Winter 2-2022

Keeping your cool: thermoregulatory performance and plasticity in desert cricetid rodents

Richard W. Ramirez
University of New Mexico - Main Campus

Eric A. Riddell
Iowa State University

Steven R. Beissinger
University of California - Berkeley

Blair W. Wolf
University of New Mexico - Main Campus

Recommended Citation

Ramirez, Richard W.; Eric A. Riddell; Steven R. Beissinger; and Blair W. Wolf. "Keeping your cool: thermoregulatory performance and plasticity in desert cricetid rodents." (2022). https://digitalrepository.unm.edu/biol_etds/347

Richard Ramirez
Candidate

Biology
Department

This thesis is approved, and it is acceptable in quality
and form for publication:

Approved by the Thesis Committee:

Dr. Blair Wolf, Chair
Dr. Christopher Witt
Dr. Joseph Cook

Keeping your cool: thermoregulatory performance and plasticity in desert cricetid rodents

By

Richard W. Ramirez,

Previous Degree

Bachelors of Science

THESIS

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Master of Science

Biology

The University of New Mexico

Albuquerque, New Mexico

May, 2022

Acknowledgements

We thank the National Park Service and the Desert Studies Center field station of CSU, especially Jason Wallace and Norma Charest. For their hard work gathering data in the Mojave heat, we thank Rosa Brasmer, Bill Talbot, Dylan Conradson, Britney Coe, Malik Alqawasmi and Armando Aispuro. Finally, we thank Dr Andrew McKechnie for feedback on the manuscript.

Keeping your cool: thermoregulatory performance and plasticity in desert cricetid rodents

By

Richard W. Ramirez,
Eric A. Riddell,
Steven R. Beissinger,
Blair O. Wolf

B.S., Biology, University of Montana, 2016

M.S., Biology, University of New Mexico, 2022

ABSTRACT

Small deserts mammals often avoid heat via nocturnality and fossoriality, and are thought to have a limited capacity to dissipate heat using evaporative cooling. Thermoregulation of small mammals exposed to high T_a is poorly understood, particularly responses across geographic and seasonal scales. We quantified the seasonal thermoregulatory performance of rodents exposed to high T_a, in the Mojave Desert. We measured metabolism, evaporative water loss and T_b using respirometry. When exposed to $T_a \geq T_b$, rodents showed steep increases in T_b, and limited evaporative heat dissipation. Most individuals were capable of maintaining T_a–T_b gradients of ~1°, resulting in low heat tolerance limits (T_a=43–45°C). We also observed significant increases in metabolism and evaporative water loss from summer to winter. Our results suggest that rodents have a limited physiological capacity to cope with environmental temperatures that exceed T_b and that a rapidly warming environment may increasingly constrain their nocturnal activity.

TABLE OF CONTENTS

Introduction

Physiological ecologists have shown a long-standing interest in the ability of small mammals to cope with the hot and arid conditions found in desert environments (Schmidt-Nielsen, 1950a). Many cricetid rodents, *Neotoma* (woodrats) and *Peromyscus* (mice), are very successful inhabitants of the extremely hot and arid Mojave, Colorado and Sonoran deserts. As a group, they show few physiological adaptations to desert life (Walsberg, 2000), and their successful occupation of hot deserts appears to be facilitated by avoidance of extreme heat via nocturnality and the use of burrows that minimize exposure to challenging conditions on the desert surface during the daylight hours (Brown, 1968; Bradley and Yousef, 1972; Lee, 1963; MacMillen, 1965, 1983). Recent work, however, suggests that these behavioral strategies may not fully buffer small mammals from high environmental temperatures (Tracy and Walsberg, 2002; Walsberg 2000) and that even nocturnal activity may be constrained by environmental temperature (Levy et al. 2016; Murray and Smith, 2012). Currently, we have little information on the thermoregulatory responses and limits of wild cricetid rodents to environmental temperatures approaching or exceeding normothermic body temperature (T_b), and as a consequence, we lack physiological and ecological contexts for understanding future responses to a warming climate.

Deserts are defined by water scarcity, and desert rodents, because of their small size, must balance their water budgets over a daily cycle. Consequently, understanding the costs of thermoregulation at environmental temperatures that approach and exceed T_b is essential for understanding the persistence of desert crictids. Avenues of water intake include water produced by metabolism, preformed dietary water, and water from drinking. Avenues of water loss include water lost via urine, feces, and evaporative losses from the skin and respiratory tract. Under benign thermal conditions (T_a <25°C), some rodents such as kangaroo rats, e.g. *Dipodomys merriami*, and a few cricetids such as the *Peromyscus crinitus*, can offset daily water losses and balance their water budgets solely via metabolic water production (MacMillen and Christopher, 1975; MacMillen and Hinds, 1983; Schmidt-Nielsen, 1964). During the spring and summer in the southwest deserts, benign environmental conditions largely disappear and burrow temperatures may exceed 30°C (Tracy and Walsberg 2002). When environmental temperatures approach and exceed normothermic T_b both metabolic heat and environmental heat loads must be dissipated through evaporative cooling to keep T_b from exceeding lethal levels. Under these conditions, rates of evaporative water loss (EWL) increase markedly and metabolic water production alone is not sufficient to offset large evaporative losses (Blackwell and Pivorun, 1979; Bradley and Yousef, 1975; Chew, 1951; Edwards and Haines, 1978; Hainsworth, 1968; MacMillen, 1983).

To date, most studies of the thermoregulatory performance of rodents at T_a above T_b have been carried out in laboratory rats and mice (*Rattus* and *Mus*). In laboratory animals and the few studies on wild rodents, evaporative cooling is accomplished by copious salivation which is sometimes accompanied by spreading of saliva onto the pelt (Chew, 1965; Hainsworth, 1968; Hart, 1971). Research on the thermoregulatory performance in wild cricetid rodents at T_a >37°C has primarily focused on metabolism (Hart, 1971; Yousef, 1980) and only a handful of studies characterized rates of EWL and variation in T_b (Brower and Cade, 1966; Layne and Dolan, 1975; Lee, 1963; Musser and Shoemaker, 1965; Nelson and Yousef, 1979; Weiner and Heldmaier, 1987). Efforts to partition evaporative heat loss into various pathways in rodents indicate that evaporative cooling via panting appears to be poorly developed (Adolph 1947; Chew 1951; Hudson, 1965; Leon et al. 2005; Wiegert 1961). Although cutaneous evaporation increases substantially in *Peromyscus* and house mice with increasing T_a, it appears insufficient to offset large exogenous heat loads (Edwards and Haines 1978). In all laboratory species studied to date, exposure to T_a above T_b results in rapid increases in T_b and a very limited evaporative cooling. In wild cricetids the capacity for evaporative cooling is poorly understood and the efficiency of the thermoregulatory response and its costs to the animal's water budget is unknown.

Rapidly increasing global temperatures (IPCC 2014) suggests that a more integrative understanding of thermoregulation in the heat would provide insight into the responses of cricetid populations to future climates. The desert rodent community has remained remarkably stable over the last century of climate change likely due to the ability to avoid extreme heat in their burrows (Riddell et al. 2021). However, predicting future responses to climate change will require an understanding of thermoregulatory performance at both the intra and interspecific levels. Few studies, however, have characterized thermoregulatory performance of rodents inhabiting hot desert environments (Brown 1968; Nelson and Yousef, 1979; McNab and Morrison, 1963); among these, Brown (1968) found that low versus high desert populations of *N. albigula* have lower body mass, higher conductance and superior vascular mechanisms for cooling, which lead to greater heat tolerance. There are no data for wild rodents that provide an integrative view of thermoregulatory performance that includes simultaneous measurements of body temperature, resting metabolic rate and EWL for animals exposed to T_a exceeding normothermic T_b. Data are also lacking which explore differences in seasonal and geographic thermoregulatory performance.

In this study, we examine both the spatial and temporal variation in thermoregulatory performance of rodents in the Mojave desert of California and characterize the costs associated with maintaining body temperature within critical thermal limits. To this end, we provide an integrated view of thermoregulatory performance by simultaneously measuring, metabolic rate (MR), evaporative water loss (EWL) and body temperature (T_b) over air temperatures (T_a) ranging from 10-48°C in four sympatric rodents (*Neotoma lepida* Thomas 1893 (desert woodrat), *Neotoma albigula* Hartley 1894 (white-throated woodrat), *Peromyscus eremicus* Baird 1858 (cactus mouse), *Peromyscus crinitus* Merriam 1891 (canyon mouse)) at different sites during both summer and winter. Our study focused on the following questions. 1) Does heat exposure produce a marked hyperthermic response and/or evoke a strong evaporative cooling response in cricetid rodents? Is the thermal response metabolically costly? We predict that heat exposure will produce rapid increases in T_b and that any up-regulation of evaporative cooling will be metabolically costly because of the costs of salivation and wiping behavior. 2) Do cricetids rodents show heat tolerance limits that are well above T_b demonstrating highly effective evaporative cooling? How does the effectiveness of this cooling strategy compare to other taxa like birds? Because most birds are diurnal and confront desert environments directly, we predict that birds will show higher heat tolerances and cooling capacity than the nocturnally active rodents 3) Do the thermoregulatory responses of cricetids across sites and season show significant plasticity within and among populations? We predict that a limited capacity for responding to heat stress within species will confer limited flexibility across sites and seasons. 4. Finally, we use our measurements to examine the potential water balance costs of cooling that might allow continued activity in a warming environment.

MATERIALS AND METHODS

Study species and sites

The Cricetidae is a large family of ubiquitous rodents that includes the New World rats and mice. Representatives of this family are found on three continents in virtually all environments. In the deserts of the American Southwest, *N. albigula* ranges from Colorado to Central Mexico and from California to Texas (Macedo and Mares, 1988), *N. lepida* and *P. crinitus* range from Oregon to the southern tip of the Baja Peninsula and from California to Utah (Johnson and Armstrong, 1987; Verts and Carraway, 2002) and *P. eremicus* occur from Nevada into Central Mexico and California into Texas (Veal and Caire 1979. *Neotoma* are nocturnal herbivorous rats that feed primarily on seeds, green vegetation and succulents. *Peromyscus* are nocturnal omnivorous mice that feed on insects, seeds and green vegetation (Orr et al. 2015).

We examined cricetidae thermoregulation during the summers (June-August) and winters (January-February) of 2017 and 2018. We collected data at two sites in the summer and winter, Joshua Tree National Monument and Zzyzx, and only during the summer at the two Midhills sites (Fig 1). The biome at the Joshua Tree National Park site (33.72898, -115.82505, elevation 1000 m) was desert dry wash and creosote brush scrub with an annual precipitation, and a mean and annual high temperatures of 137 mm, 17 °C, and 25 °C, respectively. Zzyzx (35.12731, -116.11793, 300 m) was the hottest and driest site with 108 mm of annual precipitation and , and a mean and annual high temperature of 21°C and 30°C. At Zzyzx we trapped in the salt brush scrub biome. The Midhills low site (35.1669, -115.45377, 1,400m), was predominantly Joshua tree woodland which received 175 mm annual precipitation, , and a mean and annual high temperatures were 15 °C and 22 °C. Our coolest site, Midhills high (35.14148, -115.4083, 1,600 m) was sagebrush scrub with 209 mm of precipitation, , and a mean and annual high temperatures of 14 °C and 20 °C. At the extreme, T_as at Zzyzx routinely exceed 43°C each year for more than 30 days during the summer. While minimum temperatures at Midhills high commonly drop below -5 °C during the winter. The climate data for each site above were estimated using the 30 year daily normals (1981-2010) from the PRISM Climate and Weather System (PRISM Climate Group, Oregon State University).

We used Sherman folding traps (H.B. Sherman Traps, Inc. Tallahassee, FL. XLF15) baited with mixed birdseed (Audubon Park Wild Bird Food) for animal collection. Trapping arrays were line transects approximately 120 m in length, with traps set every 3 m. We also set traps at woodrat middens and burrow entrances. We only studied adult males or adult females that did not show obvious signs of pregnancy or lactation.

