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INTRASPECIFIC VARIATION IN WATER LOSS IN A DESERT RODENT, *DIPODOMYS MERRIAMI*

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Abstract. A species' thermal and hydric environments may vary significantly throughout its range. However, geographic variation in physiological parameters related to water-saving ability has been largely ignored in mammals, even though there are dramatic differences among the environments in which many species exist. Heteromyid rodents long have been the focus of investigations concerning mammalian adaptations to severely desiccating environments. Representatives of one widely distributed subspecies of Merriam's kangaroo rat, *Dipodomys merriami merriami*, were collected from three locations that differ in environmental temperatures and aridity. Mass, evaporative water loss, urine osmolality, rate of fractional body-mass loss, fecal water content, and metabolic rate were measured under desiccating conditions. Individuals from the most arid locality were smaller, possessed lower total and mass-specific evaporative water loss (EWL), and lost proportionately less mass under dehydrating conditions than those from less arid locations. These results indicate that EWL, but not kidney function or fecal water loss, is a trait associated with conserving water in this subspecies.

Key words: desert adaptation vs. intraspecific variability; desiccation; Dipodomys; *evaporative water loss; fecal water loss vs. environment; geographic variation; intraspecific variation; kangaroo rat; phenotypic variation vs. climate; physiology and extreme environments; urine concentration; water loss vs. aridity and environmental temperature.*

INTRODUCTION

Terrestrial environments, and particularly deserts, arguably impose the greatest challenges to life with respect to extremes in temperature and potential for dehydration. Small rodents are the most common mammals in many deserts and, because physiological capacities are prominent in environmental extremes, these animals represent excellent models for studying physiology when confronted with such extreme environments. Although intraspecific geographic variation in physiological parameters related to water loss has been largely ignored in mammals (Heisinger et al. 1973, Kronfeld and Shkolnic 1996), the extent of such variation is important in understanding limits on distribution and the evolutionary origin of adaptations (see Feder and Block 1991).

The most widely distributed kangaroo rat in the southwestern United States, *Dipodomys merriami* (Merriam's kangaroo rat), has been the most extensively studied desert mammal (see Schmidt-Nielsen 1990). These rodents are nocturnal, reside in burrows, do not have access to free-standing water, and are active throughout both summer and winter (Kenagy and Bartholomew 1985). Routes of water loss are urinary loss, fecal loss, and evaporation from the respiratory tract, eyes, and skin. Urine can be highly concentrated and feces are extremely dry (Schmidt-Nielsen et al. 1948, Schmidt-Nielsen and Schmidt-Nielsen 1951, Kenagy 1973). *Dipodomys merriami* also exhibits reduced evaporation compared to mesic-adapted animals (Schmidt-Nielsen and Schmidt-Nielsen 1952). Clearly, this species exploits an extreme environment and manifests remarkable abilities for frugal use of available water.

For kangaroo rats, resistance to water loss is critical for survival in desert environments and may vary intraspecifically with geography. Because *D. merriami* ranges from central Mexico (latitude 21° N) to northern Nevada (latitude 42° N) (Schmidly et al. 1993), it is also ideal for analysis of geographic variability in physiological parameters. Within Arizona, one subspecies, *D. merriami merriami*, ranges from areas of extreme aridity and temperature in southwestern Arizona's Sonoran Desert to milder areas in northwestern Arizona (Hoffmeister 1986). Therefore, we hypothesized that resistance to water loss covaries among individuals of this subspecies with the aridity and temperature of their locations. We predicted that kangaroo rats from the more xeric locations would exhibit greater capacities to resist water loss than those from more mesic locations when tested under similar conditions.

Phenotypic plasticity can weaken the action of natural selection by allowing functional changes that are advantageous for individuals (Pohl 1976). Phenotypic plasticity, including reversible phenotypic plasticity (short-term acclimation) and developmental plasticity, can lead to covariation between physiological characteristics and environmental variables (Hewitt 1981,

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Buffenstein and Jarvis 1985). Alternatively, natural selection may act on individuals swiftly and directly because they have only fixed inherited capacities and are not phenotypically labile. Investigation of the relative importance of phenotypic plasticity and genetic variation in the production of particular phenotypes may yield insight about a species' response to climate change. It may also lead to a better understanding of basic evolutionary processes. Requisite for investigations of all of these possible modes of adaptive adjustments, however, is a quantification of physiological variables such as resistance to desiccation within a widely distributed species.

