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Urban heat and desert wildlife: rodent body condition across a gradient of surface temperatures

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Abstract

Animals in urban areas can be exposed to human-mediated land use change and radiant heat (called urban heat island effect). Few studies have empirically evaluated the effects of urban heat on wild vertebrates. We live-trapped desert wild rodents from a large metropolitan area in the Sonoran Desert, USA, across seven field sites spanning three strata of land surface temperatures. During the summers of 2019 and 2020, we captured 116 adult pocket mice (*Chaetodipus* spp. and *Perognathus* spp.) and Merriam's kangaroo rats (*Dipodomys merriami*) in mountainous urban parks and open spaces. We measured body condition, proxy for health, using percent body fat (i.e., fat mass divided by body mass). For mammals, this parameter estimates the storage of energy-rich fat, which is important for growth, survival, and reproduction. We measured body condition using a noninvasive quantitative magnetic resonance instrument. Site-level surface temperatures were measured using data loggers and long-term climate data. Results supported the prediction that body condition was greatest in cooler temperature strata compared to the hottest areas. To relate body condition to resource availability, we evaluated vegetation cover and degree of urbanization. Body fat of adult pocket mice was greater in areas with more vegetation cover and where nighttime temperatures and surface temperatures were lower and urbanization was greater. Kangaroo rats had more fat in areas with the lowest strata of surface temperature. These results demonstrate that extreme heat negatively covaries with small mammal body condition, which indicates that urbanization and climate change have the potential to reduce rodent fitness.

Keywords Body fat · Body size · Heteromyidae – kangaroo rats and mice · Quantitative magnetic resonance · Urban ecology · Urban heat island · Wildlife

Introduction

Urbanization and human-mediated land use change can transform thermal environments (Battles and Kolbe 2019). The urban heat island (UHI) effect occurs as cities grow and land cover is converted from soil and vegetation to impervious cover in buildings and roads that absorb heat during the day and radiate heat at night (Archer and Predick 2008). Emissions and heat radiating from the built environment cause the UHI effect, which results in 0.5–4.0 °C higher daytime temperatures and 1.0–4.5 °C higher nighttime temperatures in urban areas (Hibbard et al. 2017). Studies have shown negative effects of heat-related stress on human health and mortality in cities globally (Sherwood and Huber 2010; Hondula et al. 2015) and within arid cities in the Sonoran Desert of the USA (Golden et al. 2008; Harlan et al. 2014; Petitti et al. 2016). Extreme heat is predicted to increase in aridland urban systems (Archer and Predick 2008) which could exacerbate UHI effects with a warming climate. For animals, including humans, the response to thermal stress requires energy to maintain body temperature by physiological or behavioral adjustments and avoid declines in health and mortality (Collier et al. 2017).

However, few empirical studies have focused on the effects of urban heat on the health of non-human vertebrates. This study seeks to better understand the effects of extreme heat on urban wildlife. Body size variability in response to climate change in non-human animals has

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been hypothesized as a response to warming temperatures (Gardner et al. 2011). Animals, particularly endotherms, in warmer climates tend to be smaller than animals in cooler climates (Bergmann's rule, Yom-Tov 2003; Santini et al. 2018; Hantak et al. 2021). In urban areas, human-mediated land use and resource availability can increase vertebrate body size by altering habitat and food resources (Kaiser et al. 2016; McKinney 2002; Teplitsky and Millien 2014). Thus, it is difficult to predict whether vertebrates affected by UHI will have smaller body sizes such as the pattern predicted by Bergmann's rule, or whether, resources in urban areas drive animals to be larger as predicted by resource availability hypothesis. In this study, we had the opportunity to evaluate body condition across a gradient of heat from similar habitats as a proxy for similar resources to isolate effects of temperature on wildlife body condition.

Studies on animal body condition mostly focus on percent body fat or body size (mass). One study found that body mass and diet diversity were greater among urban dwelling rodents compared to non-urban populations (Santini et al. 2018; Hantak et al. 2021) found the effect of urbanization across mammal species was larger body size. Both studies predicted that urban wildlife may have benefited from increased food availability, higher calorie diets, and less predation or competition. Hantak et al. (2021) also found that animals in warmer climates, which hibernated or underwent torpor to buffer thermal stress, were more sensitive to warm temperatures and had a stronger decrease in body size. Yom-Tov (2003) found that body size of carnivore mammals increased with urbanization but not with temperature. Although studies have compared mammal body size and condition in urban and non-urban areas, our work fills an important gap that can assess how urban heat, specifically, can influence animal health without the added complication of habitat or geographic differences.

This study focuses on rodents in the arid Southwest USA, a system noted for increased susceptibility to climate change and climate variability (Archer and Predick 2008) and taxa living near their physiological limits (Walsberg 2000). Previous studies have focused on wildlife abundance or diversity in urban areas (Murray et al. 2019), but this study focuses on health of rodents because of their ecological significance and as common desert species to monitor under climate change. Rodents play important roles as bioengineers and seed dispersers and are prey for many predators (Monadjem et al. 2015). The ability of desert-adapted rodents to tolerate and survive extreme heat makes them the ideal candidate for this study. Rodent abundance and survival have been linked to temperature extremes, surface temperature, vegetation cover, food availability, and ability to persist in urban environments. Temperatures are shown to limit the range of rodent species due to their metabolic rate requirements and ability to tolerate heat (Munger et al. 1983; Walsberg 2000). Studies have found that surface temperature alters desert-adapted rodent abundance: as surface temperature increases, apparent survival decreases (Moses et al. 2012; Pianalto and Yool 2017). Vegetation coverage and food provided by plants has a positive relationship on rodent abundance, reproduction, and survival, and these resources are especially important for desert-adapted species during dry seasonal periods (Chew and Butterworth 1964; Beatley 1969; Nagy and Gruchacz 1994). Generally, cities have lower species diversity and richness and more non-native species (Cavia et al. 2009; Saari et al. 2016; Guevara and Ball 2018). Studying rodents in the Sonoran Desert, especially the Phoenix urban interface, is an opportune research area for evaluating how heat affects diverse, arid-adapted organisms that overlap urban areas (Guevara and Ball 2018).

