

Unappreciated Tolerance to High Ambient Temperatures in a Widely Distributed Desert Rodent, *Dipodomys merriami*

Randall L. Tracy*

Glenn E. Walsberg

Arizona State University, Department of Biology, Tempe,
Arizona 85287-1501

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ABSTRACT

A long-held assertion has been that nocturnality is an escape mechanism for many nocturnal desert rodents because of limited tolerances to heat. To test this claim, we used a treadmill to examine the tolerances to high ambient temperatures (T_a 's) of one subspecies of desert rodent, Merriam's kangaroo rat, *Dipodomys merriami merriami*, from contrasting environments. We simultaneously measured body temperature (T_b), evaporative water loss, and metabolic rates at an ecologically relevant speed (0.6 km h^{-1}) at different ambient temperatures ($T_a = 25^\circ\text{--}42.5^\circ\text{C}$). We hypothesized that kangaroo rats from a more xeric site would have greater abilities to remain active and maintain stable T_b than those from a more mesic site, but mesic- and xeric-site animals had comparable tolerances and were active until $T_b = 42^\circ\text{C}$. At $T_a = 42.5^\circ\text{C}$, however, T_b of mesic-site animals increased more quickly than in xeric-site animals. Although most animals could not run more than 18 min at $T_a = 42.5^\circ\text{C}$, most could run at $T_a = 40^\circ\text{C}$ for at least 30 min. Benefits of nocturnality for this species may reside more in purposes of water conservation and avoidance of predation and less on the direct regulation of T_b , as T_b is more labile than commonly thought.

Introduction

Merriam's kangaroo rat, *Dipodomys merriami*, is widespread in the deserts of southwestern North America and foremost in studies of physiological ecology and environmental physiology of desert mammals (Hall 1981; Hoffmeister 1986; French 1993). A quick glance at most introductory biology texts will dem-

onstrate that the assumption long has been that, rather than tolerating high ambient temperatures (T_a 's), nocturnal desert rodents predominantly use behavior as a means of survival within deserts by restricting activity to the night (Gordon et al. 1977; Postlethwait et al. 1991; Randall et al. 1997). Yousef and Dill (1971) asserted that *D. merriami* is poorly adapted to $T_a > 34^\circ\text{C}$ and that its survival in the desert depends on avoidance of high T_a 's. Similar conclusions have been drawn by Schmidt-Nielsen and Schmidt-Nielsen (1950). However, Dawson (1955) suggested that kangaroo rats such as *D. merriami* are frequently exposed to T_a 's near their lethal limit, and data from Schmidt-Nielsen and Schmidt-Nielsen (1950) imply that individuals may occasionally experience high T_a 's. Dawson (1955) also indicated that body temperature (T_b) in this species is somewhat labile, tending to vary directly with T_a from the zone of thermal neutrality upward, and believed that this rodent has an exceptional capacity to withstand elevated T_b as a means to tolerate high T_a 's. Individuals in his study exposed to $T_a = 40^\circ\text{C}$ suffered no ill effects. Because these animals seemingly could not prevent T_b from rising, withstanding elevated T_b 's was seen as an important physiological attribute, regardless of the nocturnality and fossorial behaviors of these animals.

The notion that kangaroo rats are very limited in their thermal tolerance has largely been inferred from indirect evidence. It is interesting to note, however, that *D. merriami* has about the same capacity for T_b regulation at high T_a 's as does the antelope ground squirrel (Dawson 1955). If such a diurnal desert rodent has no greater capacity for T_b regulation, the prevalent implication that nocturnality is an escape measure for limited thermal tolerance in kangaroo rats is not justified.

Differences in acclimation state may explain the differing conclusions of these studies. Kangaroo rats in Dawson's (1955) study were summer acclimated, while data from Yousef and Dill's (1971) study were gathered from animals from two seasons. Winter-acclimated rats had slower and less successful adjustments to heat stress than those that were summer acclimated, and this greater ability of summer-acclimated rats to tolerate heat was attributed to lower resting volumetric oxygen consumption ($\dot{V}O_2$) and thinner pelage than winter-acclimated rats (Yousef and Dill 1971). These conflicting findings warrant further investigation.

Because much of our knowledge about the thermal tolerances and ecological limits of kangaroo rats come from such analyses of resting adults, it is also important to consider the effects of activity (Wunder 1974). Gradients for heat transfer at high T_a 's decrease as T_b elevates, and the capacity for elevated T_b can

*To whom correspondence should be addressed. Present address: 330 Fitchville Road, Bozrah, Connecticut 06334; e-mail: randytracy@email.com.

reduce the need for evaporative cooling. Therefore, we examined the capacity for thermal tolerance to determine to what extent Merriam's kangaroo rats are capable of functioning at high T_a 's and, secondarily, to what extent they are capable of sustaining high T_b 's under ecologically relevant levels of activity. We tested the thermal tolerance of *D. merriami* during locomotion and determined whether this tolerance varies intraspecifically with geography. We also examined the consequences of activity at different T_a 's for evaporative water loss (EWL) and whether this loss varies intraspecifically. Based on our earlier studies, we hypothesized that the maximum T_a tolerated by this species is well over the 30°C typically used as the highest testing temperature in previous studies of kangaroo rats (Taylor et al. 1970; Raab and Schmidt-Nielsen 1972; Wunder 1974). We also hypothesized that thermal tolerance is greater and EWL is lower among xeric-site animals than among mesic-site animals.

Material and Methods

Field Sites

Two field sites that represent the broad range of conditions faced by *Dipodomys merriami* throughout its geographical range were used. The xeric site is located in the heart of the Sonoran Desert in Yuma County, southwestern Arizona (32°50'N, 113°30'W) at 150-m elevation (Turner and Brown 1994). It is typified by aeolian sand dunes, with sparse mesquite and creosote bushes. It is also one of the most arid sites inhabited by *D. merriami* (Hoffmeister 1986). Mean annual minimum and maximum daily temperatures are 14.7° and 31.9°C, respectively, and the average daily temperature range during the hottest month (July) is 26°–43°C (Green and Sellers 1964). Mean annual precipitation averages only 10.6 cm, with the greatest accumulation during the winter months and summer monsoon season (Green and Sellers 1964). The mesic site is located in north-central Arizona, within Gila County, (34°10'N, 111°15'W) at 1,200-m elevation and contains creosote bushes bordered by pinyon-juniper woodland. Daily minimum and maximum temperatures annually average 6.2° and 23.5°C, respectively, and yearly precipitation averages 43.6 cm (Green and Sellers 1964; Sellers et al. 1985). Average daily temperature range during the hottest month (July) is 24°–40°C (Green and Sellers 1964).