Methods

Field sites

Three field sites that encompass the broad scope of conditions faced by *Dipodomys merriami* throughout its range were sampled. The xeric site is located in the heart of the Sonoran Desert in Yuma County, southwestern Arizona, at 150 m above sea level (32°50′ N, 113°30′ W). This site is characterized by aeolian sand dunes with sparse mesquite and creosote bushes, and is one of the most arid locations inhabited by *D. merriami* (Hoffmeister 1986). The intermediate site is located in eastern Maricopa County in central Arizona, at 400 m above sea level (33°30′ N, 111°50′ W). It is characterized by fragmented flats of creosote bushes and paloverde–cacti–mixed-scrub desert adjacent to rocky terrain and is of intermediate aridity. The mesic site is located in north-central Arizona, within Gila County, at 1200 m above sea level. This site contains creosote bushes, and is bordered by pinyon–juniper woodland (34°10′ N, 111°15′ W). Mean annual maximum daily temperatures are 31.9°, 29.1°, and 23.5°C for the xeric, intermediate, and mesic sites, respectively, while mean annual minimum daily temperatures are 14.7°, 12.1°, and 6.2°C, respectively. Mean annual precipitation for the three respective sites is 10.6 cm, 33.6 cm, and 43.6 cm, with the greatest amount falling during the winter months and summer monsoon season (data from Green and Sellers [1964] and Sellers et al. [1985]).

Individuals belonging to one subspecies of Merriam's kangaroo rat (*D. merriami merriami*) were livetrapped at all sites from October 1996 though March 1997 (hereby referred to as ''winter'' animals). Because of the intraspecific differences found in these animals, we focused our studies on animals from the two extreme sites (xeric and mesic) and trapped them in late May 1998 for a second set of experiments. These experiments were restricted to measurements of volumetric oxygen consumption ($\dot{V}O_2$) and carbon dioxide production ($\dot{V}CO_2$), evaporative water loss, and urinary water loss (hereby referred to as ''summer'' animals). Only adults were used. Data were analyzed by means of general linear model, univariate statistics, using SPSS 7.0 (Norusis 1997) when examining potential differences among the animals from the three locations. When significant effects of location were detected, post hoc multiple comparisons of means were conducted with Scheffé's ANOVA. Data recorded across a series of temperatures for summer animals from the xeric and mesic sites were analyzed with repeated-measures ANOVA. Data recorded as percentages were arcsine transformed before analyses. Significance was accepted at the $P < 0.05$ level. Standard errors are reported with mean values.

Animal care/handling

Animals were transported to the Animal Resource Center at Arizona State University (Tempe, Arizona, USA), weighed, and maintained in an environmental chamber at 30°C and a vapor density of 12 g/m^3 (the moderately high temperature and low humidity to which they are exposed in the field; R. L. Tracy and G. E. Walsberg, *unpublished data*). Experimentation began three days after capture, and continued until the animals were in captivity for no more than three weeks. Kangaroo rats were fed moistened seeds for 12 h, then maintained on a dry seed diet ad libitum (Hartz Cockatiel Seed: 61% carbohydrate, 12% protein, 6% fat, 9% fiber, and 12% moisture [Hartz Mountain Corporation, Secaucus, New Jersey, USA]). Animals were maintained individually in cages with a dirt floor. A section of plastic pipe was supplied for shelter.

Large-scale variation in morphology

As a gross indication of ability to persist in arid environments, individuals were weighed and placed in chambers without food or water at 30°C and a vapor density of 12 g/m^3. After 12 h they were weighed again to determine percentage body mass loss ($N = 21$, 34, and 22 individuals for xeric-, intermediate-, and mesic-site animals, respectively). Differences in body size were determined by measuring cranial length ($N = 22$, 8, and 26 individuals for the respective sites) with a Mitutoyo Digimatic Model 500-351 [Mitutoyo Corporation, Aurora, Illionis, USA] digital caliper to the nearest 0.01 mm.