We evaluated the effect of UHI on rodent health by quantifying how body condition varies across an urban heat gradient in the Phoenix metropolitan area. We measured body condition using percent body fat (i.e., fat mass divided by body mass). Body condition is a parameter that estimates the storage of energy-rich molecules (e.g., lipids [fat]), which are important for growth, survival, and reproduction (Young 1976). Therefore, body condition can be used as one measure of overall animal health. We used a quantitative magnetic resonance (QMR) instrument to quantify rodent body condition. QMR has been used across taxa in animal studies (Nixon et al. 2010; Riley et al. 2016; Warner et al. 2016) as a noninvasive alternative to chemical carcass analysis, and it provides accurate measurements of body fat, lean mass, and water content (Nixon et al. 2010). Our research objectives were to evaluate (1) how rodent body condition varies across three strata of urban heat and (2) how rodent body condition relates to environmental predictors (i.e., land use, land cover, surface temperature, index of vegetation biomass, and degree of urbanization). We predicted animal body fat, lean mass, and water would be greater in individuals from cooler summer surface temperatures compared to warmer temperatures.

Methods

Study area

This study occurred in the Phoenix Metropolitan area of Maricopa County Arizona, which is situated in the Sonoran Desert of the United States (Fig. 1). The region has an estimated 4.5 million human population with rapid growth (U.S. Census Bureau 2019). We selected sampling sites based on long-term climate data in the urban heat gradient

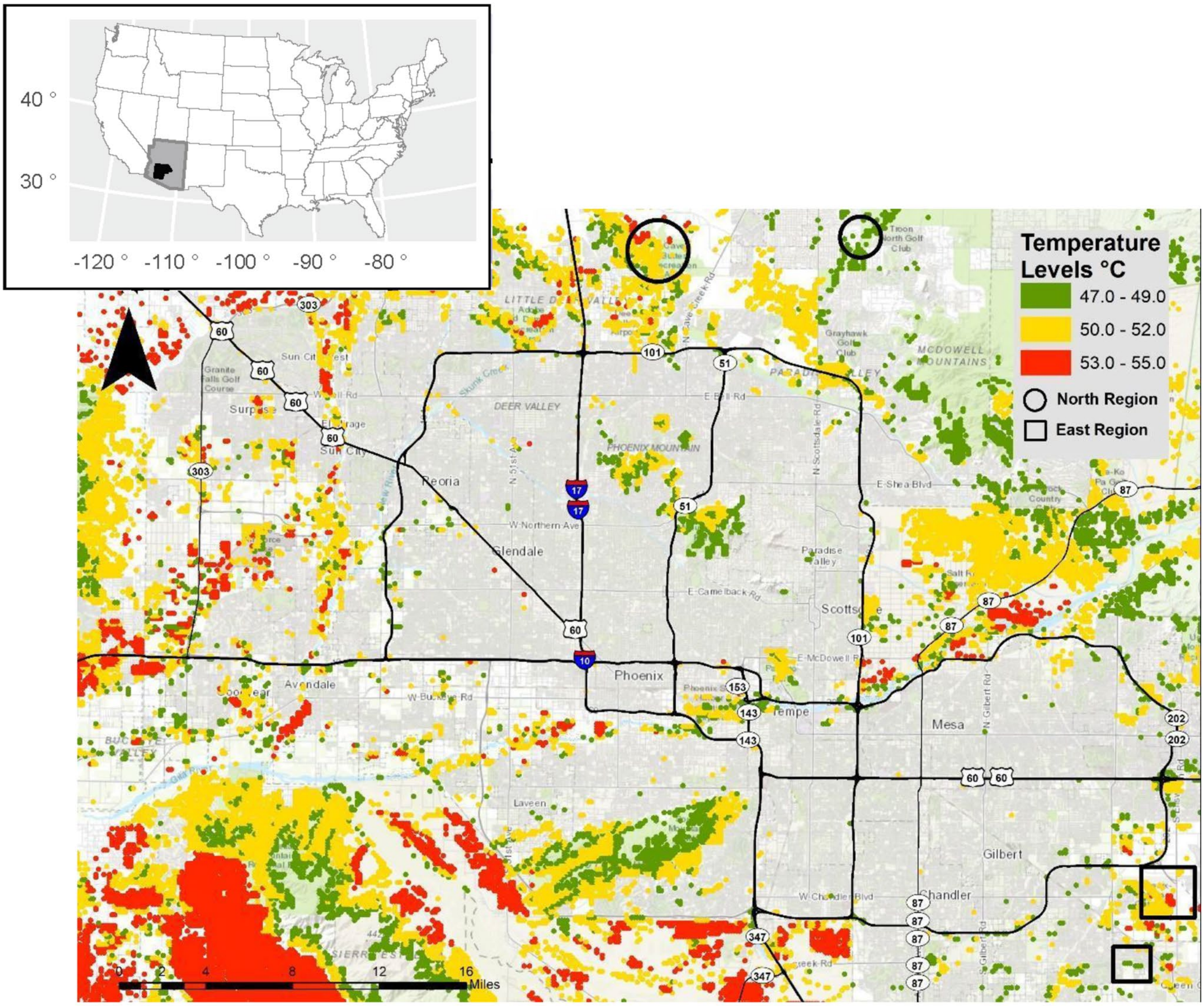

Fig. 1 Rodent capture sites occurred in northern and southeastern regions of Phoenix, Arizona, USA. Temperature strata were derived from 5-year average daily temperature in June from the long-term surface temperature LANDSAT imagery. Colors indicate regions that contained 400 square meters of open, undeveloped land with temperatures ranging from cool (green) to the hottest (red) areas. United States map (whereig.com) shows Arizona in gray and Maricopa county in black