Individuals belonging to one subspecies of Merriam's kangaroo rat (*D. merriami merriami*) were trapped using Sherman traps at each site in September and early October 1998 for all measurements. Juveniles were excluded from all experiments.

Animal Care and Handling

Captured animals from the xeric and mesic sites ($N = 16$ and $N = 15$, respectively) were transported to Arizona State University, weighed, and maintained on a 12L : 12D photocycle in

an environmental chamber at 30°C and 20% relative humidity (as measured with an Omega model 35519-050 RH digital thermohygrometer). Kangaroo rats were allowed access to moistened seeds for 12 h after capture and then maintained on a dry-seed diet (Hartz Cockatiel Seed: comprised of millet seed, oat groats, red millet seed, sunflower seed, and canary seed) ad lib. for the duration of the studies. Each animal was individually caged on a dirt floor and provided with a section of plastic piping for shelter. After they were captured, kangaroo rats were implanted with temperature transmitters and allowed to recover for 5 d before experimental measurements. Animals were weighed daily throughout their housing to ensure maintenance of mass. All animals maintained mass throughout this study.

Treadmill Specifics

The treadmill metabolic chamber was 5.5 L in volume and constructed of 0.65-cm plate aluminum. The chamber face consisted of glass, as Plexiglas was determined to be too hydroscopic to permit accurate EWL measurements. A textured vinyl tread revolved on two aluminum axles and was moved at a constant rate of 9.8 m min⁻¹ (0.6 km h⁻¹) by an external 12VDC motor (Globe Motors). From values of total foraging distance traveled in a night (Thompson 1982, 1985), we calculated the average distance that these animals would cover in 30 min and set treadmill speed accordingly. A steel brush tipped with small beads of silicone was positioned at the back of the treadmill to promote the continual movement of each kangaroo rat. Kangaroo rats ran steadily without pause at all times except during the last minute of trials at $T_a = 42.5^\circ\text{C}$. Intermittent running occurred during this minute and the trials were terminated.

Gas Exchange and Evaporation

We measured O₂ consumption, CO₂ production, EWL, and T_b simultaneously. O₂ and CO₂ values for each animal were used to determine respiratory exchange ratios (RER; the ratio of CO₂ expired/O₂ consumed) to estimate metabolic water production and metabolic heat production (MHP).

Measurements were made at $T_a = 25^\circ, 30^\circ, 35^\circ, 40^\circ,$ and 42.5°C in the open-flow metabolic treadmill. Temperatures within the chamber were measured with 26-gauge, type-T thermocouples and controlled at $\pm 0.5^\circ\text{C}$ by placing the chamber within a temperature-controlled cabinet. All measurements were made between 0800 and 1800 hours during the inactive phase of each animal's daily cycle. Animals were deprived of food for 1 h before experiments. Instrument signals were recorded by a Campbell 23x data logger and averaged at 1-min intervals. Animals were positioned within the chamber and viewed with a Magnavox observation camera mounted inside the temperature-controlled cabinet. A red fluorescent light il-

luminated the cabinet. The local red light was used to enhance the images received by our observation camera without unduly illuminating the animal during exercise. Values are reported from the end of the 30-min runs at $T_a = 25^\circ$, 30° , and 35°C and for the last minute before the run was terminated at 40° and 42.5°C . Animals were tested at $T_a = 25^\circ$, 30° , and 35°C in random order. Because of the possibility of death at $T_a = 40^\circ$ and 42.5°C , animals were tested at these temperatures last. All animals within an experimental group (eight in all) were run during 1 d at 40°C and then at 42.5°C 2 d later. Runs were terminated at $T_a = 40^\circ$ and 42.5°C when the animal was in obvious distress and continually laying prostrate, which itself corresponded with a rapid increase in vapor density (a pronounced spike above 7 mg L^{-1}) and T_b (approximately 42.5°C). After experiments were terminated at these two temperatures, each animal was quickly returned to room temperature (23°C), placed on an aluminum block ($10 \times 20 \times 1\text{ cm}$) in front of a small fan to facilitate cooling, and given a $5 \times 5\text{-cm}$ square of lettuce to compensate for water loss.

Air was passed through the chamber through nonhydroscopic, 3.2-mm i.d. tubing (Li-Cor Bev-A-Line) at $1.4\text{--}2.5\text{ L min}^{-1}$ after being dried and scrubbed of CO_2 by a Puregas model CDA112 air dryer/ CO_2 absorber system. The higher flow rates were required at $T_a = 40^\circ$ and 42.5°C to prevent the vapor density from becoming too high (exceeding 7 mg L^{-1}) and to prevent extreme hypercapnia within the chamber. Airflow was measured with Omega N112-02G rotameters, calibrated to $\pm 1\%$ with a 100 mL soap-bubble flowmeter. These flow rates allowed the entire respiratory apparatus to equilibrate in 10–20 min following the calculations of Lasiewski et al. (1966). A subsample of gas was dried with anhydrous calcium sulfate and passed to a Li-Cor model LI 6252 CO_2 analyzer that had been factory calibrated 4 mo earlier. The CO_2 analyzer resolved CO_2 concentration to 0.1 ppm, or less than 0.1% of measured values, and was calibrated daily using both CO_2 -free air and a calibration gas known to contain 2,780 ppm CO_2 . Noise level of this analyzer is typically 0.2 ppm, with a maximum of 0.4 ppm. Characteristic readings exceeded 1,200 ppm, giving a signal to noise ratio of approximately 4,000 : 1. CO_2 production was calculated using equation (3) of Walsberg and Wolf (1995) and corrected to STP (0°C , 101 kPa).