Measurements of gas exchange and evaporation

All measurements were made between 0800 and 1600, during the inactive phase of each animal's daily cycle. Measurements were made within one hour of removal from food to reduce the relative contribution of the specific dynamic action of digestion. Instrument signals were recorded by data loggers and averaged at 1-min intervals. Animals remained quiescent within the chambers, as viewed with a Magnavox observation camera mounted inside the temperature-controlled room. Fluorescent lights illuminated the temperature-controlled room. Values reported are from those periods when readings leveled for 5 min prior to data col-

lection after each animal was inactive for at least 20 min.

Measurements of $\dot{V}O_2$, $\dot{V}CO_2$, and EWL were made in four open-flow metabolic chambers (0.8 L) with positive air flow. Temperatures within the chambers were measured with 26-gauge, type-T thermocouples and controlled at 30° ± 1°C by placing the chambers within a temperature-controlled room. We determined this temperature to be within the thermoneutral zone for individuals from all sites (R. L. Tracy and G. E. Walsberg, *unpublished data*). Air was passed through the chambers at 100–150 mL/min after being dried and scrubbed of CO_2 by a Puregas model CDA112 air dryer/CO_2 absorber system [Puregas Equipment Company, Westminster, Colorado, USA]. Air flow was measured with Omega N112-02G rotameters [Omega Engineering, Stanford, Connecticut, USA], calibrated to ±1% with a 100-mL soap-bubble flow meter. These flow rates allowed the entire respiratory apparatus volume to turn over within 25–36 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 (LI-COR Incorporated, Lincoln, Nebraska, USA). The analyzer resolved CO_2 concentration to 0.1 μL/L, or <0.1% of measured values, and was calibrated daily using both CO_2-free air and a calibration gas known to contain 2780 μL/L CO_2. Because the analyzer has an upper range of 3000 μL/L CO_2, and excurrent values typically exceed this value, the air sample was diluted with a known flow of dried and CO_2-free air. A multiplier was then directly determined by diluting the calibration gas with the dried CO_2-free air. Noise level of this analyzer is typically 0.2 μL/L, with a maximum of 0.4 μL/L. Characteristic readings exceeded 1200 μL/L, giving a signal-to-noise ratio of ~4000:1. CO_2 production was calculated using Eq. 3 of Walsberg and Wolf (1995) and corrected to standard temperature and pressure (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 (Applied Electrochemistry, Sunnyvale, California, USA) that was calibrated using air drawn from outside of the building. This analyzer has a sensitivity of 0.001% O_2 and an accuracy of ±0.1%. Air drawn into the analyzer was first scrubbed of CO_2 with Ascarite (sodium-hydroxide-coated silica) and dried with anhydrous calcium sulfate. The subsample of each chamber's excurrent air was separate from that entering the CO_2 analyzer. The combined subsamples routed to the CO_2 and O_2 analyzers did not exceed that of the flow rate into the chamber. O_2 consumption was calculated using Eq. 2 of Hill (1972). Respiratory exchange ratios (ratios of CO_2 production to O_2 consumption, RER) then were determined for each animal and used to estimate metabolic water production (MWP) with the assumption that only carbohydrates and lipids were metabolized during measurement. ''Summer'' animals (N = 13 and 11 for xeric and mesic sites, respectively) were also tested at 5°C intervals from 10° to 40°C in an identical fashion using a serial arrangement of the O_2 and CO_2 analyzers. In this arrangement, samples were not sent through Ascarite, but only anhydrous calcium sulfate (Drierite), before entering the O_2 analyzer, and calculations were adjusted to accommodate for this change. The accuracy of the entire system of chambers, flowmeters, absorbants, and analyzers has been tested with introduced boluses of N_2 and CO_2 and found to yield an error of <3% for measurements of both $\dot{V}O_2$ and $\dot{V}CO_2$ (G. E. Walsberg, *unpublished data*).

Evaporative water loss (EWL) was measured using a Thunder Scientific model PC-2101C hygrometer (Thunder Scientific Corporation, Albuquerque, New Mexico, USA) that was calibrated following Walsberg et al. (1997). These values were combined with corresponding airflow rates into the chamber and the average mass of the kangaroo rat to calculate mass-specific rates of whole-body EWL. Flow rates to the chamber were kept high enough to maintain vapor density below 5 g/m^3 and low enough for O_2 concentration to be depressed by 0.65–1.0%.

