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Kangaroo rats revisited: re-evaluating a classic case of desert survival

Received: 3 December 2001 / Accepted: 16 August 2002 / Published online: 21 September 2002
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Abstract Kangaroo rats are the archetypical organisms for mammalian survival in North American deserts, yet there are contradictions in the data surrounding their physiology and ecology. The traditional view has been that these nocturnal rodents have little tolerance to high temperatures (e.g., $>30^{\circ}\text{C}$), reside in cool, humid burrows to escape the heat of the day, and nearly exclusively rely on a dry, carbohydrate-rich diet from which they metabolically derive most of their water supply. To test this view, we measured the microclimates, activity, and diet of Merriam's kangaroo rats (*Dipodomys merriami*) from a xeric location within the center of the Sonoran Desert. We arrive at the following conclusions:

1. Burrows are much hotter during the summer than previously appreciated. For over 100 days of the year, soil temperatures exceed 30°C at depths to 2 m. For over 50 days, temperatures exceed 35°C at depths to 1.5 m. These high temperatures at such depths preclude kangaroo rats from locating to cool temperatures (e.g., $<30^{\circ}\text{C}$) by burrowing.
2. Kangaroo rats remain in shallow burrows (<1 m) at relatively high ambient temperatures ($>35^{\circ}\text{C}$) throughout the daytime during the summer instead of residing deep within the soil. This finding supports recent laboratory experiments that show kangaroo rats have much higher thermal tolerances than previously realized.
3. Kangaroo rats do not restrict their activity to the coolest periods of the night, but are active immediately following sundown, during the hottest time of the night.

4. Burrows are not persistently humid, but can be quite dry.
5. Insects and succulent vegetation constitute a significant portion of a kangaroo rat's diet and may be key to their survival in the hot desert environment.

Keywords *Dipodomys merriami* · Heteromyidae · Physiological ecology · Thermal tolerance · Water loss

Introduction

Studies of kangaroo rats (*Dipodomys* spp.) have produced a prototypical case history in physiological ecology. These small, nocturnal rodents are widely distributed in North American deserts and are particularly noted for their apparent ability to survive indefinitely in nature on a dry seed diet without access to drinking water. This ability is attributed to a combination of physiological mechanisms allowing them to minimize water loss through excretion and evaporation as well as selection of microclimates that minimize exposure to high temperatures. Kangaroo rats produce highly concentrated urine (Schmidt-Nielsen et al. 1948; Carpenter 1966; Kenagy 1973) and extremely dry feces (Schmidt-Nielsen and Schmidt-Nielsen 1951). Coprophagy and high assimilation efficiencies, coupled to their ability to reclaim water from feces when water-stressed (French 1993), contribute to their ability to produce feces containing only 40% of the water content of those from white rats (Schmidt-Nielsen and Schmidt-Nielsen 1951). Likewise, at least one species of kangaroo rat, *D. merriami*, exhibits reduced evaporation when compared to mesic animals (Schmidt-Nielsen and Schmidt-Nielsen 1952; Hinds and MacMillen 1985). Given these physiological traits, and because a carbohydrate substrate yields the most metabolic water per unit energy when compared to lipids or proteins (Schmidt-Nielsen and Schmidt-Nielsen 1952), the dominant view long has been that these animals are capable of surviving solely on a diet of dry, carbohydrate-rich seeds (Schmidt-Nielsen 1964).

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Behavioral avoidance of thermal extremes is believed to be central to the ability of kangaroo rats to survive in desert environments (Bradley and Yousef 1972). The traditional views of kangaroo rat microclimate selection embrace three aspects: kangaroo rats avoid high temperatures by restricting surface activity to nighttime hours when environmental temperatures are at their minimum (Schmidt-Nielsen and Schmidt-Nielsen 1950; French 1993; Degen 1997), burrow temperatures are cool (e.g., $<25^{\circ}\text{C}$), and occupancy of a burrow suppresses evaporative water loss due to its higher ambient humidity (Schmidt-Nielsen and Schmidt-Nielsen 1950; French 1993; Degen 1997). These views have been propagated in popular ecology textbooks as well (see Pough et al. 1996). However, often-cited studies measuring temperature (e.g., Vorhies 1945) and humidity (Schmidt-Nielsen and Schmidt-Nielsen 1950) of burrows of this and other desert rodents were conducted in comparatively mesic areas or after heavy rainfall and may not reflect the typical conditions of the Sonoran Desert (Walsberg 2000). Also correlated with this portrayal of survival in desert conditions by emphasis on conservation of water and behavioral avoidance of extreme conditions is the view that kangaroo rats are intolerant of high environmental temperatures (Carpenter 1966; Yousef and Dill 1971).

The degree to which this traditional view of the mechanisms underlying the success of these common rodents holds under extreme desert conditions has been questioned (Tracy and Walsberg 2000a, 2000b, 2001a, 2001b; Walsberg 2000). One reason is that the climate experienced by small mammals in subtropical deserts is apparently more challenging than previously appreciated. During the summer, nocturnal air temperatures are high through much of the night (e.g., $>40^{\circ}\text{C}$; Walsberg 2000). Unless small mammals restrict their activity to the period immediately before dawn, they should routinely experience high environmental temperatures. The temperatures experienced by the animal while in the burrow may also be quite high ($>35^{\circ}\text{C}$), based upon soil temperature measurements and assumptions regarding the depth of burrows within the soil (Walsberg 2000). Estimates of burrow humidity based upon biophysical modeling and soil water potentials also indicate that rodent burrows in desert soils are likely to be characterized by low humidities (Walsberg 2000). For example, typically dry desert soils containing $<10\%$ water by mass should produce relative humidities within soil-enclosed air spaces of $<10\%$ (Young and Nobel 1986). *D. merriami* does not regularly plug its burrows (Bienek and Grundmann 1971; Soholt 1974). This observation, combined with the rapid air turnover predicted for multi-entrance, unplugged burrow systems (Vogel and Bretz 1972), should also prevent burrow humidity from becoming substantially higher than the humidity of air above the ground surface. In addition, soil temperatures from even comparatively mild locations within the Sonoran Desert far exceed 25°C for much of the year, even at depths >2 m (Walsberg 2000). Clearly, environmental conditions in the burrows of *D. merriami* may be hotter and drier than previously

appreciated, and known physiological adaptations appear inadequate to maintain water balance under these conditions (Walsberg 2000).