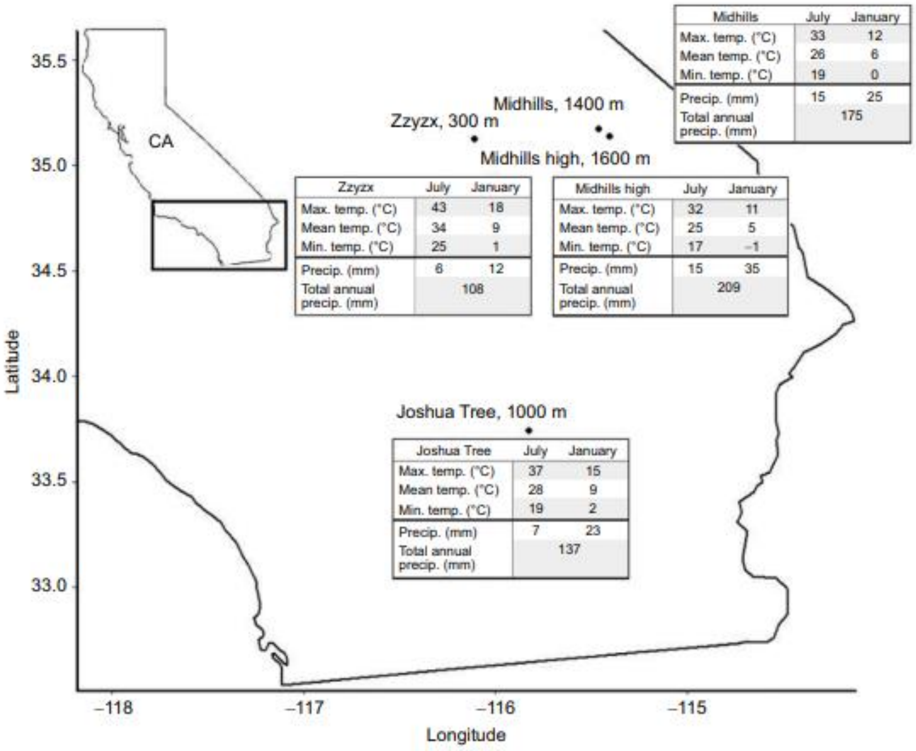


Fig. 1. Map of Southern California, showing the location of each study site. The location is denoted by a black dot, with the name of the site and elevation. The values reported are the mean 30 year climate normals for July and January at each location produced from PRISM Climate data. The minimal and maximal temperatures are the mean daily low and high temperatures from the 30 year climate normals for July and January.

All trapping occurred more than 200 m away from any occupied human structure to avoid capturing animals acclimatized to air-conditioned environments. Following each experiment, we returned rodents to their traps and offered seeds and celery for rehydration. We held animals in Sherman traps in a cool, quiet area for no longer than 12 hours and released animals at their capture location. We obtained research permits from the CA Department of Wildlife, Joshua Tree National Park (JOTR-2015-SCI-0032) and Mojave National Preserve (MOJA SC-13686, MOJA-2015-0036). The Animal Care and Use Committee of the University of New Mexico approved all protocols (16-200518-MC).

Gas exchange measurements

We measured CO_2 production and total evaporative water loss (EWL) using positive pressure flow-through respirometry. A pump (Gast, Benton Harbor, MI. DAA-V 15-EB) pushed atmospheric air through a column of Drierite^{TM}. On humid days we also used a column of silica gel before the Drierite^{TM} column. The air then passed through a mass flow controller (Alicat Scientific, Tucson, AZ. MC-5SLPM, MC-20SLPM, Mass Flow Controller, accuracy: ± 0.8% of reading + 0.2% of full scale) at flow rates ranging from 0.5 to 15 L min^{-1} STP. We adjusted the flow rate to maintain respirometry chambers at dew points < 5°C, which allowed for uninhibited evaporative cooling (Lasiewski et al.1966). Dry air then moved through clear, airtight plastic containers containing the animals (*Peromyscus* in 1.1L, 11.4 x 13.3 x 7.6 cm; *Neotoma* in 3.6L, 22.8 x 15.2 x 10.1 cm). A wire mesh platform in the bottom of the chambers suspended the animals above 2-3 cm of mineral oil. The oil captured urine and feces preventing fecal and urinary water from entering the airstream. A thermocouple (Physitemp, Clifton, NJ. model RET-4) connected to a National Instruments thermocouple module recorded the chamber temperature. We subsampled excurrent air from the chambers (~400ml min^{-1}) and directed the air to the CO_2 H_2O^{-1} gas analyzers (Li-Cor, Lincoln, NE, model 840A, accuracy ± 1ppm CO_2, ±0.01% reading for H_2O). For data acquisition, we connected the gas analyzers, thermocouples, and mass flow controllers to a National Instruments^{TM} DAQ and visualized using LabVIEW (National Instruments^{TM}, Austin, TX.).

We zeroed and spanned the CO_2 analyzers using Ascarite (Thomas Scientific, Swedesboro, NJ) and gas with a known concentration of 1840 ppm CO_2. We used Drierite^{TM} and a dew point generator (Li-Cor, Lincoln, NE, model 610) to zero and span the water channels and the zero on these analyzers were checked daily. We verified the mass flow controller calibrations at the beginning of each field season against a precision calibrated reference mass flow meter (Alicat Scientific, Tucson, AZ. M-20SLPM-D, 0 - 20L min^{-1}, accuracy: ± 0.4% of reading + 0.2% of full scale) over its full range. The mass flow controllers varied from the reference mass flow meter by < ± 0.04 L min^{-1}.

Experimental trials began with a rest period where animals were held in the dark in an unconnected metabolic chamber at a temperature of 25-28°C and allowed to sit quietly for 50-75 min. After this period, we placed the chambers in the environmental chamber and connected airflow lines and thermocouples to begin the trial. Experimental trials lasted 4-5 hours, and we held animals at each experimental air temperature until we obtained stable CO_2 readings. Once CO_2 values stabilized we recorded a 15-minute sample period for each temperature treatment, followed by a 5 minute baseline period. We ran metabolic trials during the rest phase of the circadian cycle, and we tracked animal activity continuously using infrared security cameras (Uniden® Guardian, Tokyo, Japan UDS655). Animals that showed moderate to high activity in the chambers were removed from the analysis.

Experimental air temperature (T_a) in the chamber ranged from 10-44°C, and we ramped the chamber T_a at 2-8°C intervals over 30-60 minutes during trials. We typically obtained data at five T_a values for each animal, and we limited trials to lengths where mass loss did not exceed 5% of M_b to minimize the effects of dehydration on cooling efficiency. We recorded and monitored body temperature (T_b) in real-time during trials via passive integrated transponder (PIT) (BioMark®, Boise, ID. BioThermo13, accuracy ± 0.02°C (Whitfield et al. 2015) using a Biomark® HPR Plus reader. The PIT tag was implanted sub-dermally between the shoulders of each rodent using a tag injector (Biomark® MK10) at least one hour prior to placing the animal in a chamber. Immediately prior to and after each trial, we obtained rectal temperatures and compared these values to the PIT tag readings. We used a measured approach to minimize mortality by estimating HTL values using criteria based on behavior, continuous escape attempts, physiological responses including a depression in CO_2 production, rapid spikes in T_b, or T_b increasing to 43°C (McKechnie and Wolf 2020). Animals exposed to high temperatures were cooled rapidly after removal from the experimental trial by holding the animals in front of a fan in the cool room.

Calculations

We used R version 3.5.1 (R Core Team, 2013) to calculate the MR and EWL rates from our raw values of EWL using equations 10.5 and 10.9 of Lighton (2008). Using a running mean, we selected the lowest average stable minute from each 15-minute sampling period. We assumed that animals fed in the traps before testing, and thus we assumed a respiratory quotient (RQ) of 0.95, a value derived from the proportion and nutritional content of the seeds used as bait (Walsberg and Wolf 1995). We converted rates of CO_2 production into metabolic rates using a thermal equivalent of 21.5 J ml^{-1} CO_2 (Withers, 1992). We converted rates of EWL to heat loss using 2.43 kJ g^{-1} H_2O (Lighton, 2008). We used the *segmented* package in R to identify the T_a associated with the upper and lower critical temperatures as well as inflection T_a for T_b and EWL (Muggeo 2003). We determined individual HTL as the highest air temperature where T_b remained below lethal levels (43°C). We estimated maximum values for MR, EWL and evaporative heat loss (EHD = EHL* MHP^{-1}) at the HTL using the slope intercept form from the regression lines drawn above the critical points and at the heat tolerance limit. We defined metabolic and evaporative scope as the ratio of MR or EWL at the heat tolerance limit divided by the respective value at thermal neutrality ($\frac{EWL_{HTL}}{EWL_{TNZ}}, \frac{MR_{HTL}}{MR_{TNZ}}$).

Statistical analyses

We used R version 3.5.1 (R Core Team, 2013) to conduct the statistical analyses. We compared physiological responses across seasons and sites using a species-specific analyses using Type-II analysis of covariance (ANCOVA). with individual as a random effect. To generate *p* values, we used a Type-II ANCOVA from the lmerTest() package that uses a Kenward Rogers approximation to Satterthwaite's methods for denominator degrees of freedom (Kenward and Roger 1997). We analyzed the effects of mass across sites and seasons, using linear regression analysis with a Type-II analysis of variance (ANOVA) from the *car* package to evaluate significance (Langsrud 2003). We conducted separate analyses on MR below the lower critical temperature (T_{lc}), above the upper critical temperature (T_{uc}), and within the thermal neutral zone (TNZ). Similarly, we analyzed changes in T_b at T_a above and below the inflection of the hyperthermic response. For EWL, we examined changes in rates of EWL above and below the inflection point at which animals showed a marked increase in evaporative cooling. For each analysis, we removed sites and species with only a single season of data to balance the statistical design.

Results

Body mass

N. albigula body mass (M_b = 124.1g, 95% CI: 118 to 130.2g, $N_{animals}$=13) was the largest of the species followed by *N. lepida* (M_b=112.8 g, 95% CI: 111.2 to 114.3g, $N_{animals}$=155), *P. eremicus* (M_b=18.9g, 95% CI: 18.7 to 19.2 g, $N_{animals}$=88), and *P. crinitus* (M_b=12.7, 95% CI: 12.6 to 12.8g, $N_{animals}$=111). We found significant differences among sites in the mass of *N. lepida* ($F_{4,139}$ = 5.32, $p < 0.001$) and *P. crinitus* ($F_{2,100}$ = 9.54, $p < 0.001$), with M_b varying by as much as 23.9% and 31.9% among sites, respectively (Table 1). We recorded the lowest body masses in populations from Zzyzx the warmest .habitat.

Behavioral observations

During high temperature trials, animals we observed licking their inguinal area and forearms at T_a ~ 38-39°C. Animals could clearly be seen salivating and at higher temperatures (T_a > 41°C), the fur was often noticeably wet when they were removed from the chamber at the end of a trial.

Body temperature and heat tolerance limits

In both *Neotoma* and *Peromyscus,* we found no systematic offset between our rectal T_b values and PIT tag values at any T_a (Fig. S1, S2, and Table S1). There was little variation in normothermic T_b across species with values averaging ~ 36 °C, when T_a varied between 10-

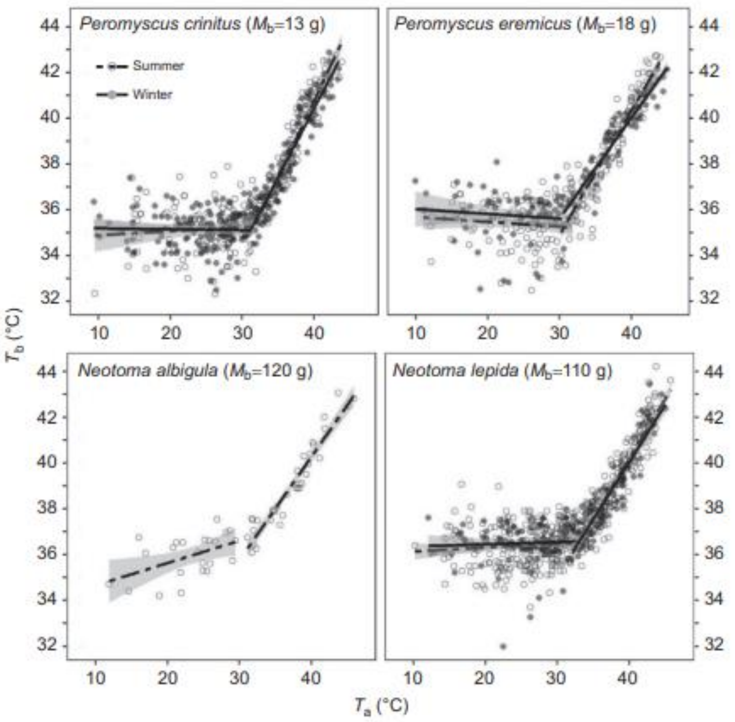


Fig. 2. Body temperature (T_b) as a function of air temperature (T_a) in four species of desert rodents. Seasonal values are displayed (summer, winter); shading denotes 95% confidence interval (CI). Little variation was observed in normothermic T_b across species, with values averaging ~35.5°C in *Peromyscus* and ~36°C in *Neotoma*. All species showed a hyperthermic response to increasing T_a, which varied by season. M_b, body mass.