The O_2 concentration of air entering and leaving the chamber was determined with an Applied Electrochemistry S3a O_2 analyzer that was calibrated using atmospheric air drawn from outside of the building and positioned upstream of the CO_2 analyzer in a serial arrangement. The O_2 analyzer has a sensitivity of 0.001% O_2 and an accuracy of $\pm 0.1\%$ of the O_2 reading. Air drawn into the oxygen analyzer was dried with anhydrous calcium sulfate (Drierite). O_2 consumption was calculated from a modified version of equation (2) of Hill (1972) because CO_2 was not removed from the samples used for O_2 analyses but only dried. F'_{EO_2} (the volume fractional concentration of O_2 in dry, CO_2 -free outlet air) was calculated from

measurements of F_{EO_2} (the volume fractional concentration of O_2 in dry outlet air) and measurements of F_{ECO_2} (the volume fractional concentration of CO_2 in dry outlet air). The accuracy of the entire system of chambers, flowmeters, absorbents, and analyzers has been tested with introduced boluses of N_2 and CO_2 and found to yield an error of 3% (G. E. Walsberg, unpublished observations) for measurements of both \dot{V}_{O_2} and volumetric carbon dioxide production (\dot{V}_{CO_2}).

EWL was measured using a Thunder Scientific model PC-2101C hygrometer that measures water-vapor concentration in milligrams per liter and was calibrated by the technique of Walsberg et al. (1997). These values were matched with corresponding airflow rates into the chamber and the mass of each kangaroo rat to arrive at mass-specific rates of whole-body EWL. Flow rates to the chamber were maintained high enough to prevent the vapor density from initially building up within the respiratory chambers in excess of 7 mg L^{-1} and low enough to depress oxygen between 0.65% and 1.0%. Evaporative heat loss (EHL) was calculated with the value of $2.42\text{ kJ g}^{-1}\text{ H}_2\text{O}$ for the latent heat of evaporation.

Although calculation of MHP from \dot{V}_{CO_2} potentially entails higher errors than calculation from \dot{V}_{O_2} , we chose to use \dot{V}_{CO_2} because of the inherently greater resolution of the CO_2 analyzer compared to the O_2 analyzer and the comparatively low signal-to-noise ratio of measured oxygen consumption at high T_a 's because of high flow rates and, therefore, limited depression of oxygen content. The thermal equivalent of CO_2 production (27.8 kJ L^{-1}) was used (Walsberg and Wolf 1995).

RERs were calculated as the ratio of \dot{V}_{CO_2} production to \dot{V}_{O_2} . A storage component was calculated by determining the derivative (and, therefore, the rate of increase of T_b) of the regression that best fit the profile of T_b versus time at a particular T_a , making the simplifying assumption that the entire mass of each animal increased uniformly in temperature and using the typical value of 3.5 J g^{-1} stored within the tissue for an increase in T_b of 1°C (Withers 1992).

Body Temperature Measurement

Minimitter model X-M temperature transmitters were implanted into kangaroo rats to determine core T_b . The transmitters were sealed in polyethylene capsules and covered with beeswax. Total mass of the transmitters did not exceed 1.4 g, or approximately 4% of the animal's body mass. The transmitters were first calibrated in water baths from 35° to 43°C . Then they were positioned within the peritoneal cavities of kangaroo rats that were anesthetized through inhalation (Mefofane; methoxyflurane). Muscular and cutaneous incisions (1 cm in length) were closed with Davis+Geck 1.5 metric surgical silk sutures (CE-4), and a topical antibiotic was administered. Animals were given $5 \times 5\text{-cm}$ pieces of lettuce postsurgery and allowed to recover for 5 d before experimentation.

The antenna used to receive the transmitter lined the inside

Table 1: Descriptive statistics for mass-specific gas and vapor exchange for all animals and total gas exchange for animals from each site from $T_a = 25^\circ$ to 42.5°C

Parameter	25°C		30°C		35°C		40°C		42.5°C	
	Mean \pm SEM	<i>N</i>	Mean \pm SEM	<i>N</i>	Mean \pm SEM	<i>N</i>	Mean \pm SEM	<i>N</i>	Mean \pm SEM	<i>N</i>
Mass-specific										
\dot{V}_{O_2} (mL g ⁻¹ h ⁻¹)	4.59 \pm .08	31	4.28 \pm .10	31	4.12 \pm .08	31	4.63 \pm .19	31	5.17 \pm .18	28
Mass-specific										
\dot{V}_{CO_2} (mL g ⁻¹ h ⁻¹)	3.47 \pm .07	31	3.32 \pm .08	31	3.17 \pm .07	31	3.81 \pm .12	31	4.38 \pm .16	28
Mass-specific										
EWL (mg g ⁻¹ h ⁻¹)	1.99 \pm .14	31	2.38 \pm .15	31	2.63 \pm .21	31	12.28 \pm 1.99	31	17.23 \pm 2.24	28
Heat storage										
(W)15 \pm .03	30	.52 \pm .04	28
\dot{V}_{O_2}										
(mL min ⁻¹)	2.72 \pm .07	31	2.55 \pm .10	31	2.43 \pm .07	31	2.65 \pm .11	31	3.22 \pm .14	28
\dot{V}_{CO_2}										
(mL min ⁻¹):										
Xeric site	1.92 \pm .06	16	1.79 \pm .08	16	1.71 \pm .07	16	2.02 \pm .09	16	2.53 \pm .09	14
Mesic site	2.20 \pm .08	15	2.17 \pm .10	15	2.05 \pm .08	15	2.28 \pm .13	14	2.91 \pm .19	14

Note. Mass-specific values were not significantly different between xeric- and mesic-site animals and were therefore pooled.

walls of the treadmill chamber. One hundred signal pulses were received by an AM radio and timed with a stopwatch at each recording session. Typically, these took 35 s to record, but the time decreased at higher T_b 's (range = 25–45 s). Although rapid pulses approached 4 Hz during these single measurements, measurements at these frequencies during calibrations were highly repeatable ($r^2 = 0.99$). We recorded T_b every 5 min at 25°, 30°, and 35°C. At 40° and 42.5°C, we recorded T_b 's every 5 min for the first 10 min of activity and every 2 min thereafter until animal failure.

