

Urban heat island mitigation strategies and lizard thermal ecology: landscaping can quadruple potential activity time in an arid city

Jeffrey W. Ackley¹ · Michael J. Angilletta Jr.¹ · Dale DeNardo¹ · Brian Sullivan² · Jianguo Wu³

Published online: 24 April 2015
© Springer Science+Business Media New York 2015

Abstract A global warming of 2 °C is predicted to drive almost half the world's lizard populations to extinction. Urban heat island (UHI) effects may further exacerbate the impacts of climate change on organisms that are sensitive to small changes in temperature. Currently, the Phoenix metropolitan region in Arizona, USA, is an average of 3 °C warmer than the surrounding desert. With continuing urbanization and climate change, thermal stress will become an increasingly important facet of urban ecology in coming decades. The main objective of our study was to investigate which landscaping styles and microhabitat variables can most effectively reduce the surface temperatures experienced by lizards. Using a bare lot as a control, we placed copper lizard models with data loggers in several vegetation and irrigation treatments that represent the dominant backyard landscaping styles in Phoenix (grassy mesic with mist irrigation, drip irrigated xeric, unirrigated native, and a hybrid style known as oasis). Our lizard models recorded 6915 estimates of potential body temperatures. We show that lizard activity time in summer was restricted to a few hours in un-irrigated native desert landscaping, while heavily irrigated grass and shade trees allowed for continual activity during even the hottest days. Shade, humidity, and sky view factor explained the majority of variation in temperature at a sub-meter scale. We suggest that maintaining the existing diversity of landscaping styles (as part of an ongoing UHI mitigation strategy targeted at humans) will be beneficial for lizards.

✉ Jeffrey W. Ackley
jwackley@asu.edu

¹ School of Life Sciences, Arizona State University, PO Box 874501, Tempe, AZ 85287-4501, USA

² School of Mathematical & Natural Sciences, Arizona State University, PO Box 37100, Phoenix, AZ 85069, USA

³ School of Life Sciences and School of Sustainability, Arizona State University, PO Box 874501, Tempe, AZ 85287-4501, USA

Keywords Landscaping · Lizards · Urban heat island · Thermal ecology · Ectotherms · Body temperature · Reptiles

Introduction

The suburbs of Phoenix, Arizona, USA, have been expanding into the Sonoran Desert at a rate of 1 km per year (MIPP 2000). This development process converts a highly reflective natural substrate into impervious urban surfaces with low solar reflectance and high heat storage capacity. The resulting urban heat island (UHI) represents a mean warming of 3 °C over the surrounding desert [with a substantial variance depending on where, how, and when temperatures are recorded (Brazel et al. 2007)]. Urban warming in Phoenix has doubled the yearly “misery hours” for humans (when the temperature-humidity index exceeds 38 °C) and increased heat stress on other organisms (Baker et al. 2002; Brazel et al. 2007; Ruddell et al. 2013). Air-conditioning can maintain indoor temperatures at desirable levels; however, compensating for a UHI has cost as much as US\$100 million per year (Akbari et al. 2001).

Strategies that mitigate the UHI effect differ in cost, effectiveness, and the scale at which benefits are realized. White paint and green plants on rooftops can reduce air temperatures within and above buildings (Kumar and Kaushik 2005). Vegetation provides additional benefits of evaporative cooling and shade, especially when irrigated regularly. Certain backyard landscaping strategies can reduce surface temperatures by over 10 °C during the day, creating a heterogeneous thermal landscape that varies more within Phoenix than between the city and the surrounding desert (Brazel et al. 2007). The cooling effect of a large park can extend several hundred meters beyond its border; Phoenix’s Tree and Shade Master Plan—a proposal to mitigate Phoenix’s UHI—aims to double canopy cover (from 12 to 25 %) by 2030, primarily by planting trees on public lands (Bowler et al. 2010; Chow et al. 2012).

Since private residences constitute the largest type of land use in Phoenix, individuals and local communities can substantially reduce the UHI through landscaping. Most residences are part of private homeowner’s associations (MIPP 2000), which control large areas of communal landscaping and dictate the type of vegetation that individuals can have on their own properties. Plant diversity is higher in wealthy areas than poor neighborhoods (Hope et al. 2003), and for every increase of \$10,000 in median household income, the mean surface temperature decreases by 0.3 °C (Jenerette et al. 2007).

Mitigation strategies targeted at improving human comfort and energy use often involve planting vegetation, but the consequences for other organisms remain uninvestigated. In particular, reptiles—a cultural icon of desert life—regulate populations of arthropods, mammals, and birds, including species considered as pests. Warming caused by urban development could have dire implications for these ectotherms. Many reptiles prefer body temperatures that enhance physiological performance, which limits their activity in space and time (Adolph 1990; Christian et al. 1983; Grant and Dunham 1988; Hertz et al. 1982). For most species of lizards, the best performance occurs at a body temperature just a few degrees below the lethal limit. Thus, an optimal microhabitat can become lethal with a small increase in temperature (Martin and Huey 2008). In summer, environments often exceed the lethal limit during midday, forcing lizards underground. Being active at a high temperature increases metabolic rate, and thus the need for energy (Angilletta 2009). Many lizards feed on arthropods that also require microhabitats with suitable microclimates. Thus, while urban lizards have the greatest need to feed during summer, they could have the fewest opportunities to do so. Recent models

showed that a warming of 2–3 °C can severely restrict activity (Buckley 2008; Kearney and Porter 2004), potentially resulting in the loss of 40 % of all lizard populations by 2080 (Sinervo et al. 2010). Strategies that increase the spatial and temporal frequency of suitable microclimates for lizards will likely promote their persistence.