Fecal water loss

Fecal water loss was measured by placing kangaroo rats in cylindrical containers with a wire mesh floor, suspended 10 cm above a vinyl mat. Fecal samples were taken during the inactive phases of their daily cycles. Food was not withheld prior to these experiments, but was not available during experimentation because animals quickly emptied cheek pouch contents when placed into their containers. As with all experiments and post-capture housing, water was withheld from the animals. Experiments lasted no more than 3 h, and containers were monitored continuously. Fecal pellets were removed within 2–3 s of defecation with forceps as they dropped onto the vinyl mat below, and at least three samples from each animal were averaged and used as a single measurement for that animal. Pellets were immediately weighed with a Mettler H10T analytical balance to the nearest 0.1 mg, then dried to a constant mass at 60°C to determine water content.

Urinary water loss

After weighing, animals were placed in urine collection chambers without food or water at 30°C and a vapor density of 12 g/m^3. Each chamber consisted of a 3.8-L aluminum can with a wire mesh floor suspended over mineral oil and a lid with ventilation holes. Because initial results for winter animals suggested that these conditions may have been too humid to elicit maximal urine concentrations, summer animals were tested in similar chambers with a continuous flow (800 mL/min) of dry air (<0.1 g/m^3).

After 12 h, individuals were weighed again and urine that was not contaminated by feces was collected with

TABLE 1. Interspecific variation in physiological parameters in winter *Dipodomys merriami merriami.*

Parameter	Field site	*N*†	Mean ± 1 SE	Comparisons‡	*P*§
Mass (g)	xeric	21	33.5 ± 0.88	X:I	**0.019**
	intermediate	40	37.3 ± 0.72	X:M	<**0.001**
	mesic	23	42.8 ± 1.25	I:M	<**0.001**
Cranial length (mm)	xeric	22	35.2 ± 0.1	X:I	**0.012**
	intermediate	8	36.0 ± 0.3	X:M	<**0.001**
	mesic	26	37.1 ± 0.1	I:M	**0.001**
Body-mass loss (%/h)	xeric	21	2.3 ± 0.22	X:I	0.097
	intermediate	36	3.0 ± 0.21	X:M	**0.050**
	mesic	24	3.2 ± 0.32	I:M	0.876
Total EWL‖ (mg H_2O/h)	xeric	21	22.88 ± 1.63	X:I	**0.019**
	intermediate	29	37.42 ± 4.43	X:M	**0.001**
	mesic	13	47.13 ± 2.89	I:M	0.258
Mass-specific EWL (mg $H_2O \cdot g^{-1} \cdot h^{-1}$)	xeric	21	0.69 ± 0.053	X:I	**0.049**
	intermediate	29	1.00 ± 0.113	X:M	**0.046**
	mesic	13	1.08 ± 0.068	I:M	0.867

† *N* = number of kangaroo rats in the sample. Only adult kangaroo rats were used.
‡ ''X,'' ''I,'' and ''M'' represent xeric-, intermediate-, and mesic-site animals, respectively. Colons between two acronyms represent comparisons of means by post hoc Scheffé's ANOVA between animals from those two sites.
§ Significant effects are shown in boldface.
‖ EWL = evaporative water loss.

glass capillary tubes. These tubes were sealed with hematocrit sealer and frozen for later analysis. They were then thawed and centrifuged for one minute at 10^5 m/s^2 in an Adams micro-hematocrit centrifuge. The supernatant was then emptied into Eppendorf tubes and diluted with distilled water to bring resultant values within range of a Wescor model 5500 ER vapor pressure osmometer (Wescor, Logan, Utah, USA) that was calibrated with standard sodium chloride solutions.

Because osmolality of a solution is not a linear function of concentration unless the solution is extremely dilute (Sweeney and Beuchat 1993), we made synthetic urine solutions that approximated both the composition of urea and sodium chloride and concentration of *D. merriami* urine (Schmidt-Nielsen and Schmidt-Nielsen 1952). These solutions were diluted, and a linear approximation of measured osmolality vs. molarity yielded an R^2 of 0.9987. Consequently, errors from extrapolating diluted samples to actual osmolalities outside the range of the osmometer appear negligible in our case. Samples of known osmolality also were treated and measured in an identical fashion as kangaroo rat urine to assure that freezing resulted in no desiccation. At least three samples from each animal within the trial were measured. The average of these values was used as a single measurement for that individual. Urine volume was estimated for summer animals with calibrated capillary tubes.