Statistical Analyses

Data were analyzed with SPSS 7.5 (Norusis 1997) using general linear model repeated-measures ANOVA to examine overall effects of T_a (within subject factor) and site (between subject factor) on physiological parameters and any interactions between site and T_a on these parameters. Significance was accepted at the $P < 0.05$ level. Data recorded as ratios (e.g., RER) were arcsine transformed before analyses. Because T_b 's of these animals were measured repeatedly over time during these experiments and at multiple T_a 's, we used repeated-measures ANOVA to investigate site and T_a effects separately on the initial and final T_b 's of these xeric- and mesic-site animals. At those points of interest, potential differences in physiological parameters from one point to another at a particular T_a or potential differences in these parameters among the animals from the two

sites at the same T_a were investigated with either paired t -tests or one-way ANOVA, respectively. Mean values are reported with standard errors.

Results

Site Effects on Physiological Parameters

Xeric-site animals averaged 33.6 ± 0.49 g ($N = 16$) and were significantly smaller than mesic-site animals, which averaged 37.9 ± 0.52 g ($N = 15$; $P < 0.001$). There was no effect of site on mass-specific \dot{V}_{O_2} ($F = 0.1519$, $df = 1$, $P = 0.229$), mass-specific \dot{V}_{CO_2} ($F = 0.396$, $df = 1$, $P = 0.535$), mass-specific EWL ($F = 1.925$, $df = 1$, $P = 0.177$), total heat storage ($F = 0.673$, $df = 1$, $P = 0.419$), nor total \dot{V}_{O_2} ($F = 1.961$, $df = 1$, $P = 0.173$). Therefore, these values were combined for animals from both sites (Table 1). However, mesic-site animals had greater total \dot{V}_{CO_2} ($F = 7.526$, $df = 1$, $P = 0.011$) than xeric-site animals. These values are presented separately for each site (Table 1).

There was no significant effect of site on total EWL nor its derived, calculated total EHL ($F = 0.981$, $df = 1$, $P = 0.331$; Fig. 1a). Similarly, there was no effect of site on mass-specific MHP ($F = 0.391$, $df = 1$, $P = 0.537$), mass-specific EHL ($F = 1.926$, $df = 1$, $P = 0.177$), nor mass-specific heat storage ($F = 0.036$, $df = 1$, $P = 0.851$; Fig. 1b). However, mesic-site animals had greater total MHP ($F = 7.624$, $df = 1$, $P =$

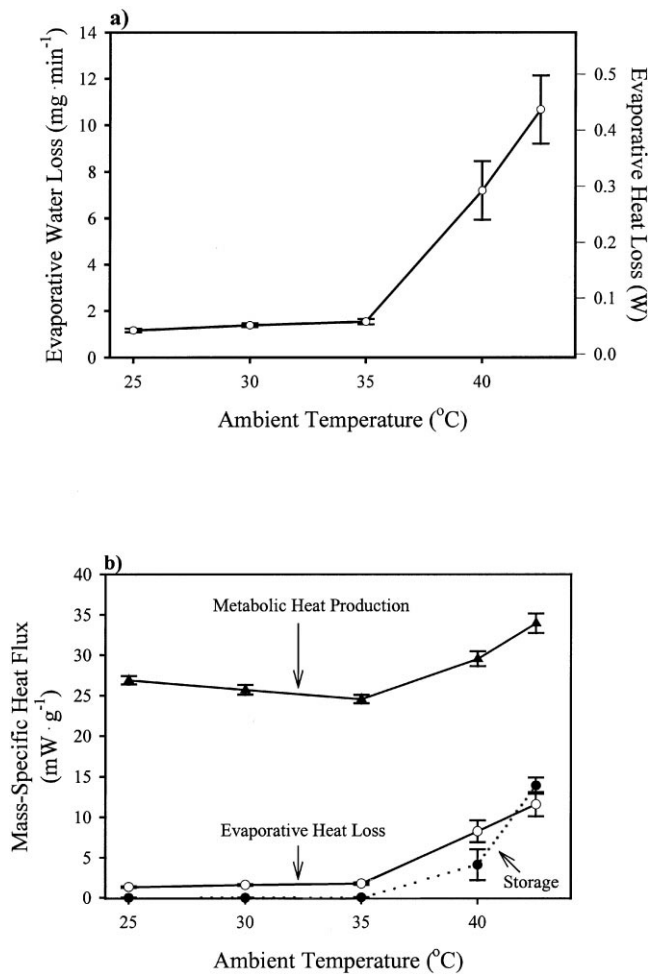


Figure 1. *a*, Total evaporative water and heat loss from all kangaroo rats at various ambient temperatures (T_a 's) with means and standard errors. *b*, Mass-specific heat flux (metabolic heat production, evaporative heat loss, and a storage component attributed to elevated body temperature) for all kangaroo rats at various T_a 's with means and standard errors. $N = 31$ for all T_a 's, except $T_a = 42.5^\circ\text{C}$ ($N = 28$).

0.010; Fig. 2) and RER ($F = 7.626$, $df = 1$, $P = 0.012$; Fig. 3) than xeric-site animals.

Ambient Temperature Effects on Physiological Parameters

There were overall effects of T_a on all parameters measured or calculated: mass-specific $\dot{V}O_2$ ($F = 10.202$), mass-specific $\dot{V}CO_2$ ($F = 26.708$), mass-specific EWL ($F = 31.170$), total heat storage ($F = 122.684$), total $\dot{V}O_2$ ($F = 18.301$), and total $\dot{V}CO_2$ ($F = 40.548$; Table 1), as well as total EWL and total EHL ($F = 28.613$; Fig. 1*a*), mass-specific MHP ($F = 26.661$; Fig. 1*b*), mass-specific EHL ($F = 31.164$; Fig. 1*b*), mass-specific heat storage ($F = 120.030$; Fig. 1*b*), total MHP ($F = 36.438$; Fig. 2), and RER ($F = 13.989$; Fig. 3; $df = 4$ and $P < 0.001$ for all pa-

rameters). All of these parameters steadily increased above $T_a = 35^\circ\text{C}$ (Figs. 1–3).