in Phoenix, Arizona (Fig. 1) across three strata of summer surface temperature (47.0–49.0 °C, 50.0–52.0 °C, and 53.0–55.0 °C). Temperature strata were derived from 5-year average daily temperature in June from the long-term surface temperature LANDSAT imagery (similar to methods of Frazier et al. 2021; Parastatidis et al. 2017). The long-term temperature data were manipulated to exclude buildings and impervious surfaces and include eligible landcover types to trap animals (compacted urban soil, inactive crops, undisturbed land, desert vegetarian, and riparian vegetation). This approach created 400 m circular plots to sample temperature strata with similar landcover types (data available from Central-Arizona Phoenix, Long-Term Ecological Research program; Li et al. 2015).

Field data collection

Rodents and sampling

The rodents of this study, pocket mice (*Chaetodipus* spp. and *Perognathus* spp.) and Merriam's kangaroo rats (*Dipodomys merriami*), live in dry, hot areas where the average maximum soil surface temperatures in June in central Arizona may exceed 60 °C (140 °F) as air temperatures reach 35 °C (95 °F) or greater. During the day, rodents live in burrows where temperatures are up to 60° less than soil and 10° less than air temperatures (Reynolds 1960; Kay 1975) found banner-tailed kangaroo rats' (*Dipodomys spectabilis*) thermal neutral zone is 20–30 °C, and their upper lethal zone is 40 °C. Desert-adapted rodents are known for their ability to conserve water by producing highly concentrated urine and dry feces (Lazaroff 1998; Tracy and Walberg 2001) and using underground burrows (Lazaroff 1998).

We captured adult pocket mice and Merriam's kangaroo rats (Online Resource 1). Reynolds (1960) summarizes life history traits of pocket mice and kangaroo rats (Family Heteromyidae), which are nocturnal, burrowing animals with fur-lined cheek pouches for storage and transportation of seeds. These rodents are primarily granivorous (seed-eating), but they also may eat some insects and a little vegetation. For Merriam's kangaroo rats, their caches (seed stores) consist primarily of *Bouteloua* spp. (annual grama grasses) or *Plantago* spp. (perennial plantain herbaceous plants). Kangaroo rats are known to be active throughout the year and are strictly nocturnal (Reynolds 1960). For pocket mice, we combined data for the genera *Chaetodipus* and *Perognathus* because pocket mice are difficult to identify in the field and have similar body sizes, metabolic rates, and genetics (Riddle 2007). Pocket mice are known to use torpor, and some species of pocket mice remain active year-round (Lazaroff 1998).

To capture live rodents, we used baited Sherman traps from mid-May to early September in mountainous urban parks and open spaces in 2019 (year 1) and 2020 (year 2). Ventilated traps with cotton batting were baited with brown rice, oats, and cereal and open from sunset to sunrise three to five days (50–100 traps/night) in sites identified as one of three strata of summer surface temperature. Sites were 400 m in diameter (200 m radius). If more than one site occurred within the stratum, we chose the site at random. Within each site, we established traps in locations with evidence of rodent activity (recently dug holes and small mammal paths). Once captured, animals were given a temporary mark on the right inner thigh to prevent resampling. Juvenile and pregnant or lactating rodents were released live on site. Animals included in analyses were transported within an air-conditioned vehicle to a climate-controlled building where the QMR machine was located. Animals were analyzed with QMR, weighed (year 1, Pesola spring scale, ± 0.01 g; year 2, Sartorius Secura analytical balance scale, ± 0.001 g), sexed, measured, then returned to the site of capture and released live in less than 24 h.

Temperature logger deployment

We deployed temperature loggers (n = 76, Maxim Integrated Products iButtons) during year 2 only at sites to obtain site-specific surface temperature. Temperature measurements were recorded every 30 min from 2 June to 24 June 2020 (22 days). Temperature data were extracted (Online Resource 2) from retrieved and functioning loggers (n = 41). The variable used for analyses was the average nighttime temperature (nighttemp) from 7 PM to 5 AM AZT based on sunrise and sunset periods, which is the period when animals in the study were most active (Walsberg 2000).

Laboratory methods

The QMR instrument uses Hydrogen (Proton)-nuclear magnetic resonance principles with measurements based on the different responses of tissues to radio waves. Radio wave disturbances cause protons to excite and relax, producing different positions and intensities that are measured reflecting the chemical composition as fat, lean muscle, and water (Jones et al. 2009). Scans are performed by placing one animal into an acrylic cylinder (animal holder), with a second, smaller cylindrical inset to limit animal movement, then placing the animal inside the machine. Each scan takes approximately 3–5 min. Animals were scanned 6–12 times to ensure the readings were accurate and the first six scans were used in analyses. The QMR output (± 0.001 g) measures body fat (g), lean mass (g), and water content (g). The QMR outputs for each animal were averaged and divided by the animal's measured mass (g); the proportion is used in this study as the dependent variable (i.e., proportion of body fat, lean mass, and water content).