31 °C (Fig. 2, Table 1). All species showed a hyperthermic response to increasing T_as starting in *Peromyscus* at T_a ~ 31°C and Neotoma at T_a ~ 33°C (Fig. 2, Table 1) Species-specific analyses indicated the differences associated with the interaction between site and season were primarily driven by *N. lepida* ($F_{1,62.3} = 25.40$, $p < 0.001$) *and P. crinitus* ($F_{1,73.7} = 3.97$, p =

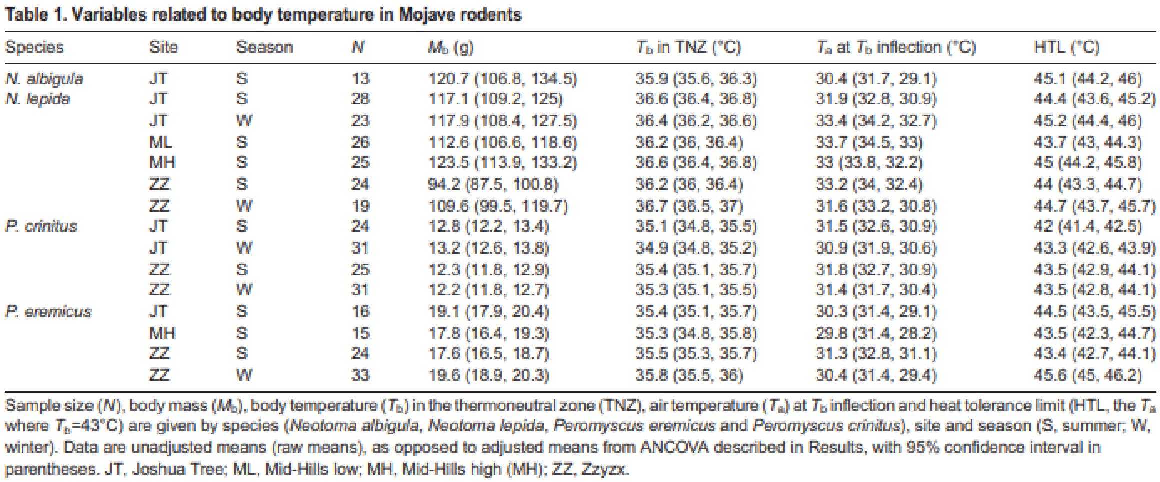


Table 1. Variables related to body temperature in Mojave rodents

Species	Site	Season	*N*	M_b (g)	T_b in TNZ (°C)	T_a at T_b inflection (°C)	HTL (°C)
N. albigula	JT	S	13	120.7 (106.8, 134.5)	35.9 (35.6, 36.3)	30.4 (31.7, 29.1)	45.1 (44.2, 46)
N. lepida	JT	S	28	117.1 (109.2, 125)	36.6 (36.4, 36.8)	31.9 (32.8, 30.9)	44.4 (43.6, 45.2)
	JT	W	23	117.9 (108.4, 127.5)	36.4 (36.2, 36.6)	33.4 (34.2, 32.7)	45.2 (44.4, 46)
	ML	S	26	112.6 (106.6, 118.6)	36.2 (36, 36.4)	33.7 (34.5, 33)	43.7 (43, 44.3)
	MH	S	25	123.5 (113.9, 133.2)	36.6 (36.4, 36.8)	33 (33.8, 32.2)	45 (44.2, 45.8)
	ZZ	S	24	94.2 (87.5, 100.8)	36.2 (36, 36.4)	33.2 (34, 32.4)	44 (43.3, 44.7)
	ZZ	W	19	109.6 (99.5, 119.7)	36.7 (36.5, 37)	31.6 (33.2, 30.8)	44.7 (43.7, 45.7)
P. crinitus	JT	S	24	12.8 (12.2, 13.4)	35.1 (34.8, 35.5)	31.5 (32.6, 30.9)	42 (41.4, 42.5)
	JT	W	31	13.2 (12.6, 13.8)	34.9 (34.8, 35.2)	30.9 (31.9, 30.6)	43.3 (42.6, 43.9)
	ZZ	S	25	12.3 (11.8, 12.9)	35.4 (35.1, 35.7)	31.8 (32.7, 30.9)	43.5 (42.9, 44.1)
	ZZ	W	31	12.2 (11.8, 12.7)	35.3 (35.1, 35.5)	31.4 (31.7, 30.4)	43.5 (42.8, 44.1)
P. eremicus	JT	S	16	19.1 (17.9, 20.4)	35.4 (35.1, 35.7)	30.3 (31.4, 29.1)	44.5 (43.5, 45.5)
	MH	S	15	17.8 (16.4, 19.3)	35.3 (34.8, 35.8)	29.8 (31.4, 28.2)	43.5 (42.3, 44.7)
	ZZ	S	24	17.6 (16.5, 18.7)	35.5 (35.3, 35.7)	31.3 (32.8, 31.1)	43.4 (42.7, 44.1)
	ZZ	W	33	19.6 (18.9, 20.3)	35.8 (35.5, 36)	30.4 (31.4, 29.4)	45.6 (45, 46.2)

Sample size (*N*), body mass (M_b), body temperature (T_b) in the thermoneutral zone (TNZ), air temperature (T_a) at T_b inflection and heat tolerance limit (HTL, the T_a where T_b=43°C) are given by species (*Neotoma albigula*, *Neotoma lepida*, *Peromyscus eremicus* and *Peromyscus crinitus*), site and season (S, summer; W, winter). Data are unadjusted means (raw means), as opposed to adjusted means from ANCOVA described in Results, with 95% confidence interval in parentheses. JT, Joshua Tree; ML, Mid-Hills low; MH, Mid-Hills high (MH); ZZ, Zzyzx.

0.050). *N. lepida* T_b rose 0.02°C and *P. crinitus* T_b increased 0.01°C above the inflection point for the onset of hyperthermia during the summer at Joshua Tree. Conversely at Zzyzx T_b above the inflection point during the summer decreased 0.01 for *N. lepida* and 0.002°C for *P. crinitus*. In contrast, *P. eremicus* exhibited a trend for a slightly higher T_b above the inflection point in the winter compared to the summer at Zzyzx ($F_{1,37.2} = 3.17$, $p = 0.083$).

We selected an endpoint T_b of 43°C for all trials as its exceedance produced rapid death (also see Leon et al. 2005). Some animals that were removed from the chamber at T_b= 43°C continued to experience increases in T_b from increased activity or thermal inertia. We observed death in individual animals at T_b = 43.5 °C in *N. lepida*; T_b = 42.7, 43.2, 44, 45°C in *P. eremicus*, and T_b = 45.8°C in *P. crinitus*. In general, *N. lepida* showed slightly higher HTL T_a ~ 44.5 °C, in comparison to *P. crinitus* T_a ~ 43.5 °C, and *P. eremicus at* T_a ~ 44 °C,. (Table 1). At the HTL, *N. lepida* and *P. eremicus* were able to defend a T_b -T_a gradient of approximately 1.5 °C, while *P. crinitus* could only defend a gradient of 0.5 °C (Table 1). We did not observe a consistent relationship between heat tolerance limit and site or season.

Metabolic rate

The larger *Neotoma* showed a slightly broader thermal neutral zone, *N. albigula* ~ 27-37 °C, *N. lepida* ~27.5-35 °C, in comparison to the smaller *P. crinitus* ~29.5-35 °C, *P. eremicus* ~28-36 °C (Fig 3, table 2). The resting metabolic rates of all species increases from summer to winter; *N. lepida* increased resting metabolism during the winter by 39.3% ($F_{1,76.3} = 47.10$,

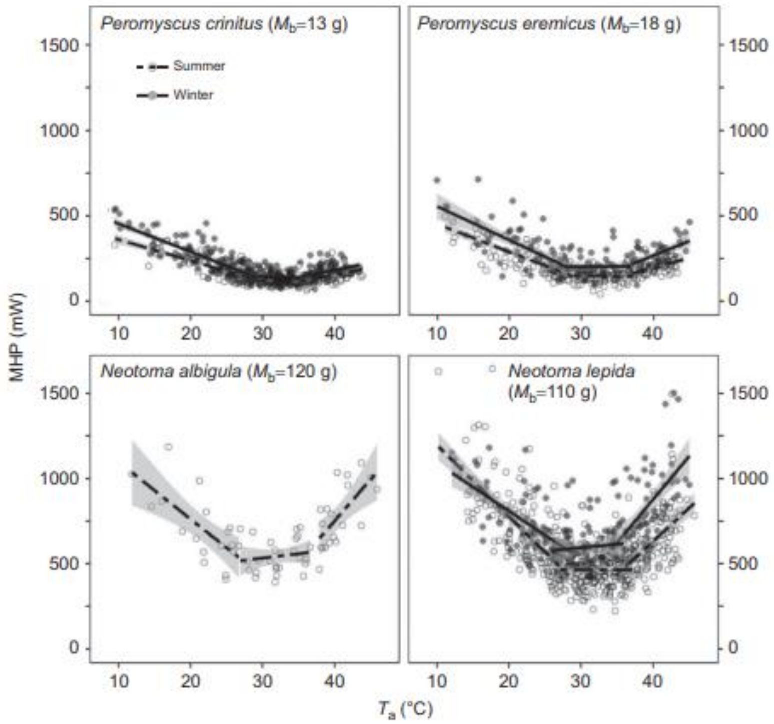


Fig. 3. Resting metabolic rate (RMR) as a function of T_a among four species of desert rodents. Seasonal values are displayed (summer, winter); shading denotes 95% CI. All species showed a general increase in metabolic heat production (MHP) during the winter. Above the upper critical temperature (T_{uc}), RMR was influenced by M_b and T_a.