Because desert rodents inhabit burrows and are nocturnal, it is possible that behavioral adjustments such as time of activity, depth to which an animal is sequestered in a burrow, or ability to relocate could compensate for physiological limitations and alleviate negative thermal and hydric effects. However, nocturnal desert rodents are not highly mobile (MacMillen 1972), and lifetime dispersal distances range only from 0 to 265 m in *D. merriami* (Jones 1989). Also, while certain nocturnal desert rodents can rely on periodic bouts of torpor or hypothermia when their usual physiological and behavioral capacities are insufficient to cope with subterranean conditions, *D. merriami* does not do so unless starved (see Yousef and Dill 1971).

Variation in time and duration of surface activity or depth within a burrow could abate some of the detrimental effects of high temperatures and low surface humidity. However, it is unclear what would be the constraints on activity given maximal water conservation through physiological means. No data exist on these attributes for this species in extreme desert habitats.

Finally, two lines of physiological evidence suggest that traditional generalizations regarding kangaroo rats may be insufficient. First, it is now clear that at least some species of *Dipodomys* are much more tolerant of high environmental temperatures than previously appreciated (Tracy and Walsberg 2000b). Second, substantial evidence now exists that kangaroo rats may routinely consume substantial amounts of two types of succulent food: green vegetation and insects (Reichman 1975; Nagy 1994; Nagy and Gruchacz 1994). These observations are consistent with analyses of body-water turnover in kangaroo rats that indicate substantially more preformed water in the diet than would be expected from a diet of air-dried seeds alone (Nagy 1994; Nagy and Gruchacz 1994). These studies suggest the existence of *D. merriami* may depend on preformed water.

D. merriami has been and continues to be the species of choice by physiological ecologists and environmental physiologists studying mammalian adaptation to desert environments, starting with the work of the Schmidt-Nielsens and their colleagues. Most of these studies were conducted in comparatively mild areas and their findings extrapolated to "the desert." Therefore, because of the seminal importance of this species, we tested in the current analysis the hypothesis that previous views surrounding the physiology and ecology of nocturnal desert rodents are based primarily on assumptions not appropriate for environments experienced by Merriam's kangaroo rats (*Dipodomys merriami*) during the summer in a hot subtropical desert. We chose to investigate individuals of this species from the area around Yuma, Arizona, which is known as being very hot and dry and, as a consequence, closer to what most would regard as a true desert. We analyzed the burrow environment in terms of both the humidity and temperature of occupied burrows,

as well as associated soil temperatures. We also quantified the surface environment experienced at night, as well as the temporal extent of surface activity by kangaroo rats. We also examine whether the portrayal of these animals as strict granivores is accurate. Finally, we analyzed consequences of occupation of these thermal and hydric environments as well as diet composition in terms of the animal's total water budget and its ability to maintain hydration under extreme desert conditions.

Materials and methods

Collection and study site

The study site was located in the heart of the Sonoran Desert in Yuma County, southwestern Arizona, at 150 m elevation (32°50'N, 113°30'W). It is characterized by aeolian sand dunes with sparse mesquite and creosote bushes. Mean annual maximum and minimum daily temperatures are 31.9°C and 14.7°C, respectively (Green and Sellers 1964). Mean annual precipitation is only 10.6 cm, with the greatest amounts falling during the winter months and summer monsoon season (Sellers et al. 1985).

Microclimate quantification

Dehydration is directly related to an organism's thermal and hydric environments; therefore, we quantified surface air temperature, long-wave radiation, humidity, and wind speed at various kangaroo rat locations to determine the conditions to which these animals are exposed while on the surface. Also, because kangaroo rats spend about 80% of the time within their burrows (Justice 1960, as cited by Soholt 1974), it was important to quantify the thermal and hydric environment of the soil in which they reside.

Soil and air temperature

Soil temperature was recorded at various soil depths beneath an open, unshaded, and unvegetated area and also beneath a shaded area north of a creosote bush (the base of which is the typical location for *D. merriami* burrows; personal observations). This procedure was followed on both a dune and on a flat area void of dunes (for a total of four locations). Prior to data collection, three 2.5-cm-diameter iron rods of varying lengths, together with sleeves of tightly fit pipes, were serially pounded into and removed from the soil down to a depth of 2.25 m. The longest rod and pipe were left in the soil. We then removed the inner rod by pulling it from the soil, leaving the outer sleeve within the soil. Thermocouples were fastened at various lengths onto a 0.32-cm-diameter wooden dowel to maintain their positions relative to one another and lowered to the appropriate depth within this sleeve. Wooden dowels were chosen as the substrate for thermocouple attachment because of their relative nonconductivity. The sleeve was then pulled out, leaving the thermocouples in place. The walls of the resulting hole collapsed around the thermocouples, and the soil was tamped around its opening. We waited 2 months to allow for adequate settling of the soil at depth before beginning data collection.

In addition to measuring temperatures at 10, 20, 30, 40, 50, 100, 150 and 200 cm below the surface, we also recorded temperature at the soil surface by placing an array of six thermocouples directly at the surface and covering it with a 1 mm coating of sand. These thermocouples were connected in parallel to yield a single, average signal. We measured air temperature 3 cm above the ground, the approximate mid-body height for a kangaroo rat. These thermocouples were shielded from direct insolation by white plastic housings that allowed air flow around the thermocouples. Data were collected once each month throughout the year, every half-hour for an entire day, using a solid-state data log-

ger (CR21X; Campbell Scientific, Utah) and associated relay multiplexer (AM416 4×16, Campbell Scientific). Programs and data were transferred to and from the data logger in the field with a palm-top computer (HP 95LX; Hewlett Packard, Calif.).

Surface humidity

Atmospheric humidity was measured 3 cm above ground with a humidity probe (PC-2101C; Thunder Scientific, N.M.). Because this instrument is temperature-sensitive, it was calibrated at multiple temperatures (0–46°C) and vapor densities (0 g m⁻³ to saturation at each temperature) that were created with saturated air pumped through slurries of various concentrations of calcium chloride (see Walsberg et al. 1997). A regression for the effect temperature and vapor density had on the output for this device (in mV) was best fit by the form of vapor density (g m⁻³) = $A+B(T_a)^{-1}+C(\text{mV})^{-1}+D(T_a)^2+E(\text{mV})^{-2}+F(T_a)$ (mV)⁻¹, where A–F are specific coefficients ($R^2=0.96$; Datafit 5.1, Oakdale Engineering, Pa.). A thermocouple was associated with the hygrometer, and the temperature was recorded along with the hygrometer's output at the same times as the soil and air temperature data were recorded. The hygrometer and associated thermocouple were kept in a white plastic tube that allowed adequate ventilation and therefore accurate measurement of vapor density, but prevented the hygrometer from being exposed to direct insolation.