Most UHI research has focused on broad scale urban climatology; little work has been conducted from an ecological perspective at small scales where organisms (including humans) experience heat (Baker et al. 2002). Thus, we compared microclimates within common types of urban landscaping. We predicted that cooler temperatures in mesic landscapes would increase the potential for summer activity by lizards in Phoenix. We also investigated which physical variables (shade, substrate type, humidity, etc.) had the greatest influence on microhabitat surface temperature. As we did not compare natural and urban sites or lizard populations, this work was not a direct investigation of UHI impacts on organisms. Our goal was to compare the thermal consequences of different residential landscaping patterns and water uses to determine the relative effectiveness of UHI mitigation strategies currently being employed, and their potential relevance for lizards.

Methods

Thermal physiology of lizards

We determined the thermal limits of motor function (a non-lethal proxy for thermal tolerance) and preferred body temperature in two of the three common urban lizard species in Phoenix: *Uta stansburiana* (Side-blotched Lizards, $N=14$) and *Urosaurus ornatus* (Ornate Tree Lizards, $N=7$). The varying sample sizes were due to *Urosaurus ornatus* being present at fewer locations and at lower abundances. Lizards from multiple urban and desert populations were captured using nooses, and housed according to Institutional Animal Care and Use Committee guidelines by veterinary staff. We did not observe a difference in thermal tolerance or preference between urban and rural populations (t-tests, all $P>0.05$). Lizards were given a minimum of two weeks to adjust to captivity and full spectrum lighting on a 12:12 cycle; and at least 48 h elapsed between all physiological tests. Our procedures followed those of Angilletta (2001) and Angilletta et al. (2002), with minor modifications described below.

Thermal tolerance limits were determined by placing lizards in plastic containers and partially submerging them in water baths. The procedure for maximum tolerable temperature was to heat each lizard gradually until it became immobile. Lizards were heated to 35 °C and then placed in a sealed plastic container (~12x12x10 cm) within a water bath set at 55 °C. After 3 min, the lizard was flipped on its back to check its righting response. If the lizard righted itself within two seconds, it was placed back into the container in the bath. This procedure was repeated every minute until the lizard was unable to right itself. At that point, its cloacal temperature was immediately recorded with a type-K thermocouple. The procedure for minimum tolerable temperature was identical, except that lizards were cooled to a body temperature of 20 °C before being placed in a bath set at 4 °C. Each lizard was randomly warmed or cooled first to avoid an artifact caused by the order of measurements.

We measured preferred body temperatures in artificial thermal gradients. Each gradient consisted of an acrylic box with an aluminum floor (250×40 cm). Hot or cold water was continuously circulated through a copper pipe welded under each end, resulting in a gradient of potential body temperatures between 18 °C and 43 °C. These extremes fall within the thermal

limits of locomotion, thus preventing animals from becoming incapacitated if they moved to the edges. Natural substrates can be modified by lizards, and were not used to ensure uniform exposure to the thermal gradient and reduce the occurrence of non-thermoregulatory behaviors. Uniform lighting was used for similar reasons, on the same 12:12 cycle used during captivity. On the evening before measurements, each individual lizard was placed in a gradient about three hours before the lights were turned off. On the following morning, lights were turned on at 07:00 h to stimulate activity. Cloacal temperatures were recorded with a type-K thermocouple every two hours, beginning at 09:00 h and ending at 17:00 h. Repeated handling at this frequency has no noticeable effect on the thermoregulatory behaviors of similar lizard species (Schuler et al. 2011). We did not fast animals before measurements because lizards often have food in their guts during activity; however, no food or water was provided in the gradients to discourage foraging behavior. We entered the room only when recording body temperatures. If we found a lizard trying to escape or showing signs of distress (e.g., running against the plastic, standing on hind legs, or panting with an elevated body), we placed it in the center of the gradient without recording its body temperature.

Estimating lizard body temperatures in different landscapes

We studied the thermal environments provided by different landscaping plots in North Desert Village: an experimental housing project owned by Arizona State University (Cook et al. 2004). This site represents the range of residential landscaping in Phoenix, within which a variety of socio-ecological interactions can be studied, such as the behavior and habitat use of desert lizards in an urban environment. In 2005, the barren common areas (~30×30 m) encircled by a ring of six houses were randomly assigned one of the four stereotypical landscaping styles found within Phoenix: 1) mesic, dense shade trees and mist-irrigated grass covering the entire plot; 2) oasis, a small patch of mist-irrigated grass, bare soil, and drip-irrigated bushes and trees; 3) xeric, drip-irrigated desert plants; and 4) native, un-irrigated local desert plants. Another housing cluster received no landscaping or irrigation, reflecting a common landscape found in backyards and undeveloped lots. All plots lie within 250 m of each other, making nutrients and rainfall similar among treatments. These landscapes are maintained by Arizona State University and residents may not modify the area.