$p < 0.001$), *eremicus* by 37.8% ($F_{1,44.04} = 9.74$, $p = 0.003$) and *P. crinitus* by 19.2% ($F_{1,89.9} = 13.41$, $p < 0.001$). At Zzyzx, *N. lepida* increased MR by 43.8% from summer to winter, which was much higher than the 13.3% increase observed at Joshua Tree ($F_{1,76.6} = 8.65$, $p = 0.004$). The upper critical temperature (T_{uc}), the T_a marked by a steep increase in metabolic rate, varied seasonally and was higher in the larger *Neotoma* compared to *Peromyscus* (Table

Table 2. Variables related to metabolism in Mojave rodents

Species	Site	Season	RMR (mW g^{-1})	RMR (mW)	T_{lc} (°C)	T_{uc} (°C)	MR slope (mW g^{-1} °C^{-1})	MR_{HTL} (mW g^{-1})	MR scope
N. albigula	JT	S	4.5 (4.1, 4.7)	546.4	26.7 (24.5, 28.8)	37.1 (35.4, 38.8)	0.6	9.7 (8.1, 11.2)	2.2
N. lepida	JT	S	4.4 (4.1, 4.7)	517.2	27.1 (25.4, 28.8)	34.7 (32.5, 36.9)	0.3	7.4 (6.4, 8.3)	1.7
	JT	W	5.2 (4.7, 5.4)	582.3	28.8 (26.1, 31.5)	34.2 (32.4, 36.1)	0.4	11.8 (9.1, 14.4)	1.7
	ML	S	4.1 (3.8, 4.3)	454.4	27 (25.2, 28.8)	37.4 (35.8, 39.1)	0.5	7 (6.1, 7.8)	1.7
	MH	S	4 (3.8, 4.3)	493.8	27.8 (26.2, 29.4)	35.6 (33.6, 37.6)	0.3	6.9 (6.3, 7.6)	1.7
	ZZ	S	4 (3.7, 4.2)	374	28.6 (27.2, 30)	36 (34.4, 37.5)	0.4	7 (6.3, 7.7)	1.8
	ZZ	W	5.5 (5.2, 5.8)	599.3	25.5 (23.4, 27.7)	36.3 (34.3, 38.3)	0.6	9.2 (7.7, 10.6)	1.7
P. crinitus	JT	S	10 (9.3, 10.7)	127.6	29.6 (27.8, 31.5)	35.8 (33.4, 38.2)	0.8	15.2 (13.3, 17.1)	1.5
	JT	W	10.8 (10, 11.5)	144.6	29.3 (28.1, 30.6)	35.5 (33.7, 37.2)	0.9	17.8 (15.8, 19.7)	1.7
	ZZ	S	8.7 (8.1, 9.3)	107.4	29.6 (28.5, 30.7)	34.9 (32.5, 37.3)	0.7	14.9 (13, 16.9)	1.7
	ZZ	W	11.3 (10.8, 11.8)	134.2	29.2 (28, 30.4)	34.9 (32.9, 36.9)	0.7	17.4 (15.6, 19.3)	1.5
P. eremicus	JT	S	8.2 (7.4, 8.9)	152.1	29.4 (26.9, 31.9)	37.3 (35.9, 38.8)	1.2	16.1 (14.4, 17.9)	2
	ML	S	7.8 (7.3, 8.4)	140.2	27.4 (24.8, 30)	35 (32.4, 37.6)	0.6	13.2 (11.5, 14.9)	1.6
	ZZ	S	8.4 (7.9, 9)	151.5	28.1 (27.5, 30.3)	35.1 (32.1, 38.1)	0.5	12.8 (11, 14.7)	1.5
	ZZ	W	10.5 (9.8, 11.5)	204.3	28 (25.7, 30.3)	36.8 (34.9, 38.7)	0.9	22.8 (19.4, 26.2)	1.7

Mass-specific resting metabolic rate (RMR), total RMR, lower critical temperature (T_{lc}), upper critical temperature (T_{uc}), metabolic rate (MR) slope ($>T_{uc}$), MR at the heat tolerance limit (HTL) and MR scope (MR_{HTL}/MR_{TNZ}, where TNZ is thermoneutral zone) are given by species (*Neotoma albigula*, *Neotoma lepida*, *Peromyscus eremicus* and *Peromyscus crinitus*), site and season (S, summer; W, winter). Data are unadjusted means (raw means), as opposed to adjusted means from ANCOVA described in Results, with 95% confidence interval in parentheses. JT, Joshua Tree; ML, Mid-Hills low; MH, Mid-Hills high (MH); ZZ, Zzyzx.

2). Above the upper critical point, *N. lepida* increased MR from summer to winter by 30.9% ($F_{1,67.9} = 37.17$, $p < 0.001$), *P. eremicus* by 32.5% ($F_{1,31.3} = 15.92$, $p < 0.001$), and *P. crinitus* by 17.5% ($F_{1,71.5} = 17.34$, $p < 0.001$). At Zzyzx, *N. lepida* increased MR from summer to winter by 64.4% which was much greater than the 19.3% increase observed in Joshua Tree animals ($F_{1,71} = 5.76$, $p = 0.019$).

Evaporative water loss

Thermoneutral EWL was highly associated with M_b and T_a at the species level for *N. lepida* (M_b: $F_{1,81.99} = 7.09$, $p = 0.009$; $T_a = F_{1,260.1} = 46.83$, p < 0.001), but not *P. eremicus* (M_b: $F_{1,39.42} = 0.093$, $p = 0.340$; $T_a = F_{1,159} = 1.98$, $p = 0.161$). For *P. crinitus*, thermoneutral EWL was associated with M_b ($F_{1,95.72} = 10.61$, $p = 0.002$) and T_a ($F_{1,347.7} = 6.71$, $p = 0.01$) (Fig 4, Table 3). Seasonally, thermoneutral values for EWL were 20.0% higher during the winter compared to summer for *N. lepida* ($F_{1,81.65} = 5.72$, $p = 0.02$), 43.7% higher during the winter

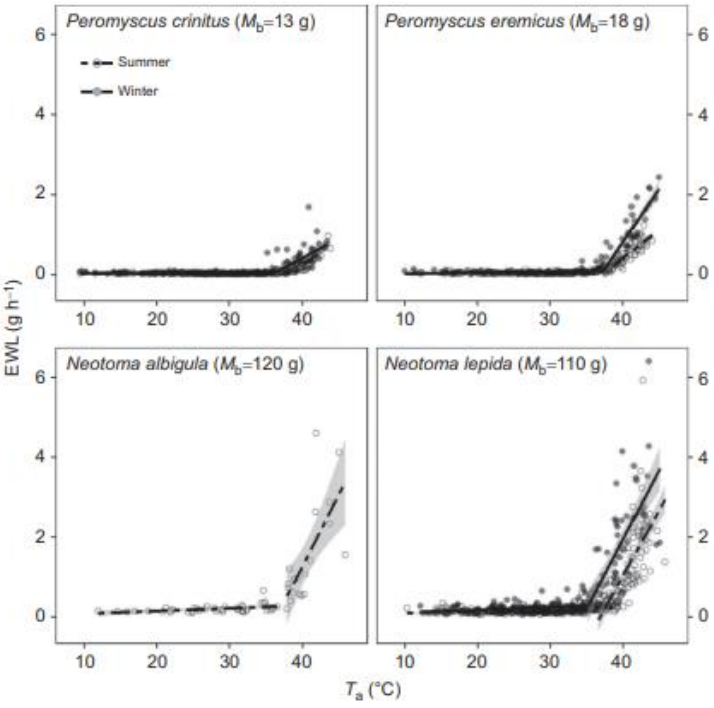
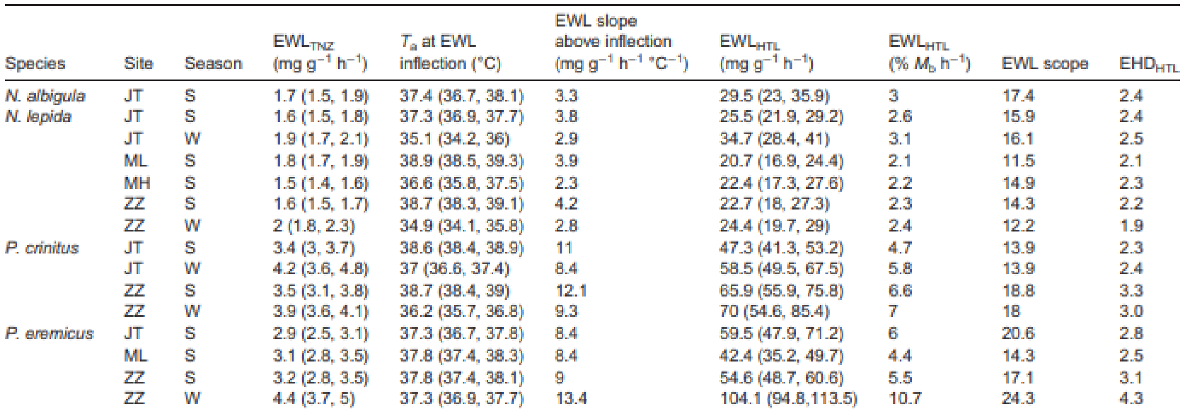


Fig. 4. Evaporative water loss (EWL) as a function of T_a in four species of desert rodents. Seasonal values are displayed (summer, winter); shading denotes 95% CI. EWL increased from summer to winter. EWL rates above the inflection point were influenced by M_b and T_a in all species.

for *P. eremicus* ($F_{1,38.4}$ = 10.18, p = 0.002), and 25.1% higher during the winter for *P. crinitus* ($F_{1,93.1}$ = 20.22, p < 0.001). Average rates of EWL within the TNZ ranged from 1.6 to 4.4 mg g^{-1} h^{-1} across all species, sites and seasons. Maximal rates of EWL at the HTL where 29.5 mg g^{-1} h^{-1} for *N. albigula*, and ranged from 20.7-34.7 mg g^{-1} h^{-1} *for N. lepida* , 42.4-104.1 mg g^{-1} h^{-1} for *P. eremicus,* and finally 47.3- 70 mg g^{-1} h^{-1} for *P. crinitus* 24.4 to 70 mg g^{-1} h^{-1} (Table 3).

Rates of evaporative water loss above the inflection point for evaporative cooling increased from summer to winter and varied among species (Table 3). EWL values increased by 65.0% from summer to winter in *N. lepida* ($F_{1,72.6}$ = 209.26, p < 0.001), and by 66.6% in *P. eremicus* ($F_{1,38.5}$ = 20.20, p < 0.001), and by 68.4% in *P. crinitus* ($F_{1,81.4}$ =18.88, p < 0.001). Seasonal responses within species also sometimes varied by site with the population at Zzyzx showing greater seasonal increase compared to the Joshua Tree population (Table 3). *N. lepida* from the Zzyzx population showed a 128% increase from summer to winter, which was much greater than the 37.5% increase observed in the Joshua Tree population ($F_{1,55.5}$ = 5.23, p = 0.026). The Zzyzx *P. crinitus* population also showed a large seasonal

Table 3. Variables related to evaporative water loss in four Mojave rodents



Species	Site	Season	EWL_{TNZ} (mg g^{-1} h^{-1})	T_a at EWL inflection (°C)	EWL slope above inflection (mg g^{-1} h^{-1} °C^{-1})	EWL_{HTL} (mg g^{-1} h^{-1})	EWL_{HTL} (% M_b h^{-1})	EWL scope	EHD_{HTL}
N. albigula	JT	S	1.7 (1.5, 1.9)	37.4 (36.7, 38.1)	3.3	29.5 (23, 35.9)	3	17.4	2.4
N. lepida	JT	S	1.6 (1.5, 1.8)	37.3 (36.9, 37.7)	3.8	25.5 (21.9, 29.2)	2.6	15.9	2.4
	JT	W	1.9 (1.7, 2.1)	35.1 (34.2, 36)	2.9	34.7 (28.4, 41)	3.1	16.1	2.5
	ML	S	1.8 (1.7, 1.9)	38.9 (38.5, 39.3)	3.9	20.7 (16.9, 24.4)	2.1	11.5	2.1
	MH	S	1.5 (1.4, 1.6)	36.6 (35.8, 37.5)	2.3	22.4 (17.3, 27.6)	2.2	14.9	2.3
	ZZ	S	1.6 (1.5, 1.7)	38.7 (38.3, 39.1)	4.2	22.7 (18, 27.3)	2.3	14.3	2.2
	ZZ	W	2 (1.8, 2.3)	34.9 (34.1, 35.8)	2.8	24.4 (19.7, 29)	2.4	12.2	1.9
P. crinitus	JT	S	3.4 (3, 3.7)	38.6 (38.4, 38.9)	11	47.3 (41.3, 53.2)	4.7	13.9	2.3
	JT	W	4.2 (3.6, 4.8)	37 (36.6, 37.4)	8.4	58.5 (49.5, 67.5)	5.8	13.9	2.4
	ZZ	S	3.5 (3.1, 3.8)	38.7 (38.4, 39)	12.1	65.9 (55.9, 75.8)	6.6	18.8	3.3
	ZZ	W	3.9 (3.6, 4.1)	36.2 (35.7, 36.8)	9.3	70 (54.6, 85.4)	7	18	3.0
P. eremicus	JT	S	2.9 (2.5, 3.1)	37.3 (36.7, 37.8)	8.4	59.5 (47.9, 71.2)	6	20.6	2.8
	ML	S	3.1 (2.8, 3.5)	37.8 (37.4, 38.3)	8.4	42.4 (35.2, 49.7)	4.4	14.3	2.5
	ZZ	S	3.2 (2.8, 3.5)	37.8 (37.4, 38.1)	9	54.6 (48.7, 60.6)	5.5	17.1	3.1
	ZZ	W	4.4 (3.7, 5)	37.3 (36.9, 37.7)	13.4	104.1 (94.8,113.5)	10.7	24.3	4.3

Evaporative water loss (EWL) in the thermoneutral zone (TNZ), air temperature (T_a) at EWL inflection, EWL slope above inflection, EWL at the heat tolerance limit (HTL) and EWL_{HTL} as a percentage of body mass (M_b), EWL scope (EWL_{HTL}/EWL_{TNZ}) and evaporative heat dissipation (EHD=EHL/MHP) at HTL are given by species (*Neotoma albigula*, *Neotoma lepida*, *Peromyscus eremicus* and *Peromyscus crinitus*), site and season (S, summer; W, winter). Data are unadjusted means (raw means), as opposed to adjusted means from ANCOVA described in Results, with 95% confidence interval in parentheses. JT, Joshua Tree; ML, Mid-Hills low; MH, Mid-Hills high (MH); ZZ, Zzyzx.

increase in EWL of 95.6% which was much greater than the 34.0% increase observed in this species in Joshua Tree ($F_{1,73.4} = 3.89$, $p = 0.052$). Seasonal increases in rates of EWL were generally did not translate into increases in specie's heat tolerance limit.