We used the EchoMRI™ Mobile Body Composition Analyzer for Birds and Bats, or other small animals up to 200 g (http://www.echomri.com). We used established protocols for animal and QMR use based on recommendations by Nixon et al. (2010). Specifically, each sample was processed using "Primary Accumulation 3," which is an average of three scans per output. Prior to year 2 field data collection, we analyzed QMR outputs from year 1 of the empty animal holder, test vials for the standard sample (two different types), and test vials with known fat samples. A known fat sample (canola oil) was used during years 1 and 2 as a standard sample to evaluate the consistency of QMR output. The expected outputs of the standard sample were 100% fat and no lean mass or water content. The standard sample mass was chosen based on a study that found deer mouse (*Peromyscus maniculatus*) fat content (mean fat (g) ± the standard deviation) was 1.06 ± 0.50 (Schulte-Hostedde et. 2001). The standard sample in year 1 (1.02 g; 13 unique runs; 119 scans) was measured before animals were processed every 1–2 days. Therefore, we established a protocol in year 2 to scan the standard sample at the beginning and end of the day and before each animal was processed in the QMR (0.80 g; 109 QMR unique runs; 833 scans). From year

1 data, we evaluated if differences were present when individual rodents were scanned six or 12 times and explored if a difference occurred between males and females for QMR outputs (body condition).

Spatial data

Environmental predictor variables were summarized from remotely sensed data at the site centers for year 1 (2019) and year 2 (2020). Temperature data were derived from 5-year average daily temperature in June from the long-term surface temperature LANDSAT imagery. To evaluate vegetation, cover, and food available to rodents, we used Normalized Difference Vegetation Index (NDVI) values derived from the MODIS vegetation index, upscaled to 1 km x 1 km pixel size (averaged from 250 m to 250 m pixels) for 22 months during 2019 and 2020 (12 months for the Queen Creek Sossaman site that was surveyed only in 2019). NDVI values ranged from − 0.2 to 1 (negative values can from clouds and water, positive values near zero are bare soil, and higher values are green vegetation). The proportion of urbanization (Online Resource 3) GIS layer was calculated as the proportion of developed area (e.g., human structures and impervious surface land covers, Li et al. 2015), within a 1 km radius buffer for each 10 × 10 m raster cell. Values ranged from 0 (no development) to 1 (complete development; J. Lewis unpublished data).

Statistical analysis

To determine the consistency of QMR output, we used a paired t-test to compare the means of 6 QMR scans and 12 QMR scans. The mean and variation were calculated from the outputs of the empty animal holder inserted into the QMR machine, outputs of the vials only for holding the standard sample, and output of vials with standard sample. Coefficient of variation (CV) was analyzed for each variable output from the QMR of the standard sample: fat content (g), lean mass (g), and water content (g). Year 1 and year 2 standard sample outputs were analyzed separately to assess the precision of the QMR outputs. To determine if body condition varied by sex, we compared fat for female and male rodents with a Levene's test to examine variance and then a two-sample t-test assuming equal variance.

Data analyses were completed separately for pocket mice and kangaroo rats with year 1 and year 2 data combined across each temperature range. Relative abundance of kangaroo rats and pocket mice included only animals used in body condition analyses. We used a Shapiro-Wilk test to examine normality of data and Levene's test to test for equal variances to analyze all data. If data were normally distributed, we used analysis of variance (ANOVA) to compare how body fat varied across urban surface temperatures then a Tukey's honestly significant difference (HSD) post hoc test to determine where differences lay. When data were not normally distributed, we used a Kruskal-Wallis test to determine if there was a significant effect of the heat strata and proportion of body fat then used post hoc pairwise comparisons using the Wilcoxon Rank Sum Test to examine where the differences lay. The tests on proportion of body fat, mass, and relative abundance in relation to heat strata were completed using R Statistical Program (R Core Team 2020).

We combined data from pocket mice and kangaroo rats to visualize relationships of the dependent variable to environmental variables. We used linear regressions to compare the proportion of body fat to nighttemp, NDVI, and urbanization using Microsoft Excel (2013). To relate species-specific responses to environmental variables we used general linear models (GLMs). To determine the independence of environmental variables, we used bivariate Pearson Correlation in SPSS version 26.0 (IBM Corp 2019). The sample unit of the ecological models was the number of trapping locations where the spatial data were independent at a 1 km scale (n = 7). We evaluated GLMs using a Corrected Akaike's Information Criterion (AICc) for small sample sizes (Burnham and Anderson 2004) to examine the response of rodents' body condition to urban heat and environmental predictors (R Core Team 2020; R version 3.6.1 with tidyverse, lme4, MuMIn, and ggplot2 packages).

Results

Rodent captures

During the 2019 and 2020 trapping seasons (33 days of trapping), we processed 69 pocket mice and 47 kangaroo rats from seven field sites spanning three strata of land surface temperature. Each season we set 25–75 traps/site/night, resulting in over 1,000 trap nights per year (Online Resource 4). Over both years of the study, pocket mice were processed from the coolest (n = 21), moderate (n = 23), and hottest (n = 25) sites. Kangaroo rats were processed from the coolest (n = 12), moderate (n = 22), and hottest (n = 13) sites. Mass of Merriam's kangaroo rat ranged from 24.0 to 48.6 g for males and 21.0–48.2 g for females and pocket mice ranged from 16.3 to 45.1 g for males and 16.0–35.0 g for females.