To estimate the temperatures that lizards could attain in each plot, we used hollow copper models molded from live animals (Bakken 1992). Such models are used to integrate the parameters that determine an animal's body temperature, such as convection from airflow, radiation from the sun and nearby objects, and conduction between surfaces. The models estimate an index known as the operative environmental temperature, which we will refer to as the estimated body temperature. This index represents the temperature of a static animal in thermal equilibrium with its environment. Our estimates ignore thermal inertia, variations in posture, color change, evaporative cooling and metabolic heating. The latter two physiological processes have a negligible impact on the body temperatures of small lizards (Bakken 1992). Models were painted with Krylon No. 1314 All Purpose Platinum Spray Primer to achieve an absorbance of 82.9 % between 290 and 2600 nm (Peterson et al. 1993); this absorbance value lies within 5 % of most lizard species (Christian et al. 1996). A temperature logger (Maxim iButton® DS1921G, San Jose, CA, USA) was integrated into the design of each model as described in Bakken and Angilletta (2013).

To validate the models, we placed several on the ground next to a restrained lizard shortly after dawn. The lizard's body temperature was measured with a type-k thermocouple wire

inserted into the cloaca. As its body temperature increased from ~ 25 °C to 40 °C, the internal temperatures of the models were recorded simultaneously. Linear regression showed that the copper models captured approximately 96 % of the variation in the body temperature of the lizard and produced a slope of 1.06 and y intercept of -2.5 (perfect models would produce a slope of 1 and a y intercept of 0). Additional comparisons between lizards of both species and models of various sizes and colors on multiple substrates and in multiple conditions (e.g., full sun, dappled sun, and shade) yielded errors typically <1 °C, which is well within the 2 °C criteria used by Dzialowski (2005).

Using the validated models, we estimated lizard body temperatures in the various yard types at North Desert Village in June and July of 2012 during ~ 13 -h periods when at least some part of the landscape was exposed to direct sunlight. The Phoenix UHI is a year-round phenomenon, but is most pronounced during this period of long days, low wind, and few clouds (Brazel et al. 2007). June and July are also among the hottest months when lizard activity is most restricted. We only collected data on nearly cloudless days with minimal wind, and waited at least three days after the rare rainfall events during this season. Models were placed by walking a random distance in a random direction from the center of the circular plots. Model placement was stratified such that 10 were on the ground and three models were in a random type of vegetation, at a random height, and a random distance from the vegetation's trunk. The 10:3 ratio roughly reflects the portion of bare ground and vegetation in the plots. Vandalism prevented us from collecting data in multiple treatments simultaneously; on any given day, models were moved between the same two treatments every hour, using new sub-locations each time. Each treatment was measured four times over 10 days to achieve one of each possible pairwise combination of treatments. The models recorded temperature at 10-min intervals. Soil temperatures were recorded at depths of 15, 30, 60, and 90 cm using type-T thermocouple wires attached to a control unit (Campbell Scientific 21 \times Micrologger, Logan, Utah, USA). Copper models were not used as differing size, shape and coloration would not alter underground temperature readings.

To determine how microhabitats influence potential body temperatures at a sub-meter scale, we recorded distances to the nearest shade and vegetation, height above ground, type of substrate, sky view factor (the inverse of canopy coverage, using a handheld densitometer), and relative humidity for each model location. These data were collected separately from plot data, and only between 10:30 and 15:30 h when the thermal variance was relatively constant and rate of change in mean temperature was lowest. Approximately 30 locations were sampled in each landscaping treatment, except for the bare lot where the nearest shade and vegetation were outside the plot ($N=137$ among all plots).

Statistical analysis

From a lizard's thermal perspective, we tested whether the fixed effect of each plot's landscaping was different from all the other plots (rather than just different from the bare lot). This required fitting a generalized additive mixed model with cubic regression splines to potential lizard body temperatures in each landscape. Our model accounted for several sources of autocorrelation: temperatures recorded at nearly the same time, on the same day, and by the same copper model were similar to one another. Spatial autocorrelation was minimized by continuously moving copper models within and between plots. Changing sun angles and dappled shade patches further reduced the correlation between individual models during the hour in which they were stationary.

Following Zuur et al. (2009), we compared the fits of several models that differed in the structures of their random effects, such as adding unique error variances for each plot and copper model. We also compared a fixed error variance with one that increased exponentially with increasing Julian date and increasing time of day. Including corrections for date and time allowed us to run one test on the entire data set, rather than conducting separate comparison tests for each of the 10 days we compared landscaping types. The latter approach would have resulted in substantial alpha-inflation. Although these model additions did not affect our conclusions qualitatively, they produced a more likely model, as judged by the Akaike Information Criterion (AIC), and reduced the confidence intervals of the parameters, indicating the improved model fit warranted the additional complexity.