Site and Ambient Temperature Effects on Physiological Parameters

There were no significant interactions between site and T_a on mass-specific $\dot{V}O_2$ ($F = 1.485$, $df = 4$, $P = 0.212$), mass-specific $\dot{V}CO_2$ ($F = 0.408$, $df = 4$, $P = 0.802$), mass-specific EWL ($F = 1.728$, $df = 4$, $P = 0.149$), total heat storage ($F = 0.013$, $df = 1$, $P = 0.911$), total $\dot{V}O_2$ ($F = 1.097$, $df = 4$, $P = 0.362$), nor total $\dot{V}CO_2$ ($F = 0.327$, $df = 4$, $P = 0.859$; Table 1). Similarly, there was no significant interaction between site and T_a on total EWL nor its derived, calculated total EHL ($F = 1.233$, $df = 4$, $P = 0.301$; Fig. 1*a*), mass-specific MHP ($F = 0.409$, $df = 4$, $P = 0.802$; Fig. 1*b*), mass-specific EHL ($F = 1.728$, $df = 4$, $P = 0.149$; Fig. 1*b*), mass-specific heat storage ($F = 0.260$; $df = 4$, $P = 0.903$; Fig. 1*b*), total MHP ($F = 0.307$, $df = 4$, $P = 0.873$; Fig. 2), nor RER ($F = 1.336$, $df = 4$, $P = 0.263$; Fig. 3). For both sites, RER significantly increased above 35°C .

Body Temperature

Repeated-measures ANOVA demonstrate that there was no significant overall effect of site on initial T_b ($F = 1.019$, $df = 1$, $P = 0.322$; Figs. 4, 5; Table 2). There was a significant effect of T_a on initial T_b ($F = 3.665$, $df = 4$, $P = 0.008$; Figs. 4, 5). Also, with respect to initial T_b , there was a significant interaction between T_a and site ($F = 2.871$, $df = 4$, $P = 0.027$), most likely as a result of the comparatively elevated initial T_b of xeric-site

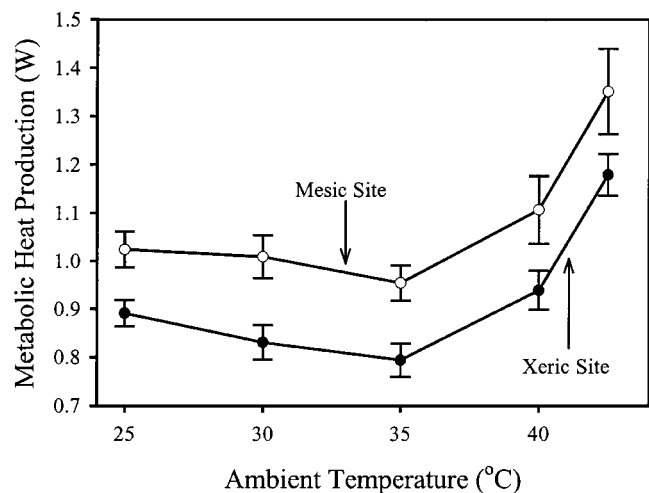


Figure 2. Total metabolic heat production for xeric- and mesic-site animals at various ambient temperatures with means and standard errors. Significant differences exist between the two sites.

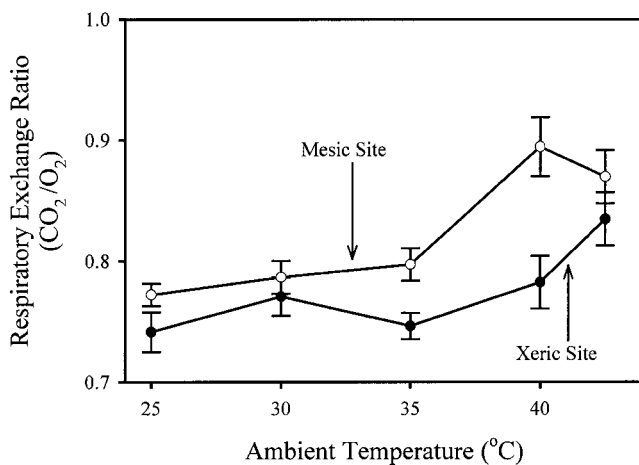


Figure 3. Respiratory exchange ratios for xeric- and mesic-site animals versus ambient temperature, reflecting metabolic water production.

animals at $T_a = 25^\circ\text{C}$. It is unclear whether this was a result of type I error.

There was no significant overall effect of site on final T_b ($F = 0.578$, $df = 1$, $P = 0.454$). There was a significant effect of T_a on final T_b ($F = 136.575$, $df = 4$, $P < 0.001$; Figs. 4, 5). Also, with respect to final T_b , there was a significant interaction between T_a and site ($F = 3.740$, $df = 4$, $P = 0.007$). Therefore, we investigated final T_b at $T_a = 42.5^\circ\text{C}$ and determined it to be greater in mesic- than in xeric-site animals and the possible origin of the aforementioned significant interaction ($P = 0.019$, one-way ANOVA; Figs. 4, 5; Table 2).

T_b leveled off (as defined by 5 min with the same T_b) within 15–20 min at both $T_a = 25^\circ$ and 30°C (Figs. 4, 5). At $T_a = 35^\circ\text{C}$, stable T_b occurred after 25 min for animals from both sites. Final T_b at this T_a for mesic-site animals was significantly greater than at lower T_a 's ($P < 0.001$, paired t -test; Fig. 5; Table 2). At $T_a = 40^\circ\text{C}$, T_b of xeric-site animals remained the same after 26 min, but stable T_b was never reached for mesic-site animals at this T_a (paired t -test; Figs. 4, 5). At $T_a = 42.5^\circ\text{C}$, stable T_b was never reached for animals from either site but steadily increased until animal failure. At this T_a , linear regressions of the specific rates of change in body temperature over time approximated $0.32^\circ\text{C min}^{-1}$ for mesic-site animals and exceeded that of $0.28^\circ\text{C min}^{-1}$ for xeric-site animals ($r^2 = 0.93$ and 0.81 , respectively).

To explore the rate of T_b increase over time at different T_a 's, T_b profiles (Figs. 4, 5) were linearized for every animal by \log_{10} - \log_{10} transformations, and repeated-measures ANOVA were performed on the resultant intercepts and slopes. Because T_b 's reached a stable plateau at the lower T_a 's and, therefore, did not exhibit the qualities of true logarithmic relationships (which are continually increasing), only data up to and including the first point of the plateau were used for these transformations.