Irradiance

A miniature net radiometer (Micromet Instruments, Mass.), modified following Walsberg (1992) to perform as an all-wave radiometer, was leveled and its output recorded by the data logger. Also, a pyranometer (8–48; Eppley Laboratory, R.I.) was positioned horizontally to receive downward short-wave radiation. Downward long-wave radiation was determined by subtracting (though insignificant) the short-wave radiation from the all-wave radiation values.

Wind speed

Wind speed was measured 3 cm from the surface with heated ball anemometers that had been calibrated against hot-wire anemometers, the latter calibrated following the techniques of Walsberg (1988). Heated spheres, though fairly omnidirectional, seem to have a substantial error only when air flow is nearly parallel to the mounting wire (Walsberg 1988). Therefore, two anemometers were placed perpendicular to one another, and the maximum wind speed of the two was determined. Values were recorded for each half-hour of the daily records. All microclimate measurements were made between March 1998, and March 1999.

Burrow hygrometry

Burrow humidity was measured in mid-November. Humidity within burrows was determined gravimetrically with capsule hygrometers. We used sintered stainless steel cylinders (SS-4F-K4-05; Swagelok, Ohio) that had 0.5- μm pores and, therefore, substantial resistance to the uptake of vapor. We filled these filters with silica gel (28–200 mesh). High resistance to the uptake of vapor is critical to the design of these hygrometers because such uptake then occurs over a significant time period and allows for more accurate data collection and calibration by reducing the possibility of the desiccant saturating prematurely. The open end of each cylinder was sealed with a threaded Teflon plug. Each unit was 2 cm long and 1.25 cm diameter and, including desiccant, weighed approximately 8 g. Eye screws (3 mm diameter) were inserted into each Teflon plug for later attachment to kangaroo rats. Hygrometers were then dried to constant mass over 4 h at 210°C and then placed in air-tight glass vials. In the field, the hygrometers were removed from the vials and quickly attached to

live-trapped kangaroo rats. Two cotton twine leads were attached to the hygrometer's eye hook and to each tarsus of the kangaroo rat so that the hygrometer was positioned 10 cm from the base of the tail of the animals. A 0.4-mm-diameter, 2-m galvanized wire lead was also attached to the eye screw. The time needed to attach the wire was typically no more than 5 min. After being released near their burrow entrance, kangaroo rats immediately dragged the hygrometer into their burrows and chewed through the twine, releasing the hygrometers. The loose end of the wire lead was fastened onto a shrub. Twenty-four hours later (to the nearest minute), each hygrometer was pulled from its burrow by its wire lead, immediately detached from the wire and cotton, and placed into a sealed glass vial. The length of wire taken underground was measured to the nearest centimeter. In every case, both cotton tethers had been chewed off at the point of attachment to the legs and remained connected to the hygrometer. The hygrometers, sealed in their vials, were transported back to the laboratory and weighed to the nearest 0.01 mg with an analytical balance (AE240; Mettler Toledo, Greifensee, Switzerland). They were then dried and weighed again to determine their dry weight. This second weighing was necessary because some fine dust may have clung to the capsules in the field.

We found that the resistance of these hygrometers to uptake of a known vapor density was temperature sensitive (~25% change with a 20°C difference in temperature). Therefore, to calibrate the hygrometers, we maintained them in containers in the laboratory at a constant temperature that correlated with the average soil temperature at depths of 10–100 cm from the field, and subjected them to air containing known vapor densities for exactly 24 h. These calibrations produced robust linear fits of mass gain over 24 h vs. vapor density ($r^2=0.997\pm 0.0005$).

Radiotelemetry

Collared temperature transmitters (G3; AVM Instrument, Calif.) that emit temperature-dependent pulses within the 151–152 MHz range were used in the field to monitor the ambient temperature that kangaroo rats experienced during the day within their burrows. Transmitter mass did not exceed 4.8 g, or approximately 12% of the animal's body mass. The transmitters were first calibrated from 20°C to 45°C in water baths in the laboratory.

Animals were captured at night with live-traps (Sherman Traps, Fla.) in August 1999. Animals ($n=6$) were anesthetized with Metofane (methoxyflurane) in the morning, and the interscapular region of the back was depilated with scissors and small razor. A drop of cyanoacrylic adhesive was used to mount the transmitter to the skin and prevented the turning of the transmitter by maintaining it in its dorsal position. Transmitters were secured onto kangaroo rats by insulated wire collars. The actual temperature sensors were located in the most dorsal area of these transmitters. An hour after recovery, the animals were reintroduced to their burrows. At 0900 hours, and every half hour until 2100 hours, ten signal pulses were received by a receiver (LA12-Q; AVM Instrument) and timed with a stopwatch (VWR Scientific Products, Pa.). Animals were recaptured the next day, anesthetized, and their transmitters removed. In all cases, each transmitter had remained in its dorsal position.

Body temperature might have affected the temperature of the attached transmitter. We quantified this effect in the laboratory. Six animals were maintained at known air temperatures (30–40°C at 1°C intervals) with transmitters attached in the same fashion as in the field, and the temperature of the transmitter was recorded. We found that attachment of the transmitters to kangaroo rats in the laboratory at known temperatures increased the temperature measured by the transmitters by at most 1°C. Values presented are corrected for the effect of body temperature on the transmitters by a third-order polynomial generated from this calibration of measured transmitter temperature vs. actual air temperature ($R^2=0.999$).

Above-surface activity

Above-surface activity was observed with a camcorder with Night-Shot capabilities (CCDTR416; Sony, Tokyo). An associated grid of 20 infrared 880 nm λ LEDs (GaAlAs; Silonex Group, Montreal) powered by two D-cell batteries added illumination to the infrared source emitting from within the camera for greater viewing range. Periods of activity, along with ambient temperature at 3 cm above surface, were recorded on six nights in August 1999.

Diet

Laboratory feeding trials

Domestic crickets (*Acheta domestica*) were presented to 12 animals that had been born in the laboratory and acclimated under wet conditions (ad libitum water, 12 g m⁻³ vapor density) and 12 animals that had been born in the laboratory and acclimated under dry conditions (no water, 3 g m⁻³ vapor density) during three separate trials to determine: (1) if these kangaroo rats would readily eat insects and if so, (2) whether there was a dependence on the hydration state of the kangaroo rat on its consumption of insects. These conditions are known to result in mass gain and loss, respectively (Tracy and Walsberg 2000a). The animals were individually housed at 30°C for 12 h in 2-l containers and presented with one cricket. The animals did not have access to other food or sources of water during, nor were they fasted prior to, these trials. The containers prevented the escape of the crickets, but allowed adequate air flow. Presence and absence of the crickets was noted, and this experiment was repeated twice.