The values for evaporative scope, (EWL at HTL/ EWL in TNZ) varied among species, season and site (Table 3) and was lowest in *Neotoma* with values ranging from14-16 compared to EWL scope values of 12-18 observed in the smaller *P. eremicus* and values of 14-24 observed in *P. crinitus*. The maximum evaporative heat dissipation values (EHD - defined as the percentage of metabolic heat dissipated via evaporation) at the HTL ranged from 1.9 to 2.5 for *Neotoma* and from 2.3 to 4.3 in *Peromyscus* (Table 3).

Discussion

Our goal was to quantify the thermoregulatory responses used by wild cricetid rodents to cope with environmental temperatures exceeding T_b and examine how these responses varied among species, sites and seasons. To this end, we made simultaneous measurements of MR, EWL and T_b on wild-caught, individuals at T_as ranging from 10 to 48°C during summer and winter from three different sites in the Mojave Desert. The common thermoregulatory pattern observed with increasing T_a started with stable body temperatures ($T_b \approx$ 35-37 °C) in the TNZ followed by marked increases in T_b as T_a increased to ~31-34 °C (Fig. 2), which then increased steeply until the animal approached its heat tolerance limit at a T_b ~43°C. Estimated heat tolerance limits for all species ranged from T_a ~ 42-46 °C. Increases in evaporative cooling lagged behind increases in T_b, with evaporation rates increasing starting at T_a ~ 33-38°C accompanied by sharp increases in metabolism. Metabolic increases represent the mechanical costs of increasing evaporative cooling (increased breathing rates, salivation, and wiping behaviors) and resulted in large metabolic scopes (2-3) at the HTL. Scopes for evaporative cooling at the HTL were also notably large (13-24) and represent the acute response needed to offset environmental and metabolic heat loads to avoid lethal hyperthermia (Table 3). Overall, we found that desert cricetids have a very limited ability to cool evaporatively and are unable to maintain a T_a - T_b gradient of more than a few degrees Celsius. We also found limited seasonal variation in evaporative cooling ability, with winter animals showing modestly higher evaporative capacities. The thermal limits within species also did not appear to vary among individuals from different elevations. Overall, evaporative cooling in cricetid rodents is a very ineffective process with high rates of evaporation and metabolism, yielding only limited cooling ability and heat tolerance.

Hyperthermic responses to heat exposure and the HTL

Increases in body temperature are common in endotherms as environmental temperatures approach normothermic body temperature (McKechnie and Wolf 2020). We observed hyperthermic responses in all species with T_b inflection points occurring at T_a ~ 31°C and ~33°C in *Peromyscus* and *Neotoma*, respectively. Increasing T_b serves to maximize the gradient for insensible heat loss with increasing T_a, minimize the gradient for heat gain between the animal and its environment, and allow for heat storage in tissues; these phenomena reduce evaporative cooling costs and conserve water (Chew 1951; Schmidt-Nielsen 1952). Our values are similar to the inflection T_as measured by Nelson and Yousef (1979) (T_a = 30°C) and Lee (1963) (T_a = 35°C) for *N. lepida* and by Brown (1968) (T_a = 32°C) for *N. albigula*. We were unable to observe any general patterns in T_bs values within and among species or across sites and seasons. Increasing T_a above the inflection points was accompanied by steep concomitant increases in T_b that rapidly drove rodent body temperatures towards lethal values.

We estimated the heat tolerance limit for each species by site and season by quantifying the T_a at which heat loads became uncompensated and result in uncontrolled increases in T_b or mortality. Our HTL values provide non-lethal means of estimating and comparing rodent thermal tolerances across sites and seasons and linking thermal limits to EWL and metabolism. These estimates of HTL represent a trade-off between the goal of establishing the maximum T_as tolerated by an individual species at differing sites and seasons and not killing all of the test subjects. Erskine (1982) determined the CT_{max} for five species of rodents using rapid heating (30-40 minutes to lethality), resulting in 100% mortality among study animals. We used a more measured approach to minimize mortality by estimating HTL values using criteria based on behavior, continuous escape attempts, physiological responses including depression in CO_2 production, rapid spikes in Tb, or Tb increasing to 43°C (McKechnie and Wolf 2020). Our HTL values for *Peromyscus* and *Neotoma* ranged from T_a 42.5 to 45.7 °C showing no clear seasonal pattern or effect of site. Our estimated heat tolerance values may be somewhat conservative because we ended experimental trials when $T_b = 43$°C, though some *Neotoma* have been observed to survive T_b of 44°C (Brown, 1968; Nelson and Yousef 1979). Our exposure times (< 1 h) to the highest temperatures were substantially less than those used in previous studies (1 – 7 h), which found lethal values (Brown 1968; Lee 1963; Nelson and Yousef 1979). The long exposure time used in earlier studies may have resulted in HTL values defined by dehydration state as opposed to acute heat stress. Our data suggest that *Neotoma* held at these high T_a would have lost 10-14% M_b of water during a 5-7 hour trial (Table 3), which would have significantly affected plasma volume and hindered cooling ability (Zurovski et al. 1991). The effect of dehydration resulting from prolonged heat exposure helps explain why our HTL values for *N. lepida* (43-46 °C) are well above the previous values of other studies (37-43°C) (Brown 1968; Lee 1963; Nelson and Yousef 1979). Determination of the values for thermal limits is also affected by how body temperature measurements are obtained. It is very difficult to obtain continuous T_b measurements without telemetry or implants due to the tendency of rodents to chew temperature leads. Most commonly, single-point T_b measurements have been obtained rectally in animals after experimental trials (e.g. Morrison and McNab 1963; Brown 1968). Our values were obtained continuously via subcutaneous PIT tag implants which were checked against rectal T_b measurements both before and after each experimental trial (see Fig S1, S2).

Resting metabolism and metabolic responses to heat exposure

In general, our metabolic values and defined critical limits agree with earlier studies on

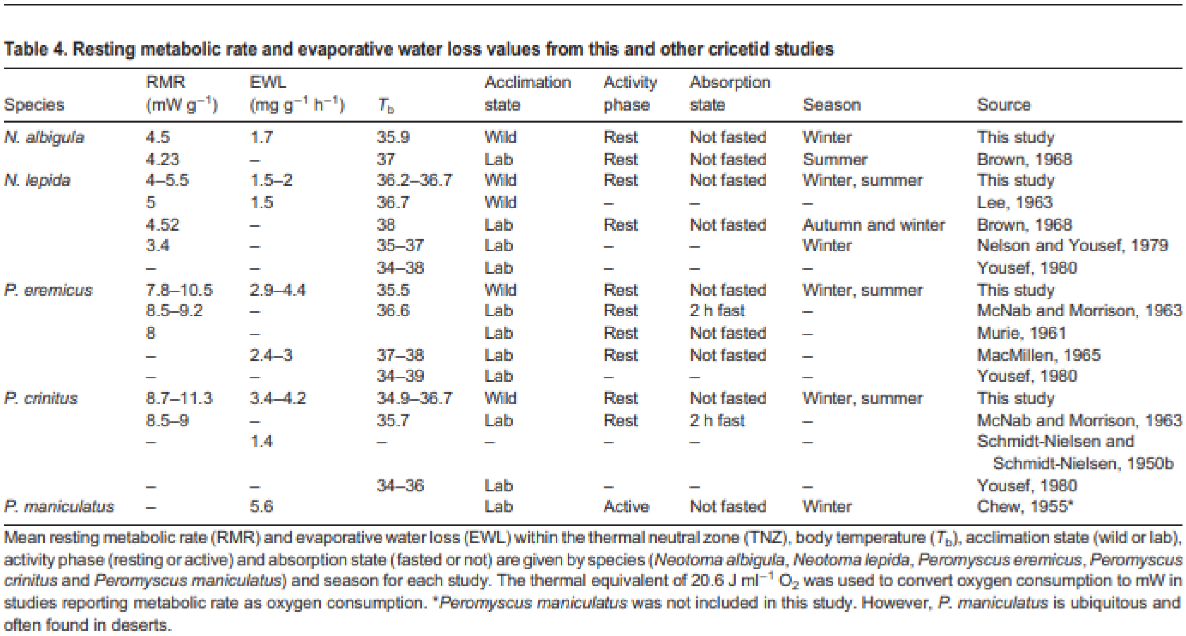


Table 4. Resting metabolic rate and evaporative water loss values from this and other cricetid studies

Species	RMR ($mW\ g^{-1}$)	EWL ($mg\ g^{-1}\ h^{-1}$)	T_b	Acclimation state	Activity phase	Absorption state	Season	Source
N. albigula	4.5	1.7	35.9	Wild	Rest	Not fasted	Winter	This study
	4.23	–	37	Lab	Rest	Not fasted	Summer	Brown, 1968
N. lepida	4–5.5	1.5–2	36.2–36.7	Wild	Rest	Not fasted	Winter, summer	This study
	5	1.5	36.7	Wild	–	–	–	Lee, 1963
	4.52	–	38	Lab	Rest	Not fasted	Autumn and winter	Brown, 1968
	3.4	–	35–37	Lab	–	–	Winter	Nelson and Yousef, 1979
	–	–	34–38	Lab	–	–	–	Yousef, 1980
P. eremicus	7.8–10.5	2.9–4.4	35.5	Wild	Rest	Not fasted	Winter, summer	This study
	8.5–9.2	–	36.6	Lab	Rest	2 h fast	–	McNab and Morrison, 1963
	8	–		Lab	Rest	Not fasted	–	Murie, 1961
	–	2.4–3	37–38	Lab	Rest	Not fasted	–	MacMillen, 1965
	–	–	34–39	Lab	–	–	–	Yousef, 1980
P. crinitus	8.7–11.3	3.4–4.2	34.9–36.7	Wild	Rest	Not fasted	Winter, summer	This study
	8.5–9	–	35.7	Lab	Rest	2 h fast	–	McNab and Morrison, 1963
	–	1.4	–	–	–	–	–	Schmidt-Nielsen and Schmidt-Nielsen, 1950b
	–	–	34–36	Lab	–	–	–	Yousef, 1980
P. maniculatus	–	5.6		Lab	Active	Not fasted	Winter	Chew, 1955*

Mean resting metabolic rate (RMR) and evaporative water loss (EWL) within the thermal neutral zone (TNZ), body temperature (T_b), acclimation state (wild or lab), activity phase (resting or active) and absorption state (fasted or not) are given by species (*Neotoma albigula*, *Neotoma lepida*, *Peromyscus eremicus*, *Peromyscus crinitus* and *Peromyscus maniculatus*) and season for each study. The thermal equivalent of 20.6 J ml^{-1} O_2 was used to convert oxygen consumption to mW in studies reporting metabolic rate as oxygen consumption. **Peromyscus maniculatus* was not included in this study. However, *P. maniculatus* is ubiquitous and often found in deserts.