RESULTS

The sex of the animals had no effect on any of the parameters tested and, therefore, was removed from all statistical analyses. Body size varied with geographic location ($F = 20.815$, df = 2, 84, $P < 0.001$). Mass of winter kangaroo rats from the xeric site averaged 90% of those from the intermediate site and 79% of those from the mesic site (Table 1). Summer xeric-site animals also weighed less than those from the mesic site (37.19 ± 1.15 g [mean ± 1 SE], $N = 12$ individuals; 40.68 ± 1.12 g, $N = 11$, respectively; $F = 4.645$, df = 1, 23, $P = 0.044$). Skull size also varied significantly with location ($F = 51.51$, df = 2, 56, $P < 0.001$). Cranial length was significantly smaller in xeric animals than both intermediate and mesic animals and smaller in intermediate animals than in mesic animals (Table 1).

Fecal water content did not vary with location ($F = 1.131$, df = 2, 83, $P = 0.328$). Pooled, mean fecal water content was 27.05 ± 1.2% ($N = 37$, 28, and 18 for the xeric-, intermediate-, and mesic-site animals, respectively). Percentage body-mass loss varied with location ($F = 3.482$, df = 2, 81, $P = 0.036$) and was significantly lower in xeric-site than mesic-site kangaroo rats (Table 1).

Urine osmolality did not vary with location ($F = 1.814$, df = 2, 61, $P = 0.172$) when animals were exposed to air with a vapor density of 12 g/m^3 ($N = 21$, 18, and 22 for the xeric-, intermediate-, and mesic-site animals, respectively; pooled mean = 9616 ± 313 kPa/kg) nor under dry (<0.1 g/m^3) conditions (pooled mean: 10 042 ± 336 kPa/kg; $F = 0.415$, df = 1, 23, $P = 0.527$; N = 12, 11 for the xeric- and mesic-site animals, respectively). Urine volume did not differ among summer animals from the xeric and mesic sites (pooled mean: 8.97 ± 1.5 μL/h; $F = 0.007$, df = 1, 23, $P = 0.933$; $N = 12$ and 11 individuals, respectively). However, it remains possible that urinary volume of winter animals (which was not measured) may

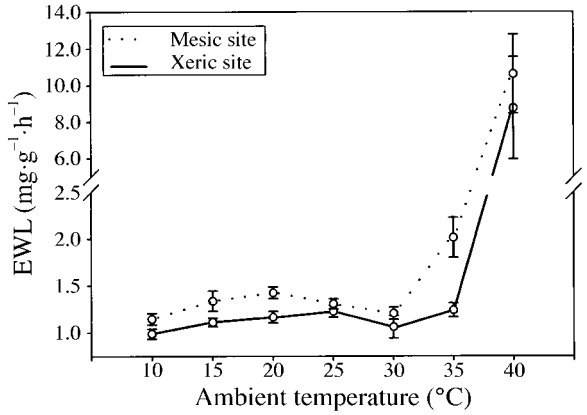

FIG. 1. Mass-specific evaporative water loss (EWL) over a series of temperatures for summer *Dipodomys merriami merriami* from the xeric and mesic sites (N = 13 and 11 animals, respectively). Data reported are means ± 1 SE. Repeated-measures ANOVA indicate significantly greater mass-specific EWL among mesic-site animals and no significant interaction between temperature and location.

have differed between kangaroo rats from the intermediate and mesic locations, despite mesic animals having more concentrated urine than the intermediate ones. Urine concentration did not vary with season at either extreme site.

Total evaporative water loss (EWL) varied significantly with location (F = 3.067, df = 2, 63, P = 0.050), but did not significantly covary with mass (F = 2.747, df = 2, 63, P = 0.103). When removing mass as a covariate, location effects on total EWL increased (F = 8.428, df = 2, 63, P = 0.001). Post hoc analyses revealed that xeric-site animals evaporated significantly less total water than intermediate- or mesic-site animals (Table 1).

Mass-specific EWL varied significantly with location (F = 3.997, df = 2, 63, P = 0.023) and mirrored differences in hourly body-mass loss. Compared to animals from the xeric site, kangaroo rats from the intermediate site exhibited a 33% greater average mass-specific EWL at 30°C (Table 1). Those from the mesic site exhibited 64% greater average mass-specific EWL than xeric kangaroo rats. Mass loss did not differ between intermediate and mesic kangaroo rats.