Stomach content analyses

Small animal live-traps (Sherman traps) were checked continually throughout the night in August 1999, and individuals were euthanized with CO₂. Their stomach contents were removed immediately and frozen with solid CO₂ in vials of distilled water for micro-analysis according to the procedures of Hansson (1970) and Reichman (1975) to determine presence of insects and vegetation. Samples were thawed and exposed under a dissecting microscope. Because most animals had consumed significant amounts of bait (rolled oats) during the short time between capture and euthanasia, we could not quantify the percentage of the constituents of their diets. Some samples were stained with iodine to visually isolate the rolled oats from the items of interest. Only those items clearly recognizable as insect or leafy vegetation were counted for these categories.

Stable isotope analyses

N isotopes fractionate depending on trophic level (Sealy et al. 1987). Values of ¹⁵N increase relative to ¹⁴N with transfer between trophic levels and therefore reflect both diet and trophic levels (DeNiro and Epstein 1981). Organisms from higher trophic levels are enriched in the heavier isotope. To explore possible consumption of insects by kangaroo rats, animals were live-trapped in August 1999, euthanized for stomach analyses, then frozen. From each individual, a gluteal muscle sample of 3 g was excised from the right hind leg, diced, and dried to constant mass at 60°C. Lipids were extracted in a Soxhlet apparatus with chloroform as the solvent for at least 8 h. Though some blood may have remained in the tissue, we expect that this residue would be extremely small compared to the bulk of the tissue measured isotopically. These lipid-free samples were then ground to a fine powder with a Wiley mill and 15 fine mesh, placed in tin vials, and weighed to the nearest microgram. The ratios of ¹⁵N:¹⁴N were measured with a mass spectrometer (20/20; PDZ Europa, Cheshire, UK). The standard used for N was atmospheric N, and stable-isotope ratios were calculated as follows: $\delta^{15}\text{N}(\%) = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3$, where $R = {}^{15}\text{N} : {}^{14}\text{N}$.

Data analysis

All data reported as “nocturnal” values were collected throughout the entire night. Statistics were performed for comparative analyses with ANOVA (SPSS 7.0, 1996; SPSS, Ill.). Percentages were arcsine-transformed before analyses. Significance was accepted at the $P < 0.05$ level. Mean values are reported with SEs.

Results

Soil and air temperatures, surface humidity, radiation, and wind speed

Data from all temperature probes exhibited nearly identical patterns. Therefore, we present only the soil temperature data from the unshaded non-dune area. Soil temperatures are high at depth for much of the year (Fig. 1A). For over 100 days of the year, mean soil temperature exceeds 30°C at least to 2 m depth. Indeed, for approximately 50 days, mean soil temperature exceeds 35°C at depths to 1.5 m. On a typical summer day, daily fluctuation in temperature was minimal at depth, averaging approximately 2°C over 24 h below 30 cm (Fig. 1B). At no time did soil temperatures at deeper than 10 cm fall below 30°C .

Yearly, nocturnal $T_{a,s}$ 3 cm above ground increased during the summer and were maximum in late August (Fig. 2A). At this height approximating the middle of a kangaroo rat’s body, mean temperature equaled 35°C during August. Maximum temperature in late August at 3 cm above ground was 40°C , while the minimum was 30°C .

Nocturnal humidity at kangaroo rat body height (3 cm) averaged $5.6 \pm 0.24 \text{ g m}^{-3}$ on a yearly basis and ranged from 1.3 to 22.5 g m^{-3} (Fig. 2A). This vapor density was relatively high in late March and again in December, but was greatest during the summer monsoon season.

Nocturnal long-wave radiation also increased during the summer and exceeded 425 W m^{-2} during July and August (Fig. 2B). Nocturnal wind speed at kangaroo rat level resembled this pattern, but also with an increase during March that was coincident with precipitation (Fig. 2B). Similarly, the high wind speed in summer coincided with summer monsoon storms. Values in late July represented a six-fold increase in wind speed compared to values for most of the year.

Nocturnal air temperature 3 cm above ground during August 1998 steadily decreased during the night and ranged from 40.3°C to 29.1°C (Fig. 3A). Temperatures measured during August 1999 exceeded the values presented for August 1998 (see Surface activity).

Burrow temperatures and humidities

$T_{a,s}$ within the burrows of six kangaroo rats averaged $35.3 \pm 0.19^{\circ}\text{C}$ during the day in August (Fig. 3B). During daylight hours, there was no significant effect of time of

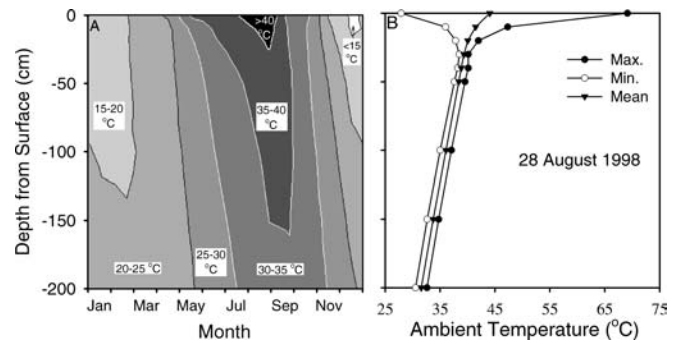


Fig. 1 A Mean soil temperatures to depths of 2 m throughout the year within a Sonoran Desert xeric site inhabited by *Dipodomys merriami*. Thermal isopleths were generated from 24-h data that was collected monthly in 1998–1999 ($n=12$). B Minimum (*min.*), mean, and maximum (*max.*) daily soil temperatures during late August 1999, at different strata. Jan January, Mar March, Jul July, Sep September, Nov November