QMR quality control

Based on the coefficients of variance analyses of the known standard sample (Online Resource 5), measurements for body fat were more consistent than measurements for lean mass and water content. Therefore, proportion of body fat was used for comparisons across surface temperature strata and in ecological models. Mean CV values indicated the standard sample from year 1 fat measurements (CV = 17.14%, SE = 0.05) and year 2 fat measurements (CV = 28.09%, SE = 0.05) had the most consistent results. For year 1 (lean mass, CV = 92.42%, SE = 0.03; water content, CV = 96.16%, SE = 0.14) and year 2 (lean mass, CV = 150.34%, SE = 0.009; water content, CV = 145.31%, SE = 0.02), lean mass and water content varied significantly.

The body fat from QMR outputs of the first 6 scans and of 12 scans (Online Resource 6) was averaged from year 1. There was no significant difference between 6 scans (M = 0.51, SE = 0.06) and 12 scans (M = 0.55, SE = 0.06; t = 1.54, df = 11, P = 0.132). For all analyses, males and females were combined per rodent genera and 6 scans were used. There was no difference in proportion of body fat between sexes (Online Resource 7) for pocket mice (t = 0.14, df = 22, P = 0.893) or for kangaroo rats (t = -0.62, df = 11, P = 0.551).

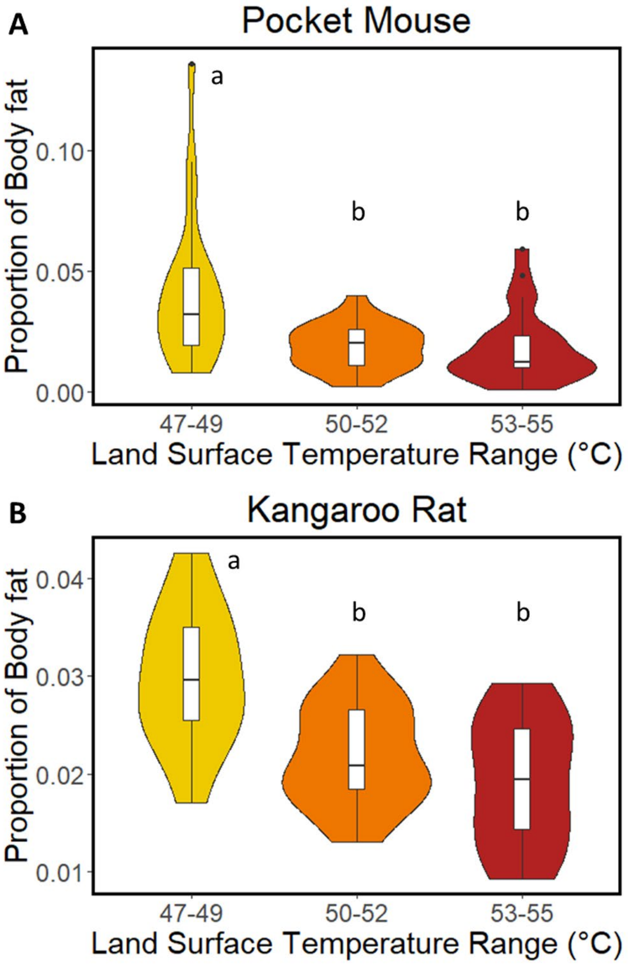

Fig. 2 Measure of proportion of body fat (%) for (A) pocket mice (*Chaetodipus* spp. and *Perognathus* spp.) and (B) Merriam's kangaroo rats *(Dipodomys merriami*) captured from three strata of land surface temperature during 2019 and 2020 in Phoenix, Arizona. For (A), analysis of variance (ANOVA) and Tukey's honestly significant difference (HSD) post hoc test were used. For (B), Kruskal-Wallis test and post hoc pairwise comparisons using the Wilcoxon Rank Sum Test. Violin plot shows density/frequency in data, solid bars are medians and quartiles are shown. Different letters above symbolize significant results of Tukey test or pairwise comparisons

Comparisons across temperature strata

For pocket mice, the proportion of body fat varied across the surface temperature strata (H = 14.11, df = 2, P = 0.0009). Pocket mice from the coolest strata had more than twice as much as mice from medium and hot strata (P = 0.003, P = 0.002, respectively; Fig. 2A). Pocket mice from the medium and hot strata did not differ (P = 1.00). For kangaroo rats, the proportion of body fat varied across the surface temperature strata (F = 10.45, df = 2, P = 0.0002). Kangaroo rats from the coolest strata had 1.6 times and 1.4 times more fat than those from medium and hot strata (P = 0.002, P = 0.0002, respectively; Fig. 2B). Kangaroo rats from the medium and hot strata did not differ (P = 0.402).

Body mass of pocket mice did not vary across the surface temperature strata (H = 4.387, df = 2, P = 0.112; Fig. 3A) but did vary for kangaroo rats (F = 12.94, df = 2, P = 0.00003; Fig. 3B). Animals from the cool and medium strata had more fat compared to those from hot strata (P = 0.00003, P = 0.003, respectively; Fig. 3B).

Temperature logger data and spatial data were summarized from the study sites (Online Resources 8). A linear regression showed that proportion of animal body fat was negatively associated with night-time temperatures (r-squared = 0.356, P = 0.031), with rodent proportion of body fat greatest in areas with the lowest temperatures (Fig. 4). We failed to find a relationship between the proportion of body fat and vegetation cover from NDVI (r-squared = 0.002, P = 0.869, Online Resource 9) or to degree of urbanization (r-squared = 0.071, P = 0.379, Online Resource 9). These results were likely because sites were consistent and showed little variability in NDVI and degree of urbanization (Online Resource 9).