Mojave *Peromyscus* and *Neotoma* (Table 4). We note, however, that our metabolism measurements and estimates of critical temperatures were made under experimental conditions that differ from most earlier studies (e.g. Murie 1961, McNab and Morrison 1963). These earlier studies focused on obtaining minimum metabolism values during long trials at “steady state”, in fasted rest-phase animals that often had been held in captivity at a T_a of ~25°C for weeks or months. These values are unlikely to represent an accurate picture of animal performance in nature. In this study, by necessity and design, we focused on making measurements of wild caught, non-fasted animals. For animals exposed to T_a near and above body temperature, we conducted measurements over shorter periods where animals were held at a single temperature for 30-60 minutes to limit total water loss and changes in the hydration state of the animal that would have diminished its thermoregulatory performance (Sawka et al., 2001). As a consequence, we urge some caution in directly comparing our values to those from earlier studies (Table 4).

As chamber T_a increased towards T_b, all animals showed increased metabolic rates due to their efforts to actively increase evaporative heat loss. Across species, seasons and sites, T_{uc} values on average ranged from 34 to 37°C with no consistent seasonal or site based difference in any species and were broadly similar to those reported by other researchers ranging from 33-35°C for *Neotoma* and 35-36°C *Peromyscus* (Table 4) (Brown 1968; Lee 1963; Murie 1961; McNab and Morrison 1963; Nelson and Yousef 1979). Increases in metabolism at the T_{uc} were closely followed by marked increases in the rates of EWL with inflection T_a for EWL of about ~0.4 °C above the T_{uc} in *Neotoma* and 1.5°C and 2.4°C above the T_{uc} in *P. eremicus* and *P. crinitus*, respectively. Animals were observed salivating at chamber T_as of 38-39°C and the steep increases in metabolism above the T_{uc} represent the costs of increasing evaporative cooling rates to maintain pace with increasing environmental heat loads. Unfortunately, increases in metabolic heat production also increase the total heat load that must be dissipated through evaporative cooling (Lee 1963; Schmidt-Nielsen and Schmidt-Nielsen, 1950a; Nelson and Yousef 1979). Overall, metabolic heat production increased by 150-250% from the T_{uc} to the HTL increasing the large burden on the evaporative heat cooling system and driving animals towards lethal T_bs.

Evaporative water loss and the capacity for evaporative cooling

At T_a within the TNZ, EWL in rodents is almost evenly divided between respiratory and cutaneous avenues. This represents the minimum obligatory water loss associated with lung ventilation and skin permeability (Baudinette, 1972; Chew, 1955; Edwards and Haines, 1978; Yousef, 1980). Our values for thermoneutral rates of EWL among species compare well to earlier studies (Table 4). In all species, we observed significant reductions in thermoneutral rates of EWL during the summer that likely reduced total water requirements by 10-15% during a period where free water is scarce and increased temperatures/decreased humidity potentially drive increased water demands. This may be largely due to reduced MR during the summer, which would tend to reduce lung ventilation rates and respiratory EWL (Schmidt-Nielsen, 1964).

Evaporative heat loss can be critical to survival when T_a approaches and exceeds T_b and in small rodents, pathways for evaporation may include panting, salivation (including extensive wiping of saliva on the animal’s surface) and increases in cutaneous water loss (Edwards and Haines, 1978; Hainsworth, 1967, 1968; Lee, 1963). For rodents exposed to environmental temperatures exceeding T_b, saliva spreading is the dominant mechanism used to increase evaporative cooling and cope with potentially lethal heat loads (Hainsworth 1967, 1968; Hainsworth and Epstein, 1966, Hainsworth and Stricker, 1968; Horowitz and Mani, 1978; Nelson and Yousef, 1979). Few studies have measured rates of EWL in Cricetids at T_a exceeding 35 °C, and this study is the first to look across multiples species at different sites and seasons (Chew, 1955; Layne and Dolan, 1975; MacMillen, 1965; Yousef, 1980). Our EWL data for these higher T_a's overlap to the few earlier studies (Table 4) that have measured water loss in *Neotoma* (Nelson and Yousef 1979) and desert *Peromyscus* (MacMillen 1965). We also found seasonal differences in rates of water loss at the highest exposure temperatures. In *Neotoma*, maximum rates of EWL were as much as 20% higher in the winter and were accompanied by higher HTL values reflecting the greater cooling abilities of winter animals. Similarly, we found that maximum rates of EWL increased in the winter in both *P. eremicus* and *P. crinitus* by as much as 96% and 23%, respectively and sometimes reflected modestly higher HTL values.

Across all species and populations of *Neotoma* and *Peromyscus* we observed maximal evaporative scopes ranging from 16 in *Neotoma* to 24 in *Peromyscus*, which suggests a significant capacity for evaporative cooling (Table 3). These values for rodents are greater than the EWL scopes observed in desert songbirds (Passeriformes) (Smith et al., 2017; McKechnie et al., 2017; Whitfield et al., 2015). However, the heat tolerance limits for cricetids rodents (~43-46°C) are significantly lower than those observed in songbirds (~48-52°C). These differences in actual cooling capacity across taxa can be illustrated by comparing relative evaporative heat loss (EWL scope) with the maximum T_a-T_b gradient that can be maintained by an animal exhibiting maximal rates of water loss. When comparing EWL scope to the maximum T_a-T_b gradient maintained in desert songbirds (summer) from

North America, southern Africa and Australia to our values for Mojave cricetid rodents during the summer (Smith et al., 2017; McKechnie et al., 2018; Whitfield et al., 2016;) we find that strikingly cricetid rodents have very high evaporative scopes - almost twice those of most songbirds. However, high evaporative scopes do not predict the relative capacities for coping with high heat loads, *N. lepida*, *P. eremicus* and, *P. crinitus* can only withstand T_a ~ 1°C > T_b. Most songbirds that show relatively low EWL scopes can withstand T_a that average 5.4 °C > T_b. Ecologically, this makes sense because we are comparing diurnally active desert birds with nocturnal desert rodents. The conundrum here is that the cricetid rodents vastly increase water loss rates at high T_a with apparently minimal cooling benefit. Songbirds pant to increase evaporative heat loss when exposed to high T_a. In contrast, few cricetid rodents are known to pant and most use salivation, which may be accompanied by wiping saliva on the fur to enhance evaporative heat loss (Hainsworth 1967, 1968; Horowithz and Mani 1978). Based on our data, salivation is a very inefficient means of evaporative heat loss. By comparing total maximum rates of EWL water and the maximum T_a-T_b gradient between taxa, we see that cricetid rodents (this study) evaporate an average of 42.2 mg H_2O g^{-1} h^{-1} and maintain an average maximum T_a-T_b gradient of 1.3 °C, which contrasts with Australian songbirds that evaporate an average 44.6 mg H_2O g^{-1} h^{-1} and maintain an average maximum T_a-T_b gradient of 4.0 °C (Fig 5) (McKechnie et al 2018). These efficiency differences among birds and rodents are striking and probably greatly overestimate salivation efficiency as a mechanism of evaporative heat dissipation, because in all cases when rodents were removed trials after being exposed to T_a >T_b, their fur was noticeably wetted. Our measurements of EWL only account for water that was evaporated and carried in the airstream to our analyzers. The wetted pelts represent an unmeasured water loss, indicating that water loss is likely much higher and that the cooling benefit is very low (Hainsworth 1967, 1968; Nelson and Yousef 1979; Brown 1968). Our data suggest that cricetid rodents have few physiological tools for coping with T_a that approach T_b in the wild.

Ecological aspects of thermoregulation

The lack of effective or efficient cooling mechanisms suggests that cricetid thermoregulation and survival are mediated almost entirely through behavioral processes. The cricetid rodents we examined are nocturnal species that persist and thrive in hot deserts like Death Valley, CA, where daytime T_a regularly exceeds 55°C, despite their limited capacity to cope with T_a > T_b. Although desert rodents seek the thermal refuges provided by burrows or nests during the day, as small endotherms their high energy and water demands require that they forage regularly. Some smaller species such as *P. eremicus* may use daily torpor to provide temporary relief from environmental extremes (MacMillen 1965). However, periods of high temperature extremes are becoming more frequent, intense, and prolonged (IPCC 2014) and nighttime T_a in these regions is increasing. Despite the stability of the rodent community in the Mojave Desert over the last century (Riddell et al. 2021), the future of rodent populations in a rapidly warming world is uncertain. Our study indicates that even modest increases in environmental temperatures could

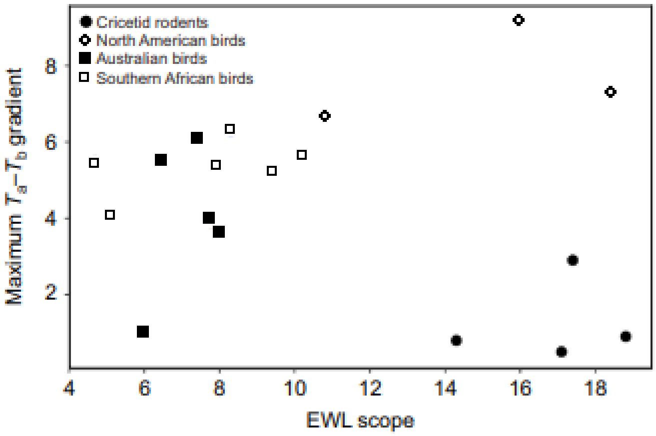


Fig. 5. EWL scope versus maximum T_a–T_b gradient for desert songbirds and cricetid rodents. EWL scope was calculated as EWL_{TNZ}/EWL_{HTL}, where TNZ is thermoneutral zone and HTL is heat tolerance limit. Although cricetid rodents have very large evaporative scope compared with that of most desert songbirds, the rodents have a very limited capacity (~1°C differential) to cope with T_a>T_b compared with songbirds (~4.5°C differential). Rodent data from this study; songbird data from Whitfield et al. (2015), Smith et al. (2017) and McKechnie et al. (2017).

importantly impact thermoregulatory costs and limit activity. Murray and Smith (2012), using animals collared with air temperature loggers found that *N. lepida* did not emerge from nests or burrows until $T_a < 42°C$, that larger animals emerged later than smaller animals, and that the active periods were reduced by nearly 50% when daily maximum $T_a > 41°C$. Our data suggest that *N. lepida* can tolerate short exposures of $T_a > T_b$ and respond by increasing evaporative heat loss via copious salivation and spreading, but the losses of water conservatively range from 2-6% M_b h^{-1} which makes lethal dehydration a risk (Table 3). Although burrows may provide a thermal refuge from extreme heat for desert rodents, burrow temperatures currently can exceed 35°C (Tracy and Walsberg 2002). Higher diurnal air and burrow temperatures will increase overall water requirements, while at the same time higher minimum air temperatures during summer nights will increasingly limit nightly activity because of thermoregulatory constraints (Murray and Smith, 2012; Tracy and Walsberg, 2002; Walsberg, 2000). The current climate trends are not promising; the numbers of days where the minimum nighttime $T_a \geq 35°C$ at Furnace Creek in Death Valley was 3, 3, and 5 days in 1962, 1990 and 2000, respectively; in 2020 there were 22 days with minimum $T_a \geq 35°C$ (NOAA/NCEI). A changing climate may also lead to changes in the availability of water rich succulent food for desert rodents by altering the plant community (Abatzoglou and Kolden, 2011; Notaro *et al*., 2012). Finally, even adaptive shifts in body size are very unlikely to keep pace with the high rate of warming (Smith et al. 2014; Quintero and Weins 2013). Our data suggest that a general lack of an ability to withstand T_a approaching or exceeding T_b and the associated high costs of responding to even modestly higher heat loads will increasing constrain desert rodents under future climate scenarios.

Appendices

This thesis has also been published in the Journal of Experimental Biology and can be found at https://doi.org/10.1242/jeb.243131.