To determine which microhabitat characteristics had the most influence on temperature, plot was treated as a random factor, since we were now interested in explanatory variables at a finer scale. As we collected these data on fewer days and during a narrower daily time window, the best error structure was fixed rather than exponential and excluded the random effect of copper model. All microhabitat variables listed above and their likely interactions were treated as fixed factors. The highest order interactions were removed sequentially until we arrived at the model with the lowest AIC. All analyses were conducted using the R software package (CDT 2005).

Results

There was not a significant difference between the tolerance limits or mean preferred temperatures of the two lizard species we tested (t-tests, all $P > 0.05$) and their preferred temperature ranges were almost identical (see Table 1). The lower and upper quartiles of body temperatures selected in our thermal gradients were 26 °C and 38 °C. This preferred range lies well within the range of temperatures that permit movement; typically, lizards became immobile when their median body temperatures fell below 10 °C or rose above 45 °C. During calibration, the 176 temperature differences between live lizards and copper models averaged 0.49 °C, and ranged from -0.9 to +3.3 °C.

We recorded a total of 6915 estimates of lizard body temperature at North Desert Village. The potential body temperatures predicted by our statistical model differed among all landscapes ($P < 0.01$), but only the oasis and mesic plots were notably cooler than the bare plot on average (Fig. 1). Temperatures commonly exceeded 60 °C in all landscapes around midday, suggesting that thermal constraints on activity have a major impact on the ecology of lizards in Phoenix. In fact, temperatures within the preferred range (<38 °C) were recorded only during the first 2–3 h of daylight in the native, xeric, and bare landscapes. At any given time, the bare

Table 1 Preferred temperature ranges and tolerance limits of lizards

| Species (N) | Mean (SD) | Preferred range | Min tolerance (SD) | Max tolerance (SD) |
|-----------------------------|------------|-----------------|--------------------|--------------------|
| <i>U. ornatus</i> (7) | 31.8 (6.4) | 25.4–37.4 | 9.8 (1.1) | 44.9 (1.1) |
| <i>U. stansburiana</i> (14) | 32.6 (6.1) | 26.8–37.9 | 10.2 (1.3) | 46.4 (1.3) |

The mean and standard deviation (SD) of lizard body temperature (°C) in a thermal gradient were not significantly different between species ($P > 0.05$). We defined the preferred range as the central 75 % of observed voluntary body temperatures. Mean involuntary tolerance limits were defined as the thermal limits of lizard motor function, again no significant difference was found between species ($P > 0.05$)

plot offered only a narrow range of temperatures ($R^2 \approx 0.95$), probably because of its homogeneous topography (Sears et al. 2011). Native landscaping had slightly greater variation in temperature ($R^2 \approx 0.9$). The addition of irrigation (xeric: $R^2 \approx 0.8$), grass (oasis: $R^2 \approx 0.5–0.6$), and trees (mesic: $R^2 \approx 0.4–0.6$) further increased the variance of temperature (Levene's tests, all $P < 0.05$). Interestingly, the highest maximum temperatures were always found in the landscaped plots when compared to the bare plot (Fig. 2a).

The heterogeneity of temperature created by landscaping had major consequences for potential lizard body temperatures. Mesic landscaping offered the greatest opportunity for activity, having 65 % more area within the preferred range than the bare habitat (Table 2). Native, xeric, and oasis landscaping resulted in 5–15 % more area of preferred thermal habitat. The mesic landscape also maximized the potential duration of activity. If we assumed that a lizard could be active when at least one of the copper models fell within the preferred range of temperatures, lizards in the mesic landscape could have been active throughout the entire day. By contrast, lizards in the bare, native, and xeric plots could have been active for less than half of the day. Temperatures underground never exceeded the thermal limits of lizards, but did approach values that trigger high metabolic demands in the bare, native, xeric and oasis plots (Fig. 3). In the mesic plot, underground temperatures varied less and were almost 10 °C cooler at a given depth than in other plots.

Three microhabitat characteristics explained more than 50 % of the variation in estimated lizard body temperatures. Not surprisingly, temperatures were cooler in more humid locations and when closer to shade ($P < 0.001$ for both). Sky view factor and distance to shade interacted to determine body temperatures ($P < 0.001$); increasing sky view increased temperatures at locations in shade but decreased temperature at locations far from shade (Fig. 4). Substrate type, height above ground, and distance to vegetation did not significantly impact estimated body temperatures ($P > 0.05$ for all).