There was a significant effect of site on mass-specific EWL for summer animals across many temperatures (repeated-measures ANOVA; F = 18.545, df = 1, 23, $P < 0.001$; Fig. 1). EWL was significantly higher among mesic-site animals than those from the xeric site (Fig. 1). There was a significant effect of ambient temperature on mass-specific EWL (F = 9.722, df = 6, 23, $P < 0.001$), and a significant interaction between location and temperature (F = 4.135, df = 6, 23, P = 0.002). The greatest variance in EWL was exhibited at 40°C by individuals from both locations.

Neither volumetric oxygen consumption, $\dot{V}O_2$ (F = 1.835, df = 2, 84, P = 0.166) nor respiratory exchange ratios (ratios of CO_2 production to O_2 consumption), RER (F = 2.364, df = 2, 84, P = 0.101) varied significantly among the three locations at 30°C for winter animals nor between individuals from the two extreme sites at all temperatures ranging from 10° to 40°C in summer animals (F = 0.160, df = 1, 23, P = 0.694 and F = 1.612, df = 1, 23, P = 0.220 for $\dot{V}O_2$ and RER values, respectively; repeated-measures ANOVA). RER significantly increased with increased temperatures in these summer animals (F = 14.748, df = 6, 23, $P < 0.001$), but there was no significant interaction between location and temperature (F = 1.48, df = 6, 23, P = 0.191). Similarly, $\dot{V}O_2$ significantly varied with increased temperatures in these summer animals (F = 105.452, df = 6, 23, $P < 0.001$), but there was no significant interaction between location and temperature (F = 1.487, df = 6, 23, P = 0.189). Mean $\dot{V}O_2$ at 30°C was 1.18 ± 0.02 mL $O_2 \cdot g^{-1} \cdot h^{-1}$ and mean RER was 0.85 ± 0.01 CO_2/O_2 for winter animals (N = 21, 40, and 23 individuals for the xeric, intermediate, and mesic sites, respectively, for both $\dot{V}O_2$ and RER).

DISCUSSION

There are at least three possible bases for the variation in body mass observed between sites. One is that competitive interactions may exist between *Dipodomys merriami* and its much larger congener, *D. deserti,* which only occurs at the xeric site. Such a case has been described for the interactions between *D. merriami* and *D. microps* in California (Kenagy 1973) and could have resulted in divergent selection body mass (see Brown and Wilson 1956). A second possibility is that body-mass differences are due to differences among the three sites in primary productivity and subsequent resources (including moisture) available for growth and development. Finally, the apparent differences in mass could result from thermal differences among the sites and may represent variable needs for heat dissipation or storage in compliance with Bergmann's rule.

Because smaller animals have a greater surface-area-to-volume ratio than do larger animals, smaller endotherms tend to have greater mass-specific heat loss. Given this greater capacity to dissipate heat, endotherms are predicted to be smaller in hotter climates than in colder climates. However, this scenario is complicated by increased rates of mass-specific evaporative water loss (EWL) through the skin of these hypothetically smaller animals and illustrates the trade-off between this increased water loss and increased heat dissipation. Nevertheless, mean masses of kangaroo rats reported here correspond to expectations of body size and climatic differences if one considers only heat dissipation, especially given the low mass-specific EWL of xeric-site animals. Also, it is unlikely that mass differences simply reflect varying fat stores given that differences in body mass parallel those in skeletal size

and all animals killed and examined from all sites were lean.

The similar fecal water losses found among locations were not unexpected. Feces account for only 7% of the water loss in this species under the conditions tested (Schmidt-Nielsen and Schmidt-Nielsen 1952). This is the same proportional water loss found in other desert mammals, such as the dorcas gazelle (Ghobrial 1970). Natural selection may very well act on this physiological parameter in *D. merriami*. Yet, fine tuning fecal water loss may have relatively little effect on the total water balance of these animals compared to other routes. Nonetheless, fecal water content was only 26.5%. Fecal water content for mammals generally exceeds 50%, even in desert rodents (see Degen 1997), and only in a few mammals such as the dik-dik (a small African antelope) is fecal water content <50% (Skadhauge et al. 1980). Fecal water content may depend on many factors such as gut retention time and time of day. Neither food intake nor fecal volume were monitored. Therefore, it is not known whether total fecal mass loss (and thus total fecal water loss) varies within this subspecies, although differences in body mass may be paralleled by differences in fecal production.