Relative abundance, as captures per 100 trap nights, was similar for all rodents across the surface temperature strata (F = 1.698, df = 2, P = 0.237). For individual species, pocket mice (F = 1.113, df = 2 P = 0.375, Online Resource 10) and kangaroo rat (F = 1.683, df = 2, P = 0.253, Online Resource 10) relative abundance did not vary across the surface temperature strata.

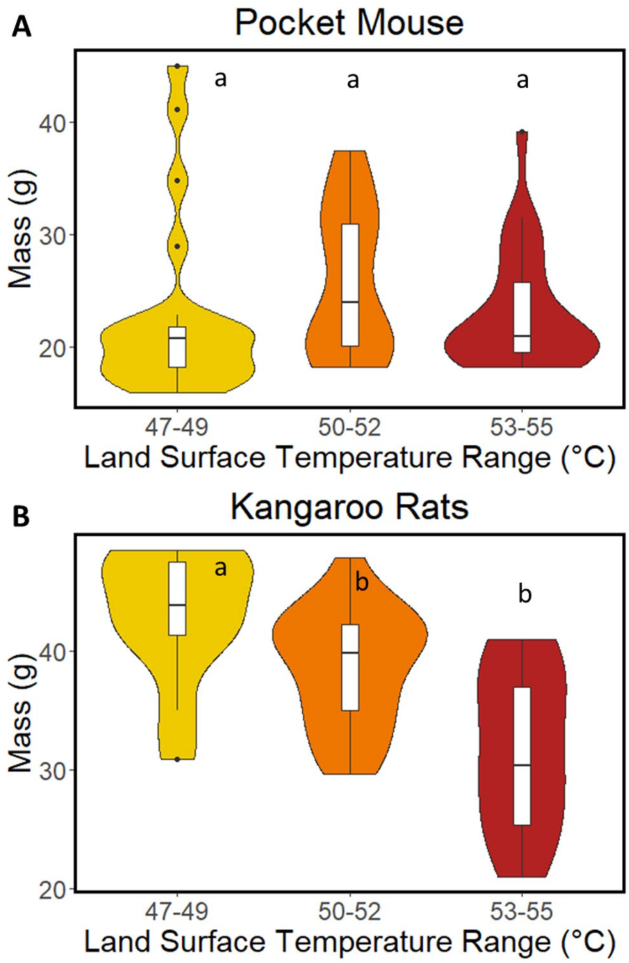

Fig. 3 Measure of mass (g) for (A) pocket mice (*Chaetodipus* spp. and *Perognathus* spp.) and (B) Merriam's kangaroo rats (*Dipodomys merriami*) captured from three strata of land surface temperature during 2019 and 2020 in Phoenix, Arizona. For (A), analysis of variance (ANOVA) and Tukey's honestly significant difference (HSD) post hoc test were used. For (B), Kruskal-Wallis test and post hoc pairwise comparisons using the Wilcoxon Rank Sum Test. Violin plot shows density/frequency in data, solid bars are medians and quartiles are shown. Different letters above symbolize significant results of Tukey test or pairwise comparisons

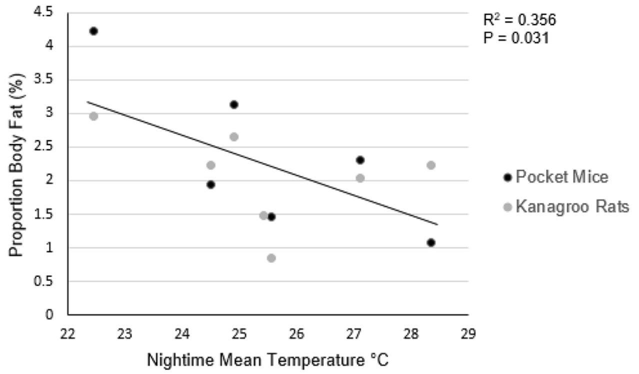

Fig. 4 Mean proportion body fat for rodents (n = 69 for *Chaetodipus* spp. and *Perognathus* spp., n = 47 for *Dipodomys merriami*) captured during 2019 and 2020 in the greater Phoenix metropolitan area, Arizona with negative association (r-squared = 0.356, P = 0.031) to nighttime temperatures. Mean proportion body obtained through quantitative magnetic resonance. Nighttime temperatures (nighttemp) record every 30 min for 22 days in June (2020) from 7 PM to 6 AM AZT based on sunrise and sunset periods

Relating proportion of body fat to environmental variables

The four environmental variables from seven sites were not sufficiently correlated ($P < 0.60$; Online Resource 11); therefore, all were included in models. We do note that urbanization and NDVI approach correlation, but overall these variables show little variability across the study sites. We considered all models with AIC weights over 2 (Burnham and Anderson 2004) and report the null model for comparison. The top model for pocket mice to predict proportion of body fat was the global model with all predictor variables (Table 1; Online Resource 12, 14). Pocket mice proportion of body fat was greatest in areas with more vegetation, lower nighttime temperatures, lower surface temperatures, and more urban land cover (Table 1). The top model for kangaroo rat to predict proportion of body fat was lower surface temperatures, which outperformed the null model (Table 2; Online Resource 13–14).