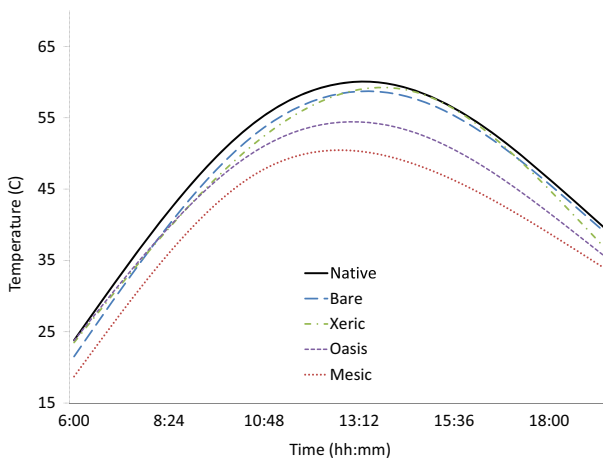


Fig. 1 Each landscaping style enabled lizards to achieve unique patterns of body temperature. The lines show the mean potential body temperatures predicted by our statistical modeling. Using almost 7000 data points, the 95 % confidence intervals are approximately equal to the line widths, thus visually discernible differences are statistically significant. Surprisingly, the native plot was warmer than the bare plot

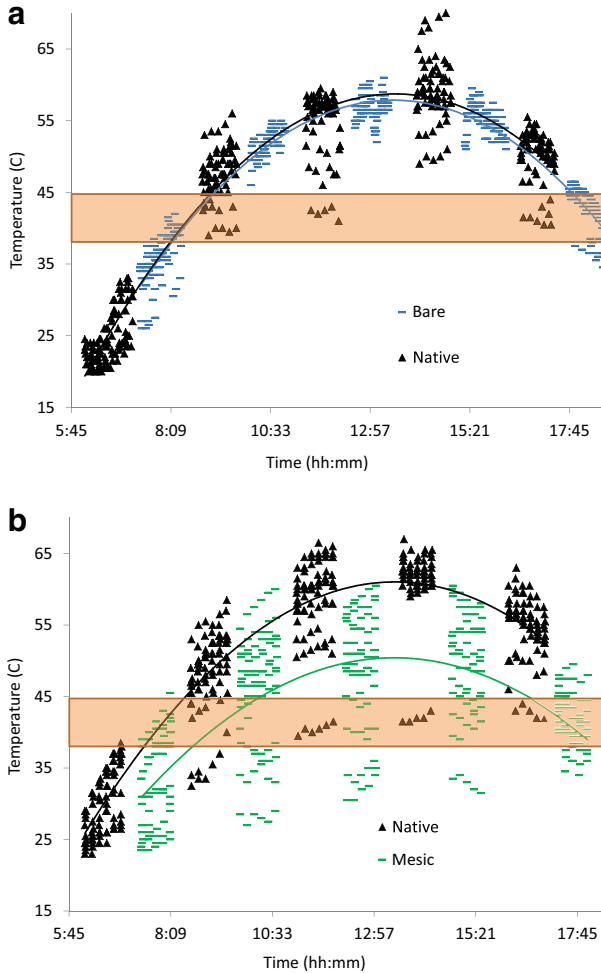


Fig. 2 **a** Un-irrigated native vegetation provided greater variation in potential body temperatures and higher maximum temperatures than bare ground. The orange rectangle indicates the temperatures that exceed a lizard's preferred range (26–38 °C) but fall below the upper limit for movement (45 °C). **b** Mesic vegetation provided even greater thermal variance and lower mean temperatures. Part of the mesic plot remained within the preferred range throughout the day. The mean temperature of the mesic plot remained preferable for approximately an hour longer than did the mean temperature of the native plot. Data depicted in panels **a** and **b** are not directly comparable, as they were recorded on different days

Discussion

Although the mean surface temperature of Phoenix exceeds that of the surrounding desert by 3 °C, microclimates in mesic landscaping are 5–10 °C cooler from a lizard's perspective than in native landscapes. These cooler microclimates come from the humidity and evaporation associated with mist-irrigated grass. The trees, bushes, shade, and drip-irrigation of native and xeric landscapes have minor effects on mean temperatures, when compared to bare ground. Although these conclusions depend on a limited sample of plots at North Desert Village, they

Table 2 The influence of landscaping type on potential lizard activity

| Landscape | Proportion of area | | Proportion of time | |
|-----------|--------------------|-----------|--------------------|-----------|
| | Preferred | Tolerable | Preferred | Tolerable |
| Bare | 0.20 | 0.29 | 0.23 | 0.41 |
| Native | 0.21 | 0.32 | 0.27 | 0.92 |
| Xeric | 0.23 | 0.41 | 0.38 | 1.00 |
| Oasis | 0.21 | 0.48 | 0.74 | 1.00 |
| Mesic | 0.33 | 0.54 | 1.00 | 1.00 |

More intensive landscaping caused a higher proportion of the habitat area to fall within a lizard's preferred and tolerable range of temperatures during the summer. Increased landscaping also resulted in an even greater increase of the proportion of time during which any part of the habitat was within the preferred or tolerable limits. The proportion of time within preferred limits is an optimistic estimate of potential lizard activity; if only a small amount of the habitat falls within a lizard's tolerance range, it is doubtful they will know where these areas exists, be able to travel to them, and achieve a net benefit by using them

should be generalizable because shade, humidity, and sky view factor are more important determinants of estimated lizard body temperatures than landscaping type.