EWL varied among kangaroo rats from the three locations and partially mirrored differences in mass loss over 12 h. At 30°C, kangaroo rats collected in the winter from the xeric site evaporated less water than those from the intermediate and mesic locations. At 10° to 40°C, kangaroo rats collected in the summer from the xeric site evaporated less water than did mesic animals. Water loss appeared to increase at 35°C from values at lower temperatures for mesic animals but not for xeric animals (Fig. 1). Only at 40°C did EWL seemingly increase in these xeric animals, indicating that they can prevent elevating evaporation at higher temperatures than can mesic kangaroo rats.

There is little information available on the partitioning of EWL in small desert rodents (MacMillen and Lee 1970; see Degen 1997), but it is evident that both respiratory and cutaneous EWL are reduced in arid species of heteromyid rodents when compared to tropical heteromyids (French 1993). Whether both routes are reduced in the xeric animals and their relative contributions remain to be tested. Mechanisms to reduce respiratory EWL might be differences in nasal reclamation of water from expired air or greater oxygen-extraction efficiencies at the lungs of xeric animals, which would reduce ventilation.

Unlike the dramatic differences in evaporation, there were no differences in ability to concentrate urine. During the urine-concentrating experiments, animals were maintained at 30°C and a vapor density of ~12 g/m^3. While 30°C represents a realistic temperature that these animals may experience for extended periods of time, vapor density may have been unrealistically high. This is substantially greater than the value of 3 g/m^3 that results in negative water balance in these animals when relying on a dry seed diet (Schmidt-Nielsen and Schmidt-Nielsen 1952). Indeed, this was the impetus for repeating urine-concentrating experiments at a lower vapor density (<0.1 g/m^3) for summer animals. Therefore, it is tempting to suggest that the humidity initially used may have been too high to elicit sufficient water loss and maximal urine concentrations, and that our values thus may not represent maximum concentrating capacities. Another explanation is that animals could have avoided high-protein seeds in favor of high-carbohydrate seeds and derived more metabolic water per unit energy and less of a urea load, as they were provided with seeds that vary greatly in their relative content of carbohydrate, fat, and protein. Even though animals lost substantial mass during experimentation, progressively more-concentrated urine could have been produced over time, whereas we sampled all the urine produced during these tests. These possibilities could have accounted for some of the reduction in urine concentration, but were not investigated.

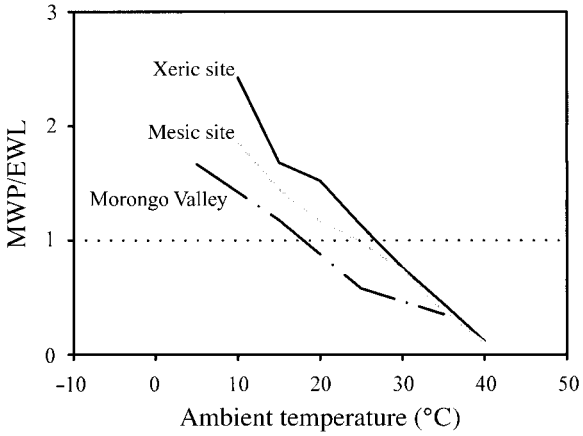

FIG. 2. Mean ratios of metabolic water production (MWP) to evaporative water loss (EWL) over a series of temperatures for summer *Dipodomys merriami* from the xeric and mesic sites ($N = 13$ and 11 animals, respectively) and from Morongo Valley (San Bernardino County, California, USA) for comparison (MacMillen and Hinds 1983). The points at which MWP/EWL intersect the line of equality indicate balance between these two major players in this species' water budget. Calculated MWP does not significantly vary between kangaroo rats from these two sites nor animals from Morongo Valley.

Nonetheless, urine concentration did not differ in these summer animals from the previous winter or between the two sites, despite the very low testing humidity. Because urinary loss can account for 18% of the total water loss from this species (Schmidt-Nielsen 1964), differences in urine volume might be expected. As urine volume determined for summer animals from the two extreme sites did not differ under dry conditions, the apparent inability of xeric-site animals to produce urine more concentrated than the intermediate- and mesic-site animals remains obscure.