Supplementary Figures and Tables

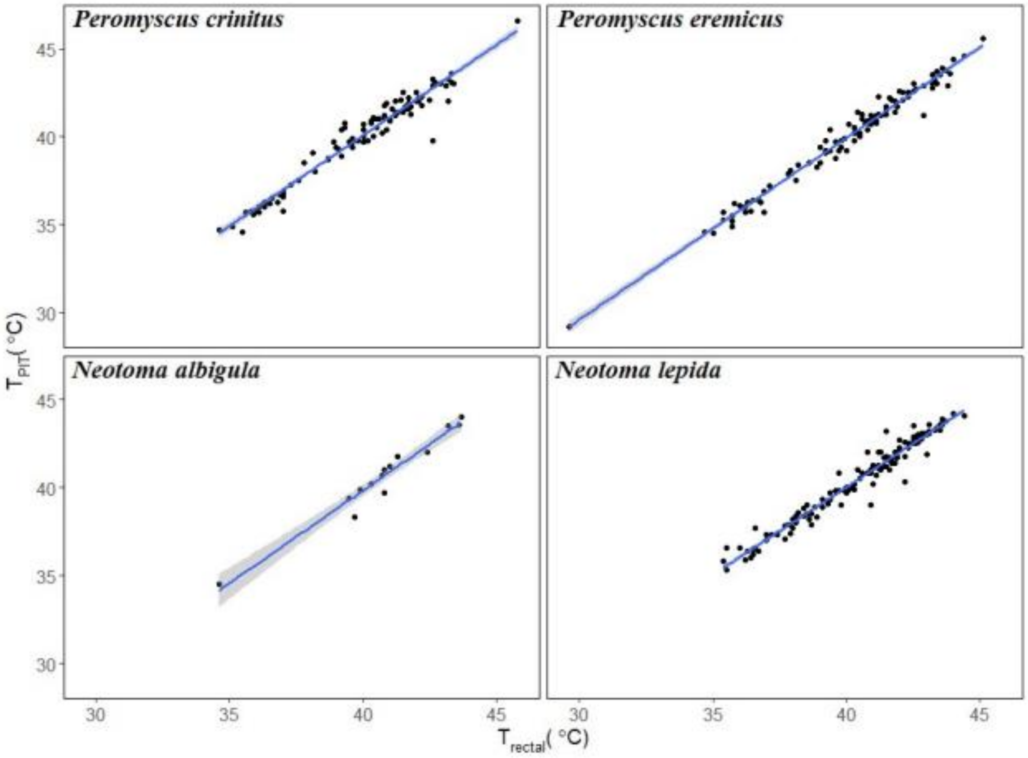


Fig. S1. PIT tag temperature as a function of rectal temperature among four species of desert rodents. Shading indicates 95% confidence intervals. Descriptive statistics are reported in table S1. The slope for each line ≈ 1 indicates as T_{ractal} increases T_{pit} increases at an equal rate.

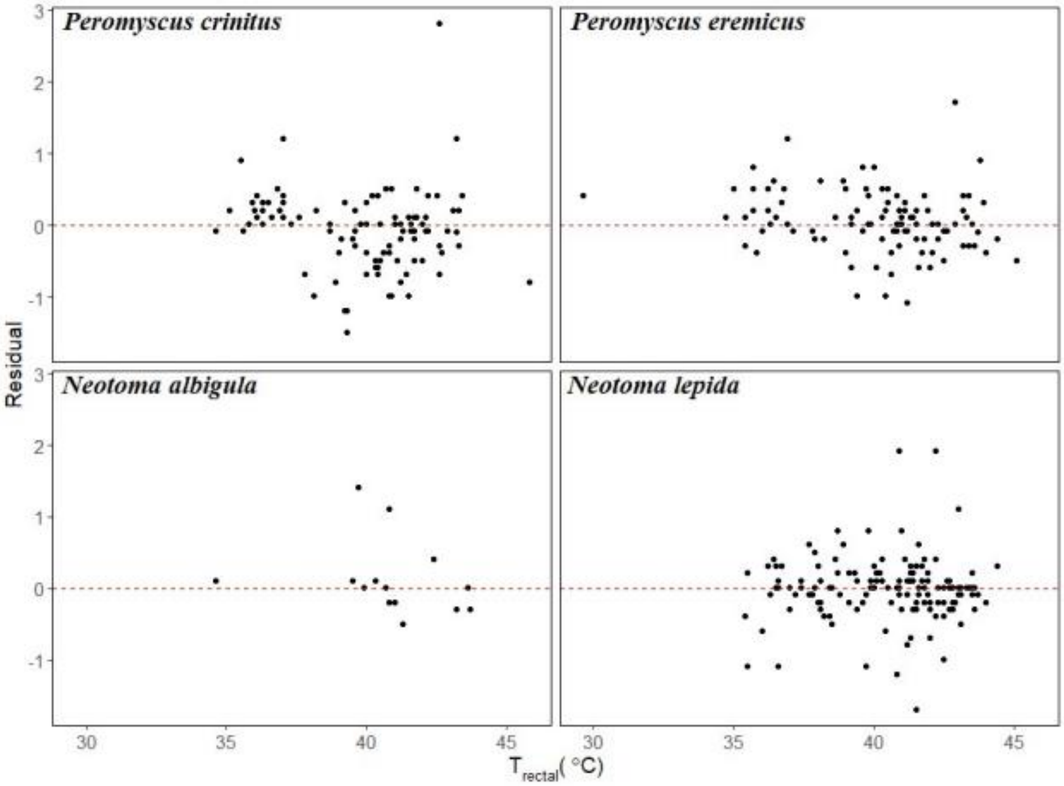


Fig. S2. Residual values from S1 as a function of rectal temp. The random values centered on the zero line, indicates that a linear model provides a good fit to the data without systematic error or bias.

Table S1. Slope ($\hat{\beta}_1$), and intercept ($\hat{\beta}_0$) for the regression of the PIT tag temps by rectal temps, with standard error, t value, p values, degrees freedom, and coefficient of determination respectively.

Species	$\hat{\beta}_0$	**SE**	**t-val**	**p-val**	$\hat{\beta}_1$	**SE**	**t-val**	**P-val**	**DF**	R^2
N. albigula	-2.32	2.69	-0.86	0.40	1.05	0.07	16.07	1.76^{10*-16}	12	0.96
N. lepida	0.28	0.68	.042	0.68	0.99	0.042	59.66	2^{10*-16}	144	0.96
P. crinitus	-1.07	0.92	-1.16	0.25	1.03	0.023	44.5	2^{10*-16}	99	0.95
P. eremicus	-1.31	0.63	-2.08	0.04	1.03	0.02	65.81	2^{10*-16}	104	0.98

Non-zero intercepts could indicate a systematic deviation from what we would expect if T_{ractal} equaled $T_{pit.}$ However, only the intercept for *P. eremicus* is statistically significant from zero. Additionally, when the intercepts are combined with slight variations from one in the slopes, we find the regressions

Table S2. Site abbreviation, elevation, dominant vegetation and Lat. Long.

Site	Elevation (m)	Dominant Vegetation	Latitude	Longitude
Death Valley (Triangle springs)	0	creosote (*Larrea tridentata*), Desert Willow (*Chilopsis linearis*) and catclaw acacia (*Senegalia greggii*),	36.72798	-117.13491
Joshua Tree (Cottonwood springs)	1000	cholla (Cylindropuntia spp), acacia (*Senegalia spp*), yucca (*Yucca baccata, Y. schidigera*) and creosote (*Larrea tridentata*)	33.72898	-115.82505
Mojave N.P. (Midhills low)	1400	cholla (Cylindropuntia spp), acacia (*Senegalia spp*), yucca (*Yucca baccata, Y. brevifolia, Y. schidigera*) and creosote (*Larrea tridentata*)	35.16690	-115.45377
Mojave N.P (Midhills high)	1600	creosote (Larrea tridentata), pinyon (*Pinus monophylla*) and juniper (*Juniperus californica*)	35.14148,	-115.4083
Mojave N.P (Zzyzx)	300	creosote (*Larrea tridentata*), Smoketrees (*Psorothamnus spinosus*), and heliotrope (*Heliotropium curassavicum*)	35.12731	-116.11793

The major location, national park/preserve, of each site is followed by the exact site name in parentheses.

References

Abatzoglou, J. T. and Kolden, C. A. (2011). Climate change in western US deserts: potential for increased wildfire and invasive annual grasses. *Rangel. Ecol. Mgmt.* **64,** 471-478.

Adolph, E. F. (1947). Tolerance to heat and dehydration in several species of mammals. *Am. J. Physiol.* **2,** 564-575.

Baayen, R. H., Davidson, D. J. and Bates, D. M. (2008). Mixed-effects modeling with crossed random effects for subjects and items. *J. Mem. Lang.* **59,** 390-412.

Baudinette, R. V. (1972). Energy metabolism and evaporative water loss in the California ground squirrel. *J. Comp. Physiol. B* **81,** 57-72.

Blackwell, T. L. and Pivorun, E. B. (1979). Influence of temperature on the water balance of three parapatric species of *Peromyscus*. *J. Mammal.* **60,** 70-75.

Bradley, W. and Yousef, M. (1972). Small mammals in the desert. In *Physiological adaptations: desert and mountain*, pp. 127-142: Academic Press New York.

Bradley, W. and Yousef, M. (1975). Thermoregulatory responses in the plains pocket gopher, *Geomys bursarius*. *Comp. Biochem. Phys. A* **52,** 35-38.

Brower, J. E. and Cade, T. J. (1966). Ecology and physiology of *Napaeozapus insignis* (Miller) and other woodland mice. *Ecology* **47,** 46-63.

Brown, J. H. (1968). Adaptation to environmental temperature in two species of woodrats, *Neotoma cinerea* and *N. albigula*. *Misc. Publ. Mus. Zool. Univ. Mich.* **135**, 1–48.

Caro, A.C., Hankenson, C.F. and Marx, J.O. (2013). Comparison of thermoregulatory devices used during anesthesia of C57BL/6 mice and correlations between body temperature and physiologic parameters. *J. Am. Assoc. Lab. Anim. Sci.* **52**, 577-583.

Chaffee, R. and Roberts, J. (1971). Temperature acclimation in birds and mammals. *Annu. Rev. Physiol.* **33,** 155-202.

Chew, R. M. (1955). The skin and respiratory water losses of *Peromyscus maniculatus sonoriensis*. *Ecology* **36,** 463-467.

Chew, R. M. (1951). The water exchanges of some small mammals. *Ecol. Monogr.* **21,** 215-225.

Chew, R. M. (1965). Water metabolism of mammals. In *Physioogicl mammalogy. Vol. 2.* (ed. W. V. Mayer and R. G. VanGelder), pp. 43-178. New York, NY.: Academic Press

Christian, D. P. (1978). Effects of humidity and body size on evaporative water loss in three desert rodents. *Comp. Biochem. Phys. A* **60,** 425-430.

Edwards, R. M. and Haines, H. (1978). Effects of ambient water vapor pressure and temperature on evaporative water loss in *Peromyscus maniculatus* and *Mus musculus*. *J. Comp. Physiol. B* **128,** 177-184.

Erskine, D. J., and Hutchison, V. H. (1982). Critical thermal maxima in small mammals. *J. Mammal.*, ***63***, 267-273.

Glanville, E. J., Murray, S. A. and Seebacher, F. (2012). Thermal adaptation in endotherms: climate and phylogeny interact to determine population-level responses in a wild rat. *Funct. Ecol.* **26,** 390-398.

Haim, A. and Izhaki, I. (1995). Comparative physiology of thermoregulation in rodents: adaptations to arid and mesic environments. *J. Arid Environ.* **31,** 431-440.

Haim, A., Racey, P., Speakman, J., Ellison, G. and Skinner, J. (1991). Seasonal acclimatization and thermoregulation in the pouched mouse *Saccostomus campestris*. *J. Therm. Biol.* **16,** 13-17.

Haines, H., MacFarlane, W., Setchell, C. and Howard, B. (1974). Water turnover and pulmocutaneous evaporation of Australian desert dasyurids and murids. *Am. J. Physiol.* **227,** 958-963.

Hainsworth, F. R. (1967). Saliva spreading, activity, and body temperature regulation in the rat. *Am. J. Physiol.* **212,** 1288-1292.

Hainsworth, F. R., Stricker, E. M. and Epstein, A. (1968). Water metabolism of rats in the heat: dehydration and drinking. *Am. J. Physiol.* **214,** 983-989.

Hainsworth, F. (1968). Evaporative water loss from rats in the heat. *Am. J. Physiol.* **214,** 979-982.

Hainsworth, F. R. and Epstein, A. N. (1966). Severe impairment of heat-induced saliva-spreading in rats recovered from lateral hypothalamic lesions. *Science* **153,** 1255-1257.

Hart, J. S. (1971). Rodents. In *Comparative physiology of thermoregulation, Vol. 2, Mammals,* (ed. G. C. Whittow) pp. 1-149, New York, London, Academic Press.