Unlike real lizards, our copper models did not move. Thus, temperatures estimated by our models reflect what a lizard's body temperature could be in specific environments without behavioral and physiological thermoregulation. Calculating potential activity time for lizards is challenging, but we can reasonably conclude that lizards would remain inactive when the entire habitat exceeds their preferred range of temperatures. At least some portions of the mesic plot fell within the preferred range throughout the day (Fig. 2b). However, surface temperatures of native and xeric landscapes exceeded the preferred range during the majority of a typical summer day (Fig. 2a). Lizard behavioral ecology will of course influence the subset of microhabitat temperatures they are commonly exposed to. Ornate Tree Lizards (*Urosaurus*

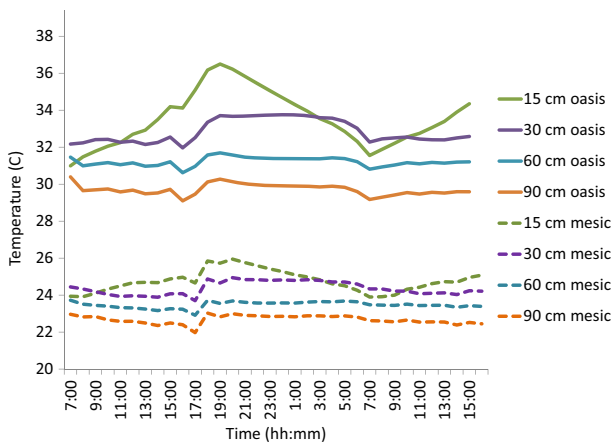


Fig. 3 During a typical summer day, underground temperatures are higher and have more variation at shallow depths. The grassy mesic plot was almost 10 °C cooler on average, sensors in the other plots were buried in bare soil. Underground temperatures in the native, xeric, and bare plots were almost identical to those of the oasis plot, and are not shown. The above ground control unit was often exposed to direct sunlight for a brief period around 7:00 and 17:00 h, which produced a small artificial dip in temperature readings

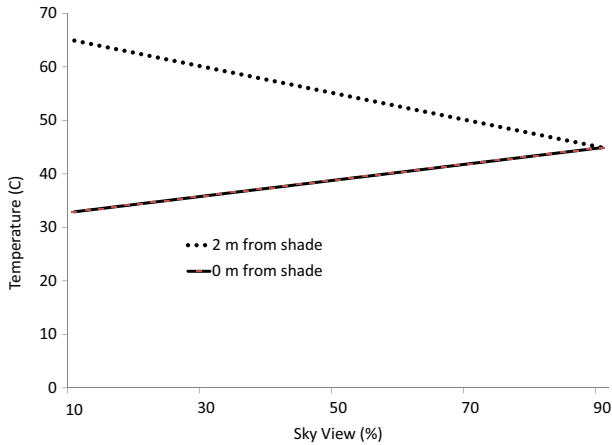


Fig. 4 An interaction was found between distance to shade and sky view. For lizards in full sun, increasing quantities of vegetation (lower sky view and greater canopy coverage) result in higher body temperatures (*dotted line*). Lizards in or near shade were cooled by increasing vegetation (*solid line*), suggesting that the high maximum temperatures found in experimental plots were the result of plants reflecting light and radiating heat onto nearby objects, rather than blocking wind and preventing warm air from moving upwards

ornatus) are primarily arboreal, but can often be found on the ground and will hide in litter and rock piles. Side-blotched Lizards (*Uta stansburiana*) are primarily terrestrial, but can often be found on trees and concrete walls and will utilize existing burrows. The complete lack of preferred surface temperatures during much of the summer could potentially require more extensive use of burrows by all urban lizards in the future.

To use preferred microclimates, lizards must (1) know when and where these microclimates exist, (2) reach them without overheating, and (3) benefit enough from the resulting body temperature to offset the associated energy demands, missed opportunity costs, and predation risks. When these conditions are not met in summer, some lizards will remain underground for days or weeks in a state referred to as aestivation (Pianka 1970). The underground temperatures that we observed in bare, native, xeric, and oasis plots were near the high end of the preferred range of the species we tested, where metabolic demands are greatest. However, the preferred range only applies to animals that are foraging on a daily basis and have adequate water availability; lower body temperatures enable lizards either to aestivate longer or to emerge from aestivation in superior condition. Further warming associated with urban or global change may produce underground temperatures that exceed the upper tolerance limits of some Sonoran Desert reptile species (Cowles and Bogert 1944). Since irrigated grass cools soils by 10 °C, mesic landscaping can extend potential aestivation periods as well as surface activity.

On the sub-meter scale at which most organisms experience heat, vegetation can raise maximal temperatures by reflecting sunlight and radiating heat toward objects already in full sun. This phenomenon would explain our most surprising result: that mean temperatures in native landscaping exceeded those of bare ground. Even mesic landscaping produced higher maximum temperatures than bare ground, despite being much cooler on average. Current plans to increase canopy cover in Phoenix could slightly increase mean surface temperatures if unirrigated native trees are used. However, the associated increase in shade and thermal variation should produce the desired outcome of enabling humans (and lizards) to

thermoregulate more effectively. Artificial shade structures could also exacerbate the UHI, depending on the method and scale of measurement. Thermal satellite images are commonly used to estimate surface temperatures (Voogt and Oke 2003), but their bird's-eye view cannot detect shaded areas beneath a canopy. However, the heat stored by the shade structures will be detected, creating an interesting conundrum: mitigation strategies will be effective on small scales at which the UHI is experienced, but may appear counter-productive on larger scales at which the UHI is monitored.