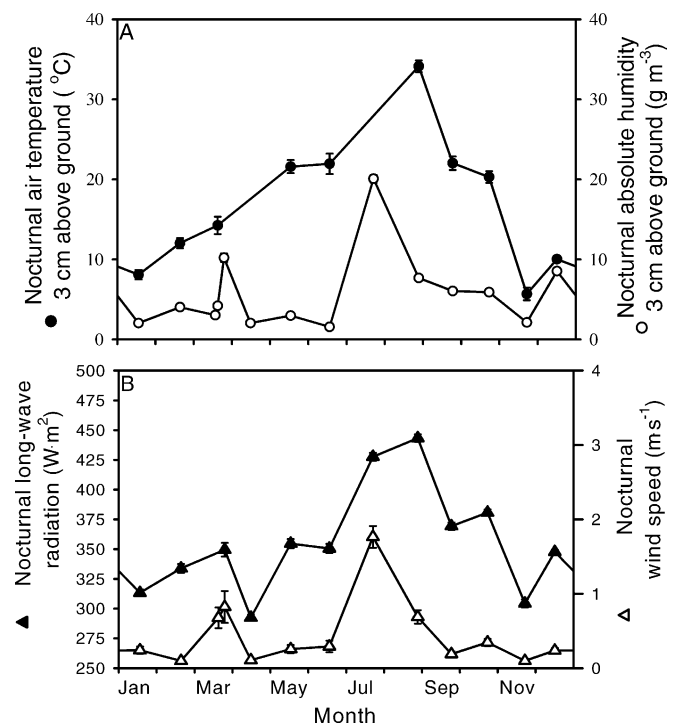
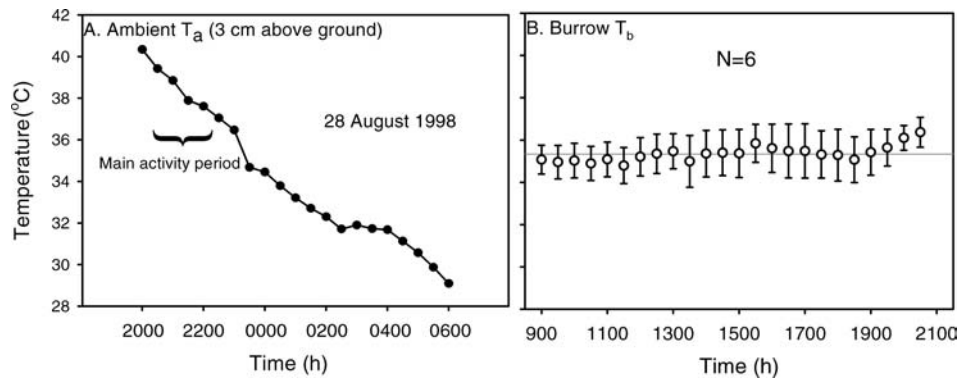


Fig. 2 A Mean±SEM nocturnal air temperature and nocturnal absolute humidity 3 cm above ground throughout the year at the xeric site. B Mean±SEM nocturnal long-wave radiation and nocturnal wind speed 3 cm above ground throughout the year. Data from 1998–1999. For abbreviations, see Fig. 1

day on the temperature recorded at the depth of the kangaroo rats ($P < 0.001$). Because the animals were not easily retrapped to regain collar temperature transmitters, they were excavated with a shovel. In all cases the kangaroo rats were found sitting at the bases of the root systems of the creosote bushes associated with their burrows. Although this was the deepest portion of their

Fig. 3 **A** Nocturnal ambient temperature 3 cm above ground for one particular night in August 1998, averaged every half hour. The main period of activity for kangaroo rats observed in August 1999 is displayed. **B** Mean \pm SEM diurnal burrow temperatures to which kangaroo rats are exposed, as measured with a radiotelemetric temperature probe harnessed to *D. merriami* in August 1999 ($n=6$)



burrow system, it was always <1 m from the surface. They quickly sprang out of this chamber and were captured by hand.

Burrow vapor density averaged $8.9 \pm 0.46 \text{ g m}^{-3}$ ($n=20$). This measurement represents an average of 22% relative humidity at the average burrow temperature of 35.3°C . Mean tunnel length from the surface to where the hygrometers had been left was $105 \pm 6.9 \text{ cm}$ ($n=20$).

Surface activity

During observations made in August 1999, animals were active on the surface every night immediately after sundown. The average temperature (3 cm above ground) when kangaroo rats were first sighted was $37.2 \pm 0.41^\circ\text{C}$ ($n=6$). The typical temperature at 3 cm above ground exceeded 35.5°C even after midnight, and kangaroo rats were regularly seen before this time. In fact, the vast majority (43 of 47) of kangaroo rats trapped during August for other portions of this study were captured within 2 h of sundown (see Fig. 3A) and, therefore, at much higher T_a s.

Diet

Feeding trials

Kangaroo rats born and raised in captivity, which were inexperienced with insectivory, readily ate insects when presented with them. There was a significant effect of hydration state of the kangaroo rats on the consumption of insects ($P < 0.001$). An average of $91.7 \pm 0.0\%$ of those 12 animals that had been raised in captivity, never before exposed to insects, and acclimated under desiccating conditions, readily consumed crickets during the three trials. Only one kangaroo rat (the same one in all the trials) refused to eat the prey item. However, an average of only $11.1 \pm 2.78\%$ of the 12 animals acclimated under water-abundant conditions ate crickets. Indeed, only two kangaroo rats consumed their crickets during the multiple feeding trials for animals acclimated under water-abundant conditions, and only one did so in more than one of the trials.

Stomach content analyses and stable isotope ratios

Eleven of the 20 stomach contents analyzed had discernible insect fragments. Each also possessed vegetation, and a total of 18 of the 20 contents had appreciable amounts of vegetation, to the extent that the contents appeared notably green. Nineteen of the 20 contents contained either insect fragments, vegetation, or both. This assessment is a conservative estimate of the stomachs containing insects, as those that had fragments that could not be distinguished between seed casings and exoskeleton were not counted as containing insects.

$\delta^{15}\text{N}$ from excised leg muscle tissue averaged $8.63 \pm 0.197\text{‰}$, and ranged from 7.185 to 11.795‰ ($n=20$). Only two individuals had a $\delta^{15}\text{N}$ value that exceeded 9.0‰ , and only two individuals had a $\delta^{15}\text{N}$ value that fell below 8.0‰ (see Discussion for comparative values and relevance).

Discussion

Kangaroo rats can routinely experience much harsher environmental conditions than previously appreciated. *Dipodomys* are active on the surface early in the evening during summer nights, when air temperatures remain quite high. While underground, they experience high burrow temperatures (average= 35.3°C) that are similar to those expected based on the high soil temperatures that prevail in the Sonoran Desert during the summer. Humidity in nest chambers is not high; the average value of 8.9 g m^{-3} represents 22% relative humidity at the prevailing average burrow temperature during summer months.