Horowitz, M., and D. Mani. (1978). Potential secretory activity of salivary glands and electrolyte concentrations in the saliva of two rodent species during heat acclimatization. *Comp. Biochem. Phys. A* **59,** 151-154.

Hudson, J. W. (1965). Temperature regulation and torpidity in the pygmy mouse, *Baiomys taylori*. *Phys. Zoo.* **38**, 243-254.

Johnson, D. W. and Armstrong, D. M. (1987). *Peromyscus crinitus*. Mammal. species, **287**, 1-8.

Kenward, M. G. and Roger, J. H. (1997). Small sample inference for fixed effects from restricted maximum likelihood. *Biometrics*, **53**, 983–997.

Langsrud, Ø. (2003) ANOVA for unbalanced data: Use Type II instead of Type III sums of squares. *Stat. Comput.* **13**,163–67.

Lasiewski, R. C., Acosta, A. L. and Bern-stein, M. H. (1966). Evaporative water loss in birds. 1. Characteristics of the open flow method of determination, and their relation to estimates of thermoregulatory ability. *Comp. Biochem. Physiol. A* **19,** 445-457.

Layne, J. N. and Dolan, P. G. (1975). Thermoregulation, metabolism, and water economy in the golden mouse (*Ochrotomys nuttalli*). *Comp. Biochem. Phys. A* **52,** 153-163.

Lee, A. K. (1963). The adaptations to arid environments in wood rats of the genus *Neotoma*: Univ. Calif. Publ. Zool. **64**, 57-96.

Leon, L.R., DuBose, D.A. and Mason, C.W. (2005) Heat stress induces a biphasic thermoregulatory response in mice. *Am. J. Physiol.* **288,** 197-204.

Lighton, J. R. (2008a). Flow-through respirometry using incurrent flow measurement. In *Measuring metabolic rates: a manual for scientists*, pp. 105-123. Oxford, New York: Oxford University Press.

Lighton, J. R. (2008b). Direct calorimetry. In *Measuring metabolic rates: a manual for scientists*, pp. 63--83. Oxford, New York: Oxford University Press.

Levy, O., Dayan, T., Porter, W.P. and Kronfeld-Schor, N. (2016). Foraging activity pattern is shaped by water loss rates in a diurnal desert rodent. *Am. Nat.* 188, 205–218.

Lovegrove, G. B. (2005). *Seasonal thermoregulatory responses in mammals*. J. Comp. Physiol. B. **175,** 231-247.

Macêdo, R. H. and Mares, M. A. (1988). *Neotoma albigula*. Mammal. Species, **310**, 1-7.

Macmillen, R. E. (1965). Aestivation in the cactus mouse, *Peromyscus eremicus*. *Comp. Biochem. Physiol.* **16,** 227-248.

MacMillen, R. E. (1983). Water regulation in *Peromyscus*. *J. Mammal.* **64,** 38-47.

MacMillen R.E. and Christopher, E. A. (1975). The water relations of two populations of noncaptive desert rodents. In *Environmental physiology of desert organisms* (ed. F. F. Hadley), pp. 117-137. Stroudsburg, PA.: Dowden, Hutchinson & Ross.

MacMillen, R. and Grubbs, D. (1976). Water metabolism in rodents. In *Progress in animal biometeorology : the effect of weather and climate on animals Vol. 1 Part 1*, (ed. H.D. Johnson), pp. 67-73. Amsterdam, Netherlangds: Swets & Zeitlinger

MacMillen, R. E. and Hinds, D. S. (1983). Water regulatory efficiency in heteromyid rodents: a model and its application. *Ecology* **64,** 152-164.

McKechnie, A. E., Gerson, A. R., McWhorter, T. J., Smith, E. K., Talbot, W. A. and Wolf, B. O. (2017). Avian thermoregulation in the heat: evaporative cooling in five Australian passerines reveals within-order biogeographic variation in heat tolerance. *J. Exp. Biol.* **220,** 2436-2444.

McNab, B. K. and Morrison, P. (1963). Body temperature and metabolism in subspecies of *Peromyscus* from arid and mesic environments. *Ecol. Monogr.* **33,** 63-82.

Muggeo, M. (2003). Estimating regression models with unknown break-points. *Stats in med.*, **22**, 3055-3071.

Murie, M. (1961). Metabolic characteristics of mountain, desert and coastal populations of *Peromyscus*. *Ecology*. **42,** 723-740.

Murray, I. W. and Smith, F. A. (2012). Estimating the influence of the thermal environment on activity patterns of the desert woodrat (*Neotoma lepida*) using temperature chronologies. *Can. J. Zool.* **90,** 1171-1180.

Musser, G. G. and Shoemaker, V. H. (1965). Oxygen consumption and body temperature in relation to ambient temperature in the Mexican deer mice, *Peromyscus thomasi* and *P. megalops*. *Occ. Pap. Mus. Zool. Univ. Mich*. **643,** 1-15.

Nakagawa, S. and Schielzeth, H. (2013). A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Meth. Ecol. and Evol.* **4,** 133-142.

Naya, D. E., Bozinovic, F. and Karasov, W. H. (2008). Latitudinal trends in digestive flexibility: testing the climatic variability hypothesis with data on the intestinal length of rodents. *Am. Nat.* **172,** 122-134.

Naya, D. E., Spangenberg, L., Naya, H. and Bozinovic, F. (2012). Latitudinal patterns in rodent metabolic flexibility. *Am. Nat.* **179,** 172-179.

Nelson, Z. and Yousef, M. (1979). Thermoregulatory responses of desert wood rats, *Neotoma lepida*. *Comp. Biochem. Phys. A* **63,** 109-113.

Noakes, M. J., Wolf, B. O., & McKechnie, A. E. (2016). Seasonal and geographical variation in heat tolerance and evaporative cooling capacity in a passerine bird. *J. Exp. Biol.* **219**, 859-869.

Notaro, M., Mauss, A. and Williams, J. W. (2012). Projected vegetation changes for the American Southwest: combined dynamic modeling and bioclimatic-envelope approach. *Ecol. Appl.* **22,** 1365-1388.

Novoa, F. F., Rivera-Hutinel, A., Rosenmann, M. and Sabat, P. (2005). Intraspecific differences in metabolic rate of *Chroeomys olivaceus* (Rodentia: Muridae): the effect of thermal acclimation in arid and mesic habitats. *Rev. Chil. Hist. Nat.* **78,** 207-214.

Price, M. and Reichman, O. (1987). Distribution of seeds in Sonoran Desert soils: implications for heteromyid rodent foraging. *Ecology* **68,** 1797-1811.

Orr, T. J., Newsome, S. D. and Wolf, B. O. (2015). Cacti supply limited nutrients to a desert rodent community. *Oecologia* **178**, 1045-1062.

Quintero, I and J. J. Wiens (2013). Rates of projected climate change dramatically exceed past rates of climatic niche evolution among vertebrate species. *Ecol. Lett.* **16**, 1095-1103

Reichman, O. J. (1975). Relation of desert rodent diets to available resources. *J. Mammal.* **56,** 731-751.

Riddell, E.A., Iknayan, K.J., Hargrove, L., Tremor, S., Patton, J.L., Ramirez, R., Wolf, B.O. & Beissinger, S.R. (2021). Exposure to climate change drives stability or collapse of desert mammal and bird communities. *Science*, **371**, 633-636.

Roberts, J. C. and Chaffee, R. (1976). Metabolic and biochemical aspects of heat acclimation in the deer mouse, *Peromyscus maniculatus sonoriensis*. *Comp. Biochem. Phys. A* **53,** 367-373.

Rodland, K. D. and Hainsworth, F. R. (1974). Evaporative water loss and tissue dehydration of hamsters in the heat. *Comp. Biochem. Phys. A* **49,** 331-345.

Sawka, M. N., Montain, S. J., & Latzka, W. A. (2001). Hydration effects on thermoregulation and performance in the heat. *Comp. Biochem. Phys. A*, **128**, 679-690.

Schmidt-Nielsen, B., Schmidt-Nielsen, K., Brokaw, A. and Schneiderman, H. (1948). Water conservation in desert rodents. *J. of Cell Comp. Physiol.* **32,** 331-360.

Schmidt-Nielsen, B. and Schmidt-Nielsen, K. (1950a). Evaporative water loss in desert rodents in their natural habitat. *Ecology* **31,** 75-85.

Schmidt-Nielsen, B. and Schmidt-Nielsen, K. (1950b). Pulmonary water loss in desert rodents. *Am. J. Physiol.* **182,** 31-36.

Schmidt-Nielsen, K. (1964). Terrestrial animals in dry heat: desert rodents. In *Handbook of Physiology: section 4 Adaptation to the Environment* (ed. D. B. Dill), pp. 493-510. Washington, D.C: American Physiological Society.

Schmidt-Nielsen, K. and Schmidt-Nielsen, B. (1952). Water metabolism of desert mammals *Physiol. Rev.* **32,** 135-166.

Scholander, P., Hock, R., Walters, V. and Irving, L. (1950). Adaptation to cold in arctic and tropical mammals and birds in relation to body temperature, insulation, and basal metabolic rate. *Biol. Bull.* **99,** 259-271.

Smith, E. K., O'Neill, J. J., Gerson, A. R., McKechnie, A. E. and Wolf, B. O. (2017). Avian thermoregulation in the heat: resting metabolism, evaporative cooling and heat tolerance in Sonoran Desert songbirds. *J. Exp. Biol.* **220,** 3290-3300.

Smith, E. K., O'Neill, J., Gerson, A. R. and Wolf, B. O. (2015). Avian thermoregulation in the heat: resting metabolism, evaporative cooling and heat tolerance in Sonoran Desert doves and quail. *J. Exp. Biol.* **218,** 3636-3646.

Smith, F. A., Murray, I. W., Harding, L. E., Lease, H. M. and Martin, J. (2014). Life in an extreme environment: a historical perspective on the influence of temperature on the ecology and evolution of woodrats. *J. Mammal.* **95,** 1128-1143.

Tracy, R. L. and Walsberg, G. E. (2002). Kangaroo rats revisited: re-evaluating a classic case of desert survival. *Oecologia* **133,** 449-457.

Veal, R. and Caire, W. (1979). *Peromyscus eremicus*. *Mammal. Species,* **118,** 1-6.

Verts, B. and Carraway, L. N. (2002). *Neotoma lepida*. *Mammal. Species,* **699**, 1-12.

Vorhies, C. T. (1945). Water requirements of desert animals in the southwest. In *Technical Bulletin No. 107*, pp. 487-525. Tucson, AZ: College of Agriculture, University of Arizona.

Walsberg, G. E. (2000). Small mammals in hot deserts: some generalizations revisited. *Bioscience* **50,** 109-120.

Weiner, J. and Heldmaier, G. (1987). Metabolism and thermoregulation in two races of Djungarian hamsters: *Phodopus sungorus sungorus* and *P. s. campbelli*. *Comp. Biochem. Phys. A* **86,** 639-642.

Whitfield, M. C., Smit, B., McKechnie, A. E. and Wolf, B. O. (2015). Avian thermoregulation in the heat: scaling of heat tolerance and evaporative cooling capacity in three southern African arid-zone passerines. *J. Exp. Biol.* **218,** 1705-1714.

Wiegert, R. G. (1961). Respiratory energy loss and activity patterns in the meadow vole, *Microtus pennsylvanicus pennsylvanicus*. *Ecology*, **42**, 245-253.

Withers, P. (1992). *Comparative physiology*, pp. 1-949. Philadelphia, Pa: Saunders College Pub.

Withers, P. C. and Cooper, C. E. (2014). Physiological regulation of evaporative water loss in endotherms: is the little red kaluta (*Dasykaluta rosamondae*) an exception or the rule? *Proc. R. Soc. Lond. B* **281,** 20140149.

Yousef, M. K. (1980). Responses of small animals to heat stress and exercise. In *Environmental physiology, aging, heat, and altitude* (ed. S. M. Hovath and M. K. Yousef), pp. 91-119. New York, NY: Elsevier.

Zurovski, Y., Eckstein, L. and Horowitz, M. (1991). Heat stress and thermal dehydration: lactacidemia and plasma volume regulation. *J. Appl. Physiol.* **71,** 2434-2439.