Table 1 General Linear Model (GLM) of environment variables (independent) to evaluate proportion body fat of pocket mice (*Chaetodipus* spp. and *Perognathus* spp.) at the site level using year one (2019) and year two (2020) data in Phoenix, Arizona. Top performing global model and null models reported. All other models did not outperform the null model. The "+" indicates a positive association while the "-" indicates a negative association to the environment variable(s)

	df	logLik	AICc	△AICc	weight	(Intercept)	NDVI	NightTemp	SurfaceTemp	Urbanization
global_model	6	27.5	-126.91	0	1	0.252	0.04	-0.003	-0.003	0.013
null	2	18.5	-29.06	97.85	0	0.024	-	-	-	-

Table 2 General Linear Model (GLM) of environment variables (independent) to evaluate proportion body fat of Merriam's kangaroo rats (*Dipodomys merriami*) at the site level using year one (2019) and year two (2020) data in Phoenix, Arizona. Top performing model and null models reported. All other models did not outperform the null model. The "-" indicates a negative association to the environment variable

	df	logLik	AICc	△AICc	weight	(Intercept)	NDVI	NightTemp	SurfaceTemp	Urbanization
model5	3	33.680	-53.359	0.000	0.971	0.150	-	-	-0.002	-
null	2	26.203	-45.407	7.952	0.018	0.022	-	-	-	-

Discussion

This is among the first studies to investigate how the UHI affects body condition of vertebrate wildlife in cities. Results supported the prediction that animals from hotter locations (both from long-term and field-collected data sources) had poorer body condition. However, this was somewhat unexpected because the focal species are desert-adapted rodents and have evolved to live in hot, arid environments. Models further corroborated the patterns by showing that proportion of body fat was related to areas with high vegetation, lower nighttime and surface temperatures, and greater urbanization for pocket mice. Models for kangaroo rats showed body fat was related to areas with lower surface temperatures. These results suggest aridland and urban species may be increasingly at risk, despite their adaptations to hot environments, due to a changing climate and the UHI effect. Species already persisting near their physiological limits (Walsberg 2000) may be especially vulnerable to increasing temperatures.

In this study, rodent body fat was negatively related to field collected nighttime temperatures. When fat is reduced, the chance of reproduction and survival is reduced for rodents (Moitra et al. 1998) and for mammals generally (Young 1976; Speakman 2008; Heldstab, 2017). Mice with no fat have been found to have decreased reproductive success and experienced premature death (Moitra et al. 1998). In female rabbits, Rödel et al. (2016) found that higher fat reserves could boost reproduction by increased litter size and total offspring growth. Additionally, Rödel et al. (2016) found decreased feeding effort during lactation. Similarly, Myers and Master (1983) found prairie deer mouse (*Peromyscus maniculatus bairdii*) mass was positively correlated with the number of young and average mass of young at birth. Studies on birds, which have similarly high metabolic demands from being endothermic, show similar patterns. The brood size of collared flycatchers (*Ficedula albicollis*) is decreased in females with poor body condition (Cichon et al. 1998). Adult female great white-fronted geese (*Anser albifrons frontalis*) body condition was positively related to survival (Schmutz and Ely 1999). These studies show a link between body fat and mass with reproduction and survival, implying that our results suggest that high environmental temperatures could have negative consequences on urban wildlife.

Environmental variables were also good predictors of body fat in this study for one of the focal species. The ability of rodents to survive and reproduce may be highly influenced by the availability of vegetation (Munger et al. 1983), and increases in desert rodent abundance and reproductive success after plant growth has been well documented (Chew and Butterworth 1964; Van de Graaff and Balda 1973; Petryszyn 1982). Petryszyn (1982) found increased plant production resulted in six times more heteromyid rodent density in the Sonoran Desert, Arizona. One study monitored rodent abundance in semi-arid areas and found a strong positive correlation with NDVI (Chidodo et al. 2020; Moses et al. 2012) found vegetation production to be among the highest supported models to predict kangaroo rat apparent survival. Overall, we did see a positive relationship between pocket mice proportion of fat and vegetation cover; however, values of NDVI across our study sites showed little variation (Online Resource 9) suggesting that sites were similar in habitat resources.

The built environment, consisting of buildings and paved surfaces, can raise temperatures in cities from from 3.6 to 14.4 °C (2 to 8 °F) (Golden et al. 2008). It is expected by 2030 that up to 60% of the world's population will live in urban areas (United Nations, 2002), and most of this population growth is expected to occur in arid areas (Baker et al. 2004). The increase in temperature due to the UHI effect and climate change may affect arid-adapted mammals greater, as many live at their physiological limits and are at risk of hyperthermia and mortality (Speakman and Król 2010). Our findings support these predictions, for both pocket mice and kangaroo rats. Additionally, we found that rodents had a greater proportion of body fat where site level nighttime temperatures were lower. Pocket mice body mass did not show this same trend, perhaps because we combined species of pocket mice with different maximum adult body masses. Nevertheless, the same trend is likely to hold true based on our findings with the kangaroo rats and on the results of other studies. For example, one study in New Mexico found a negative impact on apparent survival of banner-tailed kangaroo rats as daytime surface temperatures increase (Moses et al. 2012). Since kangaroo rats are known for their behavioral and physiological adaptations that allow them to survive in harsh desert conditions (Moses et al. 2012), their own struggle with rising temperatures forecasts potentially worse implications for less arid-adapted organisms.