Mean r^2 for all linear transformations for xeric-site animals was 0.91 ± 0.010 , while that for all mesic-site animals was 0.94 ± 0.005 (Table 2).

There was an overall effect of site ($F = 4.701$, $df = 1$, $P = 0.039$) and T_a ($F = 207.463$, $df = 4$, $P < 0.001$) on the slopes of T_b versus time but no significant interaction between site and T_a on these slopes ($F = 1.779$, $df = 4$, $P = 0.139$). Slopes steadily increased with increasing T_a and were steeper for mesic-site than xeric-site animals (Figs. 4, 5; Table 2).

There was no significant effect of site on the intercepts of T_b versus time ($F = 0.617$, $df = 1$, $P = 0.439$) but a significant effect of T_a ($F = 12.913$, $df = 4$, $P < 0.001$) and a significant interaction between site and T_a ($F = 3.067$, $df = 4$, $P = 0.020$) on these intercepts (and therefore initial T_b 's). The latter most likely arose from the high initial T_b 's of xeric-site animals at $T_a = 25^\circ\text{C}$.

Collectively, cubic regressions best fit these T_b profiles over time for animals from both sites and for all T_a 's (r^2 range: 0.986 – 1.000). Representative of this is the regression for xeric-site animals at 25°C ($T_b = 36.9951 + 0.2335 \times \text{Time} - 0.0089 \times \text{Time}^2 + 0.0001 \times \text{Time}^3$; $r^2 = 0.998$). Except at $T_a = 25^\circ\text{C}$ for xeric-site animals, where $T_b = 37.0^\circ\text{C}$ at $\text{Time} = 0$, all other intercepts ranged from 36.1° to 36.4°C .

All animals completed 30 min of activity without distress at $T_a = 25^\circ$, 30° , and 35°C . Time to failure did not differ between xeric- and mesic-site animals at $T_a = 40^\circ\text{C}$ ($P = 0.914$; Fig. 6a) and averaged 27.4 ± 0.6 min. Time to failure also did not vary between animals from these sites at $T_a = 42.5^\circ\text{C}$ ($P = 0.218$; Fig. 6b) yet averaged only 19.2 ± 0.6 min. This time to failure

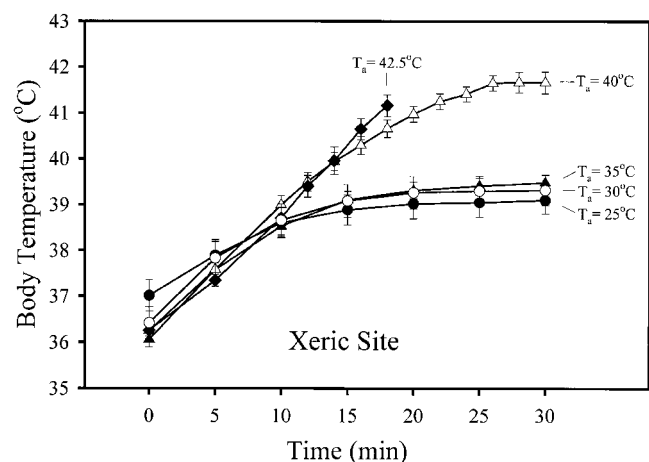


Figure 4. Mean body temperatures \pm SE for xeric-site animals versus time at different ambient temperatures (T_a 's). $N = 15$ for all times at $T_a = 25^\circ$, 30° , and 35°C . At $T_a = 42.5^\circ\text{C}$, means \pm SEs are shown until the sample size fell to half its original value from failing animals (see Fig. 6a, 6b to determine sample sizes due to failing animals at $T_a = 40^\circ$ and 42.5°C).

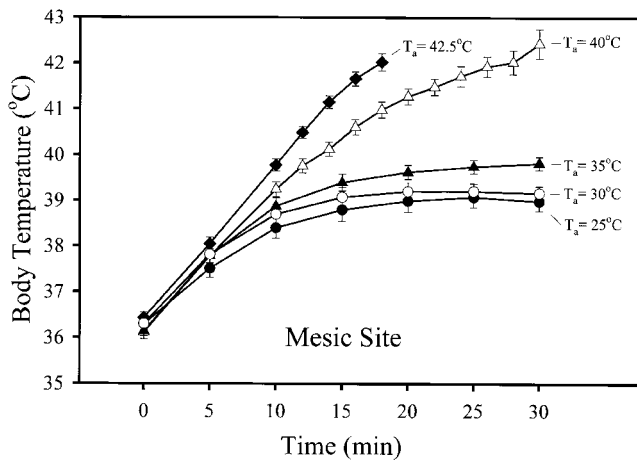


Figure 5. Mesic-site animal body temperatures at different ambient temperatures (T_a 's) versus time. $N = 15$ for all times at $T_a = 25^\circ$, 30° , and 35°C , except at time = 15 and 20 min at $T_a = 35^\circ\text{C}$ ($N = 14$). At $T_a = 42.5^\circ\text{C}$, means \pm SEs are shown until the sample size fell to half its original value from failing animals (see Fig. 6a, 6b to determine sample sizes due to failing animals at $T_a = 40^\circ$ and 42.5°C).

occurred significantly more quickly than at $T_a = 40^\circ\text{C}$ ($P < 0.001$).

Discussion

Evaporative Water Loss and Heat Flux

The consistently low EWL from $T_a = 25^\circ$ to 35°C (Fig. 1a) indicates that these animals have the capacity to remain active at these temperatures for long periods of time without incurring substantial water loss. However, it is not surprising that EWL increased strongly when T_a exceeded 35°C . When T_a exceeded typical T_b (i.e., at $T_a = 40^\circ$ and 42.5°C), EWL increased nearly an order of magnitude to offset the added metabolic heat load from the kangaroo rat and input from the environment. Correspondingly, EHL increased above $T_a = 35^\circ\text{C}$. Though initially compensating less than 10% of the metabolic heat being produced at $T_a < 35^\circ\text{C}$, soaring EHL offset approximately 30% of the metabolic heat being produced at $T_a = 40^\circ$ and 42.5°C (Fig. 1b). At these T_a 's, the increased heat storage associated with the increase in MHP contributed to the elevated T_b 's exhibited by all animals (Fig. 1b).