Landscaping projects such as the Tree and Shade Master Plan are more viable components of an UHI mitigation strategy in Phoenix than in other similarly warm and arid climates (Chow and Brazel 2012; Chow et al. 2012). Phoenix has a relatively abundant water supply from groundwater, local rivers, and Colorado River water imported through a canal system (Gober and Kirkwood 2010; Guhathakurta and Gober 2007). Maintaining existing mesic areas could have numerous benefits beyond historical preservation, human comfort, and energy savings, while avoiding the expense and disturbance of converting these established habitats for the purposes of water conservation. We certainly do not advocate increasing overall urban water use or believe that lizards should have a large influence on urban planning, however many local governments may wish to reconsider offering rebates of up to \$3000 for property owners who convert grassy areas to xeriscapes.

The non-thermal effects of mesic landscaping may be mixed for lizards. The greater abundance of water and arthropods in Phoenix's mesiscapes may be beneficial, but reduced arthropod diversity compared to xeriscapes may be detrimental for lizards that specialize on certain prey species (Bang and Faeth 2011). Fortunately, landscapes dappled by various forms of human activity can offer diverse ecological opportunities. The existing variation of backyard landscaping styles are often available within the range of a lizard's daily movements, and could benefit habitat selection on multiple scales: including hourly thermal variation in microhabitats, daily energy requirements, seasonal temperature shifts, and progressive life history stages.

Habitat loss and fragmentation, novel predators and diseases, road mortality, chemical and light pollution, invasive species, and even mountain biking have raised concern among herpetologists (Mitchell et al. 2008). These factors can strongly influence the distribution and relative abundance of species. Nevertheless, temperature dictates when ectotherms can be active, and potentially whether they can survive in an anthropogenic thermal landscape. This widely-overlooked consideration will become increasingly important in an era of climate change and aggressive urban development.

Acknowledgments Greg Adrian and Davina Kumar assisted with data collection. Stevan Earl provided logistical support. This research was supported by the National Science Foundation Central Arizona-Phoenix LTER (BCS-1026865), the National Science Foundation IGERT in Urban Ecology at Arizona State University (DGE 05040248), and the Environmental Protection Agency STAR (FP-91742701-0).

References

- Adolph SC (1990) Influence of behavioral thermoregulation on microhabitat use by two *Sceloporus* lizards. *Ecology* 71:315–327
- Akbari H, Pomerantz M, Taha H (2001) Cool surfaces and shade trees to reduce energy use and improve air quality in urban areas. *Sol Energy* 70:295–310