Higher temperatures are likely to threaten rodent health and survival in a host of ways. High nocturnal surface temperatures may reduce foraging times if they exceed the TNZ of desert rodents (Kay 1975; Kay and Whitford 1978) and simultaneously reduce food resources since high temperatures could desiccate plant and seed materials. It is possible that desert rodent populations could acclimate to higher temperatures by increasing heat tolerance and adjusting rates of water loss or could respond by an upward shift in their TNZ or upper lethal zone (ULT; Tracy and Walsberg 2001). However, rodents may not be able to expend additional energy to dig deeper burrows or reduce surface activity for foraging, so environmental conditions that drive body temperatures above ULT could result in rodent mortality (Speakman and Król 2010; Moses et al. 2012) found temperatures in the Chihuahuan Desert, New Mexico taken 30 years previously had reached a maximum land surface temperature of 34 °C while measurements at the same site from 2006 to 2010 were 44–50 °C. To maintain water and food reserves, desert rodents may need to increase foraging activity, which could also increase the risk of predation (Moses et al. 2012). These threats are likely to be concerns for rodents worldwide due to global warming, but rodents living in cities may have an especially urgent need for climate acclimation due to the further temperature increases from the UHI effect.

With an 11.2% population increase over the last decade, the Phoenix metropolitan area is growing at a faster rate than any other major city in the USA (US Census Bureau, 2020). This growth makes Phoenix an ideal location to study the effect of urbanization on wildlife health. Our study showed that body condition, as measured by body fat, in pocket mice was positively related to degree of urbanization and kangaroo rat body condition was not impacted by urbanization. However, the relationship to urbanization may have been influenced by the presence of riparian forest at some sites. For instance, the Queen Creek Sossaman site contained one such riparian corridor, this forest area had a high urbanization index which could have influenced the model. However, similar to the variable of NDVI, degree of urbanization had low variation across our study (Online Resource 9).

Although we found no significant differences in relative abundance, the study was not designed to evaluate abundance and was instead focused on capturing the most animals efficiently for body measures. Future studies with trap grid designs may find differences in rodent abundance across temperature strata. Although our sample size for number of animals in the study was high to evaluate body condition across strata, there were limitations in relating body condition to specific environmental variables. Our sample size for the ecological models was limited to the number of field sites instead of individual animals. For future studies, increasing the number of sites of each treatment area could increase power to relate rodent body condition to environmental predictors. The results are robust, however, because over 100 animals were included in the study and both the comparison across land surface temperature strata and the ecological models point to temperature being a major predictor of animal fat.

Previous research on animal body condition uses methods that require euthanasia; however, we used the novel method of QMR, which allowed for the release of animals live back to their point of capture. QMR has been used to assess many organisms (Taicher et al. 2003; McGuire and Guglielmo 2010; Nixon et al. 2010; Riley et al. 2016) but hasn't been previously used to assess rodent health and the effect of heat on body condition. We found the least variation of QMR values occurred in fat measurements when compared to a known standard sample. These findings may suggest lean mass and water content may be imprecise compared to fat measurements by QMR. As such, body fat ensured the most consistent results for evaluating body condition across the urban heat interface. We found that QMR fat measurements were consistently accurate and precise. We suggest that future studies evaluate QMR results using a standard sample or other forms of body composition analysis to evaluate variability in QMR instrument measurements.

Conservation implications

Arid ecosystems are among the fastest areas to be urbanized (United Nations 2014). Moreover, the US southwest is predicted to become hotter and drier with climate change (National Oceanic and Atmospheric Administration 2013), which will potentially exaggerate the patterns found in this study. Climate change could have negative consequences for heteromyid rodent fitness because it may reduce their activity to forage during hot periods (Moses et al. 2012; Schweiger and Frey 2021). Climate change and the UHI effect could especially reduce survival during summer months due to increased heat stress, severe summer showers ruining food caches, desiccation of seeds, and increased snake predation resulting from longer active periods (Moses et al. 2012; Schweiger and Frey 2021) predict that climate change will reduce rodent activity during early summer periods, the period when females gather resources for reproduction, which will reduce fitness and reproductive success. Climate change and urban heat may result in poorer body condition and increased mortality for mothers and offspring. As Johnson et al. (2019) found that extreme heat slowed the growth of urban spiderlings and increased mortality. With the prediction of reduced reproductive success and increased mortality due to the rapid expanse of arid urban areas and the southwest climate change, urban arid wildlife could be especially vulnerable in the future. Our results suggest that high environmental temperatures could affect a rodent's ability to survive and reproduce. This research brings attention to the need to mitigate the effects of extreme heat on urban wildlife to protect these species.

Conclusion

Our study has implications for wildlife conservation in urban areas under increasingly warm conditions. The desert adapted rodents in this study are specialists of dry aridland conditions but may be unable to combat the rising global temperatures from climate change and urban infrastructure, which can reduce body fat. In mammals, lower body fat relates to lower rates of survival and reproductive success. Rodents and other small mammals are important links in trophic webs, and loss of these small consumers will likely have ramifications on predator abundance, as well. Therefore, measures to reduce urban heat stress, such as increasing urban green and blue infrastructure (such as riparian corridors), are needed to preserve wildlife and benefit human health and environments.

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Author contributions All authors contributed to the study conception and design. Original conceptualization, field methods and data collection, data archiving, data analyses and visualization, supervision, and project administration by Heather Bateman. Field and lab data collection, data summarization, and literature review were performed by Brittany Allen. QMR methodology and material preparation by Marianne Moore. Urban heat methodology and field temperature materials by David Hondula. The first draft of the manuscript was written by Brittany Allen as a thesis and all authors commented on previous versions of the manuscript. Final version edits by Heather Bateman.

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Code Availability Contact the authors for code.

Declarations

Conflict of interest The authors have no conflicts to declare.

Ethics approval Method protocol involving animal use was granted from Arizona State University Institutional Animal Care and Use Committee (Protocol #19-1719R to Marianne Moore) and Arizona Game and Fish Department Scientific Collection Permit (LIC #SP648546 to Heather Bateman).

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