Metabolism is intimately tied to water balance be-

cause of its effects on water production and loss. Based upon the constituents of the diet and on expected RER values for the catabolism of different substrates (see Kleiber 1975), and assuming indiscriminate consumption of all seed types, an RER of 0.95 is predicted. Yet, the mean RER for all animals tested was 0.85. It therefore is unclear exactly what proportions of the substrates were catabolized during experiments or to what extent kangaroo rats relied on stored fat. Given the similar RER displayed by individuals from the three locations, however, similar levels of metabolic water production (MWP) and substrate utilization are suggested.

In heteromyid rodents, the sources of water gain and loss of overwhelming importance are, respectively, MWP and EWL. For instance, under the chamber conditions of this study, 88% of the total water intake should originate from metabolic production and 71% of the total water loss through evaporation (Schmidt-Nielsen and Schmidt-Nielsen 1951). Therefore, the environmental temperature at which MWP balances EWL is a useful index of the thermal conditions required for maintenance of hydration (MacMillen and Hinds 1983; Fig. 2). Below the temperature at which production equals loss, the animal has excess water. Above this temperature, the animal dehydrates. The average temperature that results in equal MWP and EWL differed among sites for animals collected during the summer. The temperature for the mesic site averaged 24.5°C, while that of the xeric site averaged 27.0°C. Because inferred MWP rates differed only slightly between kangaroo rats from the two extreme sites, it is differences in EWL that contribute to different temperatures of net water balance. The 2.5°C difference in the temperature that results in balance between MWP and EWL between the xeric and mesic sites summarizes the consequences of differential resistance to desiccation—water balance was achieved at higher temperatures in the animals collected at the more xeric site.

Our data, however, differed substantially from those of MacMillen and Hinds (1983), who studied *D. merriami* collected in Morongo Valley of the southern Mojave Desert of California (34° N, 117° W; altitude about 780 m) and observed that the temperature required for MWP to balance EWL was 17°C. This is 7.5°–10°C below the temperature observed in our animals. As MWP for Morongo Valley animals approximates those for the animals of this study, it may be that the EWL of the former is greater because of reduced selective pressures of an unclear origin (e.g., differences in vegetation or insect abundance). An alternative possibility is that EWL differences reflect contrasting conditions of animal maintenance and acclimation. Our results, however, clearly demonstrate that *D. merriami* is substantially better at conserving water lost through evaporation than formerly appreciated.

This is noteworthy, as the literature is replete with studies of the urine concentrations of heteromyid rodents and the dominant role that it plays in these species' abilities to survive in deserts (see French 1993), even though it comprises only 18% of their water loss (Schmidt-Nielsen et al. 1948). It was EWL and not urine-concentrating capacity that varied most significantly in *D. merriami merriami* from contrasting environments. Because animals from the xeric site were smaller than those from the other two locations, these xeric-site animals are expected to have greater mass-specific EWL. This was not the case.

We have shown that increased aridity is correlated with a decrease in size and mass-specific water loss in *D. merriami merriami.* However, we have not yet demonstrated the processes that lead to this variation. Physiological adjustments to changing conditions such as the desiccating potential of the environment can occur through three, nonexclusive, avenues that differ in their time courses. That requiring the longest time is natural selection, whereby populations exhibit adaptations to local conditions. A second avenue is developmental plasticity, by which exposure to particular environments early in life defines an individual's physiological capacities. In some rodent species, for example, post-weaning water restriction has caused kidney hypertrophy that allows production of more highly concentrated urine (Blount and Blount 1968, Hewitt 1981). The third avenue is acclimation, in which an individual changes its physiological responses over relatively short time periods. Certainly, natural selection acts on the last two avenues; yet, by increasing the range of conditions in which an individual can survive, they otherwise buffer individuals from natural selection's potential effects.

Understanding the evolution of physiological traits requires understanding these mechanisms that can underlie a particular phenotype. Phenotypic plasticity can operate relatively quickly and therefore might blunt the time course of natural selection. Understanding the extent and nature of such flexibility therefore is critical to our comprehension of the consequences of processes such as global climate change. By defining the presence and extent of intraspecific variation in physiology, this study resolved the necessary first step towards this understanding for one species of common, and widely distributed, desert rodent.

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