- Angilletta MJ (2001) Thermal and physiological constraints on energy assimilation in a widespread lizard (*Sceloporus undulatus*). *Ecology* 82:3044–3056
- Angilletta MJ Jr (2009) Thermal adaptation: a theoretical and empirical synthesis. Oxford University Press, Oxford
- Angilletta MJ, Hill T, Robson MA (2002) Is physiological performance optimized by thermoregulatory behavior?: a case study of the eastern fence lizard, *Sceloporus undulatus*. *J Therm Biol* 27:199–204. doi:10.1016/S0306-4565(01)00084-5
- Baker LA et al (2002) Urbanization and warming of phoenix (Arizona, USA): impacts, feedbacks and mitigation. *Urban Ecosyst* 6:183–203
- Bakken GS (1992) Measurement and application of operative and standard operative temperatures in ecology. *Am Zool* 32:194–216. doi:10.1093/icb/32.2.194
- Bakken GS, Angilletta MJ (2013) How to avoid errors when quantifying thermal environments. *Funct Ecol* 28:96–107
- Bang C, Faeth SH (2011) Variation in arthropod communities in response to urbanization: seven years of arthropod monitoring in a desert city. *Landsc Urban Plann* 103:383–399. doi:10.1016/j.landurbplan.2011.08.013
- Bowler DE, Buyung-Ali L, Knight TM, Pullin AS (2010) Urban greening to cool towns and cities: a systematic review of the empirical evidence. *Landsc Urban Plann* 97:147–155. doi:10.1016/j.landurbplan.2010.05.006
- Brazel A, Gober P, Lee S-J, Grossman-Clarke S, Zehnder J, Hedquist B, Comparri E (2007) Determinants of changes in the regional urban heat island in metropolitan Phoenix (Arizona, USA) between 1990 and 2004. *Clim Res* 33:171–182. doi:10.3354/cr033171
- Buckley LB (2008) Linking traits to energetics and population dynamics to predict lizard ranges in changing environments. *Am Nat* 171:E1–E19
- Chow WTL, Brazel AJ (2012) Assessing xeriscaping as a sustainable heat island mitigation approach for a desert city. *Build Environ* 47:170–181. doi:10.1016/j.buildenv.2011.07.027
- Chow WTL, Brennan D, Brazel AJ (2012) Urban heat island research in Phoenix, Arizona: theoretical contributions and policy applications. *Bull Am Meteorol Soc* 93:517–530. doi:10.1175/bams-d-11-00011.1
- Christian K, Tracy CR, Porter WP (1983) Seasonal shifts in body temperature and use of microhabitats by Galapagos land iguanas (*Conolophus pallidus*). *Ecology* 64:463–468
- Christian KA, Bedford GS, Shannahan ST (1996) Solar Absorptance of some Australian lizards and its relationship to temperature. *Aust J Zool* 44:59–67
- Cook WM, Casagrande DG, Hope D, Groffman PM, Collins SL (2004) Learning to roll with the punches: adaptive experimentation in human-dominated systems. *Front Ecol Environ* 2:467–474. doi:10.1890/1540-9295(2004)002[0467:ltrwtp]2.0.co;2
- Cowles B, Bogert CM (1944) A preliminary study of the thermal requirements of desert reptiles. *Bull Am Mus Nat Hist* 83:265–296
- Dzialowski EM (2005) Use of operative temperature and standard operative temperature models in thermal biology. *J Therm Biol* 30:317–334. doi:10.1016/j.jtherbio.2005.01.005
- Gober P, Kirkwood CW (2010) Vulnerability assessment of climate-induced water shortage in Phoenix. *Proc Natl Acad Sci* 107:21295–21299. doi:10.1073/pnas.0911113107
- Grant BW, Dunham AE (1988) Thermally imposed time constraints on the activity of the desert lizard *Sceloporus Merriami*. *Ecology* 69:167–176. doi:10.2307/1943171
- Guhathakurta S, Gober P (2007) The Impact of the phoenix urban heat island on residential water use. *J Am Plan Assoc* 73:317–329. doi:10.1080/01944360708977980
- Hertz PE, Huey RB, Nevo E (1982) Fight versus flight: body temperature influences defensive responses of lizards. *Anim Behav* 30:676–679. doi:10.1016/S0003-3472(82)80137-1
- Hope D et al (2003) Socioeconomics drive urban plant diversity. *Proc Natl Acad Sci* 100:8788–8792. doi:10.1073/pnas.1537557100
- Jenerette GD, Harlan SL, Brazel A, Jones N, Larsen L, Stefanov WL (2007) Regional relationships between surface temperature, vegetation, and human settlement in a rapidly urbanizing ecosystem. *Landsc Ecol* 22:353–365
- Kearney M, Porter WP (2004) Mapping the fundamental niche: physiology, climate, and the distribution of a nocturnal lizard. *Ecology* 85:3119–3131. doi:10.1890/03-0820
- Kumar R, Kaushik S (2005) Performance evaluation of green roof and shading for thermal protection of buildings. *Build Environ* 40:1505–1511
- Martin TL, Huey RB (2008) Why “suboptimal” is optimal: Jensen’s inequality and ectotherm thermal preferences. *Am Nat* 171:E102–E118
- MIPP (2000) Hits and misses: fast growth in metropolitan phoenix. Morrison institute for public policy. Arizona State University, Tempe
- Mitchell JC, Jung RE, Bartholomew B, Society for the Study of A, Reptiles (2008) Urban herpetology. Society for the Study of Amphibians and Reptiles, Salt Lake City, Utah

- Peterson CR, Gibson AR, Dorcas ME (1993) Snake thermal ecology: the causes and consequences of body temperature variation. In: Seigel RA, Collins JT (eds) Snakes: ecology and behavior. McGraw-Hill, New York, pp 241–314
- Pianka ER (1970) Comparative Autecology of the lizard *Cnemidophorus Tigris* in different parts of its Geographic range. *Ecology* 51:703–720. doi:10.2307/1934053
- R CDT (2005) R: A language and environment for statistical computing. ISBN 3-900051-07-0. R Foundation for Statistical Computing, Vienna, Austria, 2013. url: <http://www.R-project.org>
- Ruddell D, Hoffman D, Ahmad O, Brazel A (2013) Historical threshold temperatures for Phoenix (urban) and Gila Bend (desert), central Arizona. *USA Clim Res* 55:201–215. doi:10.3354/cr01130
- Schuler MS, Sears MW, Angilletta MJ (2011) Food consumption does not affect the preferred body temperature of Yarrow's spiny lizard, *Sceloporus Jarrovi*. *J Therm Biol* 36:112–115
- Sears MW, Raskin E, Angilletta MJ (2011) The world is not flat: defining relevant thermal landscapes in the context of climate change. *Integr Comp Biol* 51:666–675. doi:10.1093/icb/acr111
- Sinervo B et al (2010) Erosion of lizard diversity by climate change and altered thermal niches. *Science* 328:894–899. doi:10.1126/science.1184695
- Voogt JA, Oke TR (2003) Thermal remote sensing of urban climates. *Remote Sens Environ* 86:370–384. doi:10.1016/s0034-4257(03)00079-8
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York