The greater total MHP of mesic-site than xeric-site animals (Fig. 2) is consistent with the greater mass of mesic-site animals. One would have expected mesic-site animals to have greater total levels of EWL than xeric-site animals to counteract the added heat load the former generate metabolically. Also, the larger mass of the mesic-site animals allows them to store more heat for a given increase in T_b . Nevertheless, the rate of increase in T_b at $T_a = 42.5^\circ\text{C}$ and final T_b of mesic-site animals (Fig. 5) exceeded that of the xeric-site animals (Fig. 4). This could

have occurred because EWL (and therefore EHL) was insufficient to offset the comparatively high MHP in mesic-site animals.

Metabolic Water Production

The increases in RER with T_a (Fig. 3) may represent a shift from predominantly lipid metabolism at lower T_a 's to increasing glycolysis above $T_a = 35^\circ\text{C}$. As carbohydrates yield an RER of 1.0 while lipids yield an RER of 0.70 (Schmidt-Nielsen 1990), an increased dependence on (proportion of) anaerobic metabolism would likely contribute to an increase in RER, at least over the short term in a whole animal. This increase in RER may also be the passive result of behavioral changes at high T_a (increased escape behavior) that resulted in a heightened recruitment of glycolytic muscle fibers or slight hyperventilation. A consequence of this increase in RER may have been increased metabolic water production because carbohydrates yield more water per unit energy than lipids. One can estimate the metabolic water produced at these temperatures based on the substrates catabolized (Schmidt-Nielsen 1990). For instance, catabolism of a purely carbohydrate substrate would yield $0.031 \text{ g H}_2\text{O kJ}^{-1}$ energy (the greatest energy-specific yield of metabolic water per gram of carbohydrates, lipids, or proteins). Even if RER rose to 1.0 at higher temperatures (indicating exclusive catabolism of carbohydrates), metabolic water production would increase, at most, an additional 1.34 mg min^{-1} from $T_a = 35^\circ$ to 40°C . However, evaporative water loss rose a minimum of 5.93 mg min^{-1} from $T_a = 35^\circ$ to 40°C during this study (Fig. 1a). Therefore, the potentially increased metabolic water production due to changing fuel usage at higher temperatures would have only a limited effect in compensating for the high levels of EWL at these high T_a 's.

Body Temperature and Thermal Tolerance

Glycogen depletion occurs sooner at high temperatures because muscles and surface tissues compete for blood and therefore glucose. Failure at $T_a = 40^\circ$ and 42.5°C in part may have been due to muscle glycogen depletion. We did not wish to test muscular fatigue but instead the ability to remain active at an ecologically relevant speed at high T_a 's (tolerance to high T_a 's). Nonetheless, fatigue (*sensu stricto*) and tolerance may be inextricably linked at these high T_a 's. Importantly, though, it has been claimed that the highest T_a 's that kangaroo rats can tolerate may be substantially lower than diurnal rodents that can tolerate T_a 's as high as 42.5°C (Carpenter 1966). The thermal tolerance of *Dipodomys merriami* exhibited in this study is greater than formerly appreciated and corroborates those data gathered by Dawson (1955). Carpenter (1966) suggested that because he saw no evidence of salivation in kangaroo rats at T_a 's near 40°C , these species are rarely subjected to temperatures above thermoneutrality (30° – 35°C). In that study of the ther-

Table 2: Slopes, intercepts, and coefficients of determination of values obtained from the relationship between T_b versus time ($^{\circ}\text{C min}^{-1}$) that were \log_{10} - \log_{10} transformed and final T_b 's ($^{\circ}\text{C}$) for xeric- and mesic-site animals from $T_a = 25^{\circ}$ to 42.5°C

	25 $^{\circ}\text{C}$	30 $^{\circ}\text{C}$	35 $^{\circ}\text{C}$	40 $^{\circ}\text{C}$	42.5 $^{\circ}\text{C}$
Xeric site:					
Slope017 \pm .002	.024 \pm .001	.028 \pm .001	.045 \pm .001	.045 \pm .001
Intercept	1.57 \pm .004	1.56 \pm .004	1.56 \pm .002	1.55 \pm .002	1.55 \pm .002
R^289 \pm .028	.92 \pm .015	.97 \pm .006	.90 \pm .017	.80 \pm .029
Final T_b ($^{\circ}\text{C}$)	39.1 \pm .30	39.3 \pm .33	39.5 \pm .18	41.7 \pm .14	41.2 \pm .18
Mesic site:					
Slope023 \pm .002	.024 \pm .001	.030 \pm .001	.048 \pm .002	.049 \pm .001
Intercept	1.56 \pm .003	1.56 \pm .002	1.56 \pm .002	1.55 \pm .002	1.55 \pm .002
R^294 \pm .013	.93 \pm .012	.97 \pm .004	.93 \pm .008	.89 \pm .009
Final T_b ($^{\circ}\text{C}$)	39.0 \pm .20	39.2 \pm .15	39.8 \pm .14	42.1 \pm .21	42.0 \pm .20

Note. Values are means \pm SEM.

moregulation of this species at rest, all *D. merriami* at $T_a > 37.5^{\circ}\text{C}$ died, and all animals studied at $T_a = 40^{\circ}\text{C}$ had T_b 's approaching 42°C and died. From these data, Carpenter (1966) concluded that the lethal T_a for *D. merriami* was 39° – 40°C . The results of this study, however, suggest that this species is much more thermally tolerant than formerly appreciated. Only two of 32 animals failed to recover after 30 min of continuous exercise at 40°C . At $T_a = 42.5^{\circ}\text{C}$, all survived, and most tolerated 15 min of continuous exercise (Fig. 6b). All animals that survived (30 of the 32) recovered completely and lived more than 30 d after the completion of this study. That all survived at this higher temperature and two did not at $T_a = 40^{\circ}\text{C}$ appears paradoxical but may be the result of our increased awareness of behavior representative of distress and critical levels of evaporative water loss in these animals during the higher-temperature runs. Therefore, it may have been increased vapor density that directly contributed to the death of those two animals, as they were two of the first animals tested at these temperatures, and we may have unnecessarily allowed them to continue with questionable levels of activity under conditions of high humidity. The long-term survival of the rest of the animals demonstrates that there were no delayed negative effects.