The high levels of nocturnal long-wave radiation, windspeed, and air temperatures paint a very different picture of the nocturnal habitat of this species during the summer than commonly described in reviews (French 1993; Reichman and Price 1993; Degen 1997). Nocturnal temperatures are much greater than previously appreciated, especially during the summer months. When these high T_a s are combined with the increased wind speed during the summer, increases in evaporative water loss and heat loads may occur due to increased convection.

Temperatures exceeded 35°C to depths of 1 m for a great part of the year and are consistent with the excep-

tional thermal and desiccation tolerance exhibited by *D. merriami* when subjected to ecologically relevant levels of activity in the laboratory (Tracy and Walsberg 2000b). These burrow temperatures (Fig. 3B) and depths of excavation of kangaroo rats parallel direct measurements of soil temperatures (Fig. 1A, B). At no time during the day are these animals exposed to temperatures that would be regarded as cool.

Our data on insect consumption in the laboratory and insect and succulent vegetation consumption in the field corroborate those of Reichman (1975), Nagy (1994), and Nagy and Gruchacz (1994) on the significance of non-seed resources to *D. merriami*. The hot summer months, despite the increased monsoonal humidity, may necessitate the consumption of significantly more insects and succulent vegetation than during other times of the year. Interestingly, almost all of the water-stressed and almost none of the well-hydrated kangaroo rats consumed insects in the laboratory. Some studies have suggested that succulent vegetation and insects may be necessary for reproduction in these animals (Reichman and Van De Graaf 1975; Soholt 1977), due to increased water intake (Beatley 1969) and coupled increases in hormones that trigger ovulation. However, the degree to which consumption of these added water sources varies on a seasonal basis has yet to be determined. It is possible that the very dry and moderately hot conditions in early fall may be the most critical time with respect to water loss for this species.

Our analyses of stomach contents, isotopic ^{15}N enrichment, environmental conditions, and physiological capacities suggest the intake of significant amounts of succulent food. Stable isotope analyses of nectivorous bats that reside within the Sonoran Desert and primarily feed at nonsucculent (C3) plants throughout the year have revealed typical $\delta^{15}\text{N}$ values between 8 and 9‰, but higher $\delta^{15}\text{N}$ values between 11 and 12‰ during the wet season (Ceballos et al. 1997). It has been suggested that this increase is linked to the consumption of insects and, thus, the occupancy of a higher trophic level by these bats during the wet season. Had we obtained mean $\delta^{15}\text{N}$ values exceeding 12‰, we could have strongly suggested that such enrichment was due to significant consumption of insects, especially when combined with our stomach-contents data. However, the $\delta^{15}\text{N}$ values we recorded for *D. merriami* are similar to those of many of the plant species found in this field site (Shearer et al. 1983). As muscle tissue is a good seasonal indicator of diet, insects therefore may not significantly contribute to the diet of *D. merriami* seasonally, despite their prevalence in the stomachs of Merriam's kangaroo rat. It may be that insects are ephemeral food sources. Our isotopic results, combined with the stomach contents and feeding trials results, instead, are consistent with the conclusion that green vegetation contributes more significantly to the intake of preformed water in these animals than does the consumption of insects.

The consequences of occupying such a hot and arid environment can be approximated by estimating the net

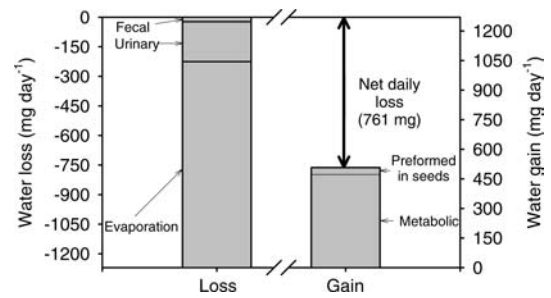


Fig. 4 Daily water loss and gain for *D. merriami* on a dry-seed diet at $T_a=35^\circ\text{C}$, with the respective contributions of preformed water and metabolic water production from the oxidation of food-stuffs and water loss through evaporation, urine production, and feces. \leftrightarrow Represents the net daily loss at this temperature assuming no consumption of succulent foods (i.e., insects and green vegetation)

water balance of a kangaroo rat. Only estimates for resting animals are possible, however, as appropriate data for active animals are not yet available. Metabolic water production, evaporative water loss, and urinary water loss are calculated for a typical 35-g animal from the mass-specific values of Tracy and Walsberg (2001a). Fecal water loss and preformed water contained in seeds consumed are both minor avenues of loss or gain, respectively, and were estimated by the methods of Schmidt-Nielsen and Schmidt-Nielsen (1951). The mass of seeds consumed was calculated using Schmidt-Nielsen's (1964) ratio of seed mass to metabolic water production (53.7 g H_2O per 100 g seed). Preformed water in the seeds was estimated as 3.7% of seed mass (Schmidt-Nielsen 1964). Fecal water loss was assumed to be proportional to mass of food ingested, and to equal 2.5% intake (Schmidt-Nielsen 1964).

A reasonable estimate of the average environmental temperature experienced by kangaroo rats over a daily cycle during summer in the Sonoran Desert probably is about 35°C , and all empirical data except urinary loss were measured at this temperature. Urinary water loss was measured at 30°C (Tracy and Walsberg 2000a).

At 35°C for a resting animal, maintenance on a seed diet is expected to lead to substantial net water loss: 761 mg or 2.2% of body mass per day (Fig. 4). Therefore, even if water loss equaling the extreme value of 12–14% of body mass could be tolerated by these animals [see Schmidt-Nielsen (1964) for mammalian dehydration tolerance], our calculations show kangaroo rats can probably survive less than a week on a dry seed diet when exposed to the environmental conditions normally prevailing in the field.

This inability to survive on a dry diet is consistent with evidence of the animals consuming substantial amounts of succulent food. In our study, this consisted mostly of leaves. This finding was remarkable, because during this period little green vegetation was apparent in the region. Nevertheless, this vegetation itself may be dependent on the summer monsoon. In contrast, insects are abundant on the soil surface during summer nights in the Sonoran Desert, almost all kangaroo rats readily con-

sumed insects in laboratory trials when water-stressed, and most kangaroo rats trapped in the field had some insect parts in their stomach. Our subjective impression, however, is that these insect parts were a much smaller fraction of the stomach contents than was green vegetation. This finding agrees with data derived from stable isotope analyses of kangaroo rats, which indicate that insects do not comprise a dominant fraction of their diet.

