in response to urbanization may last several weeks.

Overall, our results demonstrate different responses to urbanization by our study species, with geckos, but not agamas, showing increased water loss in cities. This highlights that water availability might be an important factor for reptile physiological changes and should be further explored. It further highlights the need for more studies on various reptile species representing different families with differing life history, morphology, ecology, thermal biology, and evolutionary history (Putman & Tippie, 2020). Indeed, species' responses and survival in urban habitats may vary depending on their evolutionary history (Sih et al., 2011) as well as their recent history in urban environments (Vardi et al., 2021). These responses may further vary based on diets, morphology, scale characteristics (Putman et al., 2019), or activity times. Furthermore, different aspects of the urban environment may exert different pressures on the studied species. However, we did not find significant differences in size or metabolic rates between urban and natural environments. The similar metabolic rates we found suggest that urban reptiles may rely on plastic physiological responses or behavioral changes to deal with urban conditions. Moreover,

the similar body sizes (length and mass) suggest that agamas and geckos in urban habitats may not experience different overall costs. Still, with increasing urbanization worldwide, better understanding the different effects of urbanization on different species is essential for future reptile conservation and understanding urbanization effects in both space and time.

Acknowledgments

We would like to thank Simon Jamison, Tao Liang, Yan-Ronen Liberman, Anuj Shinde, and Eli Finarov for their assistance in the field. We also thank Berry Pinshow for the fruitful discussion and two anonymous reviewers whose helpful suggestions greatly improved our manuscript. RV is partly supported by the Alexander and Eva Lester postdoctoral fellowship.

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