The 15 min tolerated by these animals at $T_a = 42.5^{\circ}\text{C}$ is a reasonable time for kangaroo rats to forage actively on the surface at potentially high temperatures before returning to their burrows. Likewise, the salivation apparent after 30 min of continuous locomotion at $T_a = 40^{\circ}\text{C}$ or 15 min of locomotion at $T_a = 42.5^{\circ}\text{C}$ in this study are testaments to the ability of these animals to evaporatively cool and suggests that they may at times be exposed to such conditions.

Burrows of *D. merriami* have been described as simple and 25–30 cm deep (Carpenter 1966). As soil temperature is greater than 35°C at these depths for greater than 30% of the year at our xeric site (Walsberg 2000), it seems likely that either bur-

rows are much deeper or these animals are exposed to these high temperatures for much of the day and year. This contention remains to be resolved.

Acclimation to milder conditions than this species experiences in the wild has been shown to result in relaxed physiological capacities, such as the ability to concentrate urine or restrict evaporative water loss (Tracy and Walsberg 2000b). Acclimation before or during animal maintenance in previous studies may have led to the comparatively low measures of thermal tolerance in this species. Furthermore, geographic dissimilarities could account for these physiological differences.

Collection Site Effects

While the differences in allowable T_b increases between xeric- and mesic-site animals were minimal, they still occurred in the direction our hypothesis predicted. Xeric-site animals do appear to possess slightly greater capacities to tolerate high T_a 's than mesic-site animals with respect to prevention of T_b increase. At high T_a 's (40° and 42.5°C), mesic-site animals never appeared to reach a stable T_b . Yet xeric-site animals did show evidence of reaching a stable T_b at $T_a = 40^{\circ}\text{C}$, even if it is was only for the last 4 min. T_b of xeric-site animals on trial completion was not elevated above that of lower T_a 's until $T_a = 40^{\circ}\text{C}$. However, T_b on trial completion for mesic-site animals became elevated at a lower T_a (35°C). Also, at $T_a = 42.5^{\circ}\text{C}$, the rate of T_b increases over time, and final T_b 's were greater in mesic-site animals than xeric-site animals. Nonetheless, the ecological relevance of these differences are questionable, as there were no differences in time to failure or EWL between these two groups at $T_a = 40^{\circ}$ and 42.5°C .

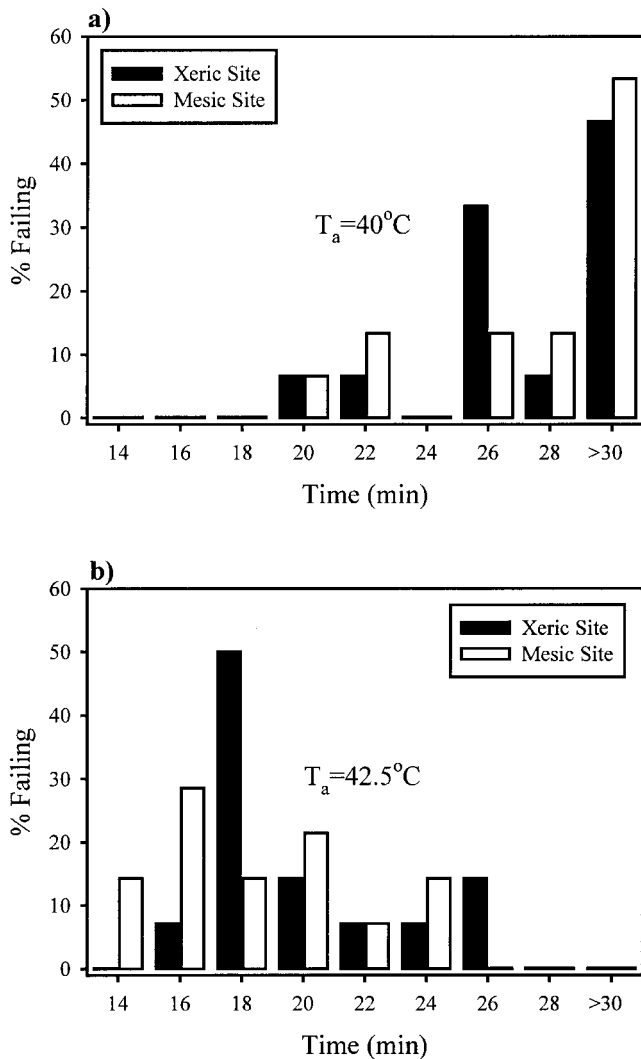


Figure 6. *a*, Tolerance of xeric- and mesic-site animals at $T_a = 40^\circ\text{C}$ ($N = 15$ for each respective site). Percentage at time = 30 min represents animals that completed 30 min and were removed from the treadmill but still had not failed. *b*, Tolerance of xeric- and mesic-site animals at $T_a = 42.5^\circ\text{C}$ ($N = 14$ for each respective site).

Effects of Activity on Body Temperature

We have already demonstrated this species' capacity to tolerate T_a 's of up to 42.5°C at rest for at least an hour (Tracy and Walsberg 2000a). How do kangaroo rats fare when active at such T_a 's? In Wunder's (1974) investigation of Ord's kangaroo rat (*Dipodomys ordii*), activity was found to have a dramatic effect on the thermal tolerance range for this inhabitant of less extreme deserts. While resting animals could withstand 30°C with very little elevation in T_b , they lost this T_b stability with only moderate activity (Wunder 1974). We agree that activity should be taken into account when determining thermal tol-

erances. However, *D. merriami* appears to employ semistable hyperthermia, as well as evaporation, as a means to tolerate moderately high T_a 's and has greater thermal tolerances than realized. This species certainly possesses a suite of coevolved adaptations that couple it to nocturnality. Although T_b and EWL increased in these kangaroo rats at high T_a 's, their activity persisted. Therefore, contrary to previous thought, it appears that these animals avoid the rigors of diurnality more for purposes of conservation of water combined with predator avoidance and, importantly, not avoidance of high T_a 's because they may at least temporarily endure mild hyperthermia and tolerate prolonged activity at these high T_a 's.

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