Concluding comments and broader significance

We have arrived at a much different view of kangaroo rat existence within the deserts of North America than that which is traditional. Rather than being strictly granivorous, weakly heat-tolerant animals that are exposed to cool, humid burrows, they are omnivorous, facultatively consuming significant amounts of vegetation and insects to maintain water balance during harsh desert summers. Moreover, they are tolerant of high temperatures and exposed to substantial potential desiccation and thermal stress. Finally, burrows are not cool and humid refugia from surface conditions.

Kangaroo rats, specifically *Dipodomys merriami*, were one of the first desert animals to be extensively and systematically studied. The overall conclusion or assumption of these studies was that these animals are able to occupy desert conditions on a diet of dry seeds without drinking (Schmidt-Nielsen and Schmidt-Nielsen 1950, 1951, 1952; Schmidt-Nielsen 1964; MacMillen 1964, 1972; MacMillen and Hinds 1983; Hulbert and MacMillen 1988). This ability, which was attributed to a combination of physiological mechanisms for conserving water and behavioral avoidance of extreme conditions, has strongly influenced our general view of desert mammals. It is now clear that this portrayal is not broadly accurate, at least for animals in hotter desert regions. Instead, kangaroo rats in such areas may be challenged normally by hot, arid conditions both on the surface and in their burrow, exhibit substantial tolerance to high environmental temperatures, and apparently rely critically on water from succulent food.

Part of the basis for this disparity between traditional views and current knowledge is lack of appreciation for the wide range of environments subsumed under the generic term of "desert." Deserts perhaps can be best defined as regions in which precipitation is so low that it plays the dominant role in controlling biological productivity (Noy-Meir 1973). Such arid regions vary widely in temperature regimes, from hot subtropical deserts to colder deserts at high altitudes or high latitudes. The dominant physiological challenges that such habitats present to animals are similarly variable. For small mammals occupying northern deserts, for example, the most critical thermal challenge in the annual cycle may be coping with very low temperatures during winter nights. For mammals in subtropical deserts, the effects of very high summer temperatures are likely to be overwhelming.

In a general sense, the adaptive tactics traditionally ascribed to nocturnal desert rodents certainly do occur.

In fact, it is likely that these traditional views may hold true in colder deserts and cool seasons in the Sonoran Desert. The results of our current studies are not meant to replace one dogma with another. Rather, our data demonstrate that the traditional views do not apply when conditions are truly challenging (i.e., the most interesting situations). Workers must be careful to recognize the role of geographic variation, even within what is usually classified as a single habitat (as in the case of "the desert"). Related to this is the issue that the Schmidt-Nielsens and similar founding investigators studied animals in a relatively mild area, yet extrapolated the results to "the desert." Our earlier comparisons of animals from xeric, intermediate, and mesic sites show how critical such choices are, and important it is that we refrain from unwarranted generalizations (Tracy and Walsberg 2001a).

Another point worth mentioning is that physiological ecologists and environmental physiologists have spent a great deal of effort studying animals from extreme environments in the hopes of finding nice examples of "adaptation," and this may have biased our views as to how common adaptations really are. As Garland and Adolph (1991) have stated, "The predilection of comparative physiologists for choosing extreme species for comparison may have led to a bias in our data base and hence in our view regarding the commonness of physiological adaptation to the environment." Again, our comparative work with *Dipodomys merriami* from contrasting environments (Tracy and Walsberg 2000a, 2000b, 2001a, 2001b) illustrates some of these issues.

Workers also must be careful to recognize that what they see as "adaptations" can be achieved through evolution, ontogeny, acclimation, or some combination of the three. Although this was not the focus of this investigation, our comparisons of animals from xeric and mesic sites in a previous study (Tracy and Walsberg 2001b) illustrate this precisely. In this study, we found developmental plasticity and acclimation together can overwhelm physiological differences manifested by Merriam's kangaroo rats from areas of contrasting temperature and aridity that otherwise strictly would be attributed to genetic differences.

Finally, it is notable that a recurrent theme in discussions of the status and future of ecological physiology is that this discipline has largely achieved its initial, major goals of describing how animals function in their natural environments and how they are adapted to them (see, for example, New directions in ecological physiology, Feder et al. 1988). Presumably, this assertion should apply most safely to desert animals, given the seminal importance in the history of physiological ecology of studies of animals occupying extreme environments, particularly deserts. It is striking, therefore, that the most broadly accepted generalizations regarding a long-studied species of desert mammal are now known to include important misconceptions.

Acknowledgements We thank A. Borek and P. Dockins for their assistance with animal husbandry. We also thank J. F. Harrison, J. R. Hazel, T. C. M. Hoffman, F. H. Pough, A. T. Smith, and K. M. Wooden for their comments relating to this study. We trapped all

animals under Arizona Game and Fish scientific collecting permit no. SP785298 and conducted all studies in compliance with Arizona State University's Institutional Animal Care and Use Committee protocols nos. 96-367R and 98-417R. All experiments complied with the legal requirements of the state of Arizona and the USA. Funding was assisted by the Research Support Program at Associated Students of Arizona State University, the Graduate College and Vice President for Research (grant no. 97-410) to R. T. and by NSF grant IBN 9725211 to G. W.

References

- Beatley JC (1969) Dependence of desert rodents on winter annuals and precipitation. *Ecology* 50:721-724
- Bienek GK, Grundmann AW (1971) Burrowing habits of two subspecies of *Dipodomys merriami* in California and Utah. *Great Basin Nat* 31:190-192
- Bradley WG, Yousef MK (1972) Small mammals in the desert. In: Yousef MK, Horvath SM, Bullard RW (eds) *Physiological adaptations: desert and mountain*. Academic Press, New York
- Carpenter RE (1966) A comparison of thermoregulation and water metabolism in the kangaroo rats *Dipodomys agilis* and *Dipodomys merriami*. *Univ Calif Publ Zool* 78:1-36
- Ceballos G, Fleming TH, Chavez C, Nassar J (1997) Population dynamics of *Leptonycteris curasoae* (Chiroptera: Phyllostomidae) in Jalisco, Mexico. *J Mammal* 78:1220-1230
- Degen AA (1997) *Ecophysiology of small desert mammals*. Springer, Berlin Heidelberg New York
- DeNiro MJ, Epstein S (1981) Influence of diet on the distribution of nitrogen isotopes in animals. *Geochim Cosmochim Acta* 45:341-351
- Feder ME, Bennett AF, Burggren WW, Huey RW (1988) *New directions in ecological physiology*. Cambridge University Press, New York
- French AR (1993) Physiological ecology of the Heteromyidae: economics of energy and water utilization. In: Genoways HH, Brown JH (eds) *Biology of the Heteromyidae*. *Spec Publ Am Soc Mammal* 10:509-538
- Garland T Jr, Adolph SC (1991) Physiological differentiation of vertebrate populations. *Annu Rev Ecol Syst* 22:193-228
- Green CR, Sellers WD (eds) (1964) *Arizona climate*. University of Arizona Press, Tucson, Ariz.
- Hansson L (1970) Methods of morphological diet micro-analysis in rodents. *Oikos* 21:255-266
- Hinds DS, MacMillen RE (1985) Scaling of energy metabolism and evaporative water loss in heteromyid rodents. *Physiol Zool* 58:282-298
- Hulbert AJ, MacMillen RE (1988) The influence of ambient temperature, seed composition and body size on water balance and seed selection in coexisting heteromyid rodents. *Oecologia* 75:521-526
- Jones WT (1989) Dispersal distance and the range of nightly movements in Merriam's kangaroo rats. *J Mammal* 70:27-34
- Justice KE (1960) Nocturnalism in three species of desert rodents. Unpublished PhD dissertation. University of Arizona, Tucson, Ariz.
- Kenagy GJ (1973) Daily and seasonal patterns of activity and energetics in a heteromyid rodent community. *Ecology* 54:1201-1219
- MacMillen RE (1964) Population ecology, water relations, and social behavior of a southern California semidesert rodent fauna. *Univ Calif Publ Zool* 71:1-66
- MacMillen RE (1972) Water economy of nocturnal desert rodents. *Symp Zool Soc Lond* 31:147-174
- MacMillen RE, Hinds DS (1983) Water regulatory efficiency in heteromyid rodents: a model and its application. *Ecology* 64:152-164
- Nagy KA (1994) Seasonal water, energy and food use by free-living, arid-habitat mammals. *Aust J Zool* 42:55-63
- Nagy K, Gruchacz MJ (1994) Seasonal water and energy metabolism of the desert-dwelling kangaroo rat (*Dipodomys merriami*). *Physiol Zool* 67:1461-1478
- Noy-Meir I (1973) Desert ecosystems: environment and producers. *Annu Rev Ecol Syst* 5:195-214
- Pough FH, Heiser JB, McFarland WN (1996) *Vertebrate life*, 4th edn. Prentice Hall, Upper Saddle River, N.J.
- Reichman OJ (1975) Relation of desert rodent diets to available resources. *J Mammal* 56:731-751
- Reichman OJ, Price MV (1993) Ecological aspects of heteromyid foraging. In: Genoways HH, Brown JH (eds) *Biology of the Heteromyidae*. *Spec Publ Am Soc Mammal* 10:509-538
- Reichman OJ, Van de Graaf KM (1975) Association between ingestion of green vegetation and desert rodent reproduction. *J Mammal* 56:503-506
- Schmidt-Nielsen B, Schmidt-Nielsen K (1950) Evaporative water loss in desert rodents in their natural habitat. *Ecology* 31:75-85
- Schmidt-Nielsen B, Schmidt-Nielsen K (1951) A complete account of the water metabolism in kangaroo rats and an experimental verification. *J Cell Comp Physiol* 38:165-181
- Schmidt-Nielsen K (1964) *Desert animals: physiological problems of heat and water*. Clarendon Press, London
- Schmidt-Nielsen K, Schmidt-Nielsen B (1952) Water metabolism of desert mammals. *Physiol Rev* 32:135-166
- Schmidt-Nielsen K, Schmidt-Nielsen B, Brokaw A (1948) Urea excretion in desert rodents exposed to high protein diets. *J Cell Comp Physiol* 32:361-380
- Sealy JC, Van Der Merwe NJ, Lee Thorp JA, Lanham JL (1987) Nitrogen isotopic ecology in southern Africa: implications for environmental and dietary tracing. *Geochim Cosmochim Acta* 51:2707-2717
- Sellers WD, Hill RH, Sanderson-Rae M (eds) (1985) *Arizona climate: the first hundred years*. University of Arizona Press, Tucson, Ariz.
- Shearer G, Kohl DH, Virginia RA, Bryan BA, Skeeters JL, Nilsen ET, Sharifi MR, Rundel PW (1983) Estimates of N₂-fixation from variation in the natural abundance of ¹⁵N in Sonoran Desert ecosystems. *Oecologia* 56:365-373
- Soholt LF (1974) Environmental conditions in an artificial burrow occupied by Merriam's kangaroo rat, *Dipodomys merriami*. *J Mammal* 55:859-864
- Soholt LF (1977) Consumption of herbaceous vegetation and water during reproduction and development of Merriam's kangaroo rat, *Dipodomys merriami*. *Am Midl Nat* 98:445-457
- Tracy RL, Walsberg GE (2000a) Prevalence of cutaneous evaporation in Merriam's kangaroo rat, and its adaptive variation at the subspecific level. *J Exp Biol* 203:773-781
- Tracy RL, Walsberg GE (2000b) Unappreciated tolerance to high ambient temperatures in a widely distributed desert rodent, *Dipodomys merriami*. *Physiol Biochem Zool* 73:809-818
- Tracy RL, Walsberg GE (2001a) Intraspecific variation in water loss in a desert rodent, *Dipodomys merriami*. *Ecology* 82:1130-1137
- Tracy RL, Walsberg GE (2001b) Developmental and acclimatory contributions to water loss in a desert rodent: investigating the time course of adaptive change. *J Comp Physiol B* 171:669-679
- Vogel S, Bretz WL (1972) Interfacial organisms: passive ventilation in the velocity gradients near surfaces. *Science* 175:210-211
- Vorhies CT (1945) Water requirements of desert animals in the Southwest. *Univ Ariz Coll Agric Exp Stn Tech Bull* 107:487-525
- Walsberg GE (1988) Consequences of skin color and fur properties for solar heat gain and ultraviolet irradiance in two mammals. *J Comp Physiol B* 158:213-221
- Walsberg GE (1992) Quantifying radiative heat gain in animals. *Am Zool* 32:217-224
- Walsberg GE (2000) Small mammals in hot deserts: some generalizations revisited. *Bioscience* 50:109-120
- Walsberg GE, Weaver T, Wolf BO (1997) Seasonal adjustments of solar heat gain independent of coat coloration in a desert mammal. *Physiol Zool* 70:150-157
- Young DR, Nobel PS (1986) Predictions of soil water potentials in the northwestern Sonoran. *J Ecol* 74:143-154
- Yousef MK, Dill DB (1971) Daily cycles of hibernation in the kangaroo rat, *Dipodomys merriami*. *Cryobiology* 8:441-446