

Foraging Activity Pattern Is Shaped by Water Loss Rates in a Diurnal Desert Rodent

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ABSTRACT: Although animals fine-tune their activity to avoid excess heat, we still lack a mechanistic understanding of such behaviors. As the global climate changes, such understanding is particularly important for projecting shifts in the activity patterns of populations and communities. We studied how foraging decisions vary with biotic and abiotic pressures. By tracking the foraging behavior of diurnal desert spiny mice in their natural habitat and estimating the energy and water costs and benefits of foraging, we asked how risk management and thermoregulatory requirements affect foraging decisions. We found that water requirements had the strongest effect on the observed foraging decisions. In their arid environment, mice often lose water while foraging for seeds and cease foraging even at high energetic returns when water loss is high. Mice also foraged more often when energy expenditure was high and for longer times under high seed densities and low predation risks. Gaining insight into both energy and water balance will be crucial to understanding the forces exerted by changing climatic conditions on animal energetics, behavior, and ecology.

Keywords: foraging, climate, microhabitat, energy expenditure, water loss, predation.

Introduction

Energy acquisition is key to individual fitness; therefore, foraging behavior is studied extensively by ecologists using both empirical research and a growing body of theory (e.g., Stephens and Krebs 1986; Brown 1988; Huey 1991; Bozinovic and Vasquez 1999; Porter et al. 2002; Bacigalupe et al. 2003; Sears et al. 2006). Many studies focus primarily on the effects of interspecific interactions, such as predation and competition, on foraging decisions (e.g., Brown et al. 1994a; Kotler et al. 1994; Werner and Peacor 2003; Butler et al. 2004; Gutman and Dayan 2005; Preisser et al. 2005).

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Much less attention has focused on the effects of abiotic conditions (e.g., Bozinovic and Vasquez 1999; Porter et al. 2002; Bacigalupe et al. 2003; Sears et al. 2006) or on the combination of both (Kotler et al. 1993; Mitchell and Porter 2001; Mitchell et al. 2004), although abiotic conditions clearly exert strong selective pressures on animal ecology, behavior, and evolution.

Although animals fine-tune their activity to avoid unfavorable climatic conditions, we still lack a mechanistic understanding of such behaviors. In an era of climate change, such understanding is particularly important if we aim to predict how populations and communities may alter their activity times and microhabitat use. The ecological and physiological challenges that shape activity vary at different temporal and spatial scales; hourly to seasonal changes in activity and behavior reflect the interplay between abiotic and biotic interactions. Foraging behavior, for example, is influenced by different magnitudes of pressures such as predation risk, competition, and resource availability (Brown 1989; reviewed by Kotler et al. 2002; Brown and Kotler 2004), as well as ambient temperature, solar radiation, and other climatic variables. These and other abiotic and biotic pressures may have similar, different, or even conflicting effects. Since climatic conditions vary rapidly throughout the day, it is crucial that we study activity at fine temporal scales, while accounting for other possible explanatory variables.

We studied the effects of ecological and physiological factors, and the interactions between them, on foraging decisions, focusing on the golden spiny mouse (*Acomys rus-satus*), a small diurnally active desert mammal. We carried out a field study, in which we monitored mouse activity decisions, in terms of foraging intensity and quitting-harvest rates, which represent the rates of energy and water gain at which mice ceased foraging in our foraging patches. We used a mechanistic approach, Niche Mapper (Porter and Mitchell 2006), to estimate how physiological costs during foraging vary with temporal (hourly to seasonal) and spatial (between-microhabitat) changes in climatic conditions (see

Porter et al. 1994, 2000, 2006; Porter and Kearney 2009). This method was previously used to predict the climatic constraints on the distribution of mammals (e.g., Natori and Porter 2007) and to model the preferred activity phase or temporal niche in golden spiny mice (Levy et al. 2012). While Levy et al. (2012) compared the energy and water required for thermoregulation (i.e., to keep homeothermy) during day versus night activity, here we tested how hourly variation in predicted foraging activity costs (in terms of energy and water) may explain observed variations in foraging behavior throughout the day.

We also took the giving-up density approach developed by Brown (1988) and used extensively to investigate how foraging behavior is affected by perceived predation risk (Brown 1988; Brown et al. 1988; Kotler and Brown 1988), competition (e.g., Ovadia and zu Dohna 2003), and climatic pressures (e.g., Orrock and Danielson 2009). By combining these approaches, we aimed to shed light on the forces underlying temporal and spatial foraging patterns at the diel scale.

We modeled foraging behavior as two decisions in which the animal (i) chooses whether to forage at a given habitat and (ii) chooses how long to stay in it. We tested how the energy and water costs of thermoregulation, resource availability, and predation risks affected foraging decisions as well as quitting-harvest rates. This analysis enabled us to gain insight into the relative roles of ecological and physiological factors in shaping the foraging ecology of diurnally active desert rodents.

Material and Methods

Our study involved seven main components. (1) We collected data on foraging decisions of golden spiny mice using artificial foraging patches with an automatic monitoring system that allows individual recognition. We ran the experiments during both summer and winter, under new moon and full moon conditions. (2) For each foraging observation, we collected body temperature data in or near the foraging patches and ambient temperature data in each foraging patch. (3) We parameterized a biophysical model according to the golden spiny mouse's morphological and physiological properties and validated it using published data. (4) For each hour in the study, we used the validated biophysical model, together with the body and ambient temperature observations, to estimate the energy and water costs during foraging. (5) For each day, we collected the quantity of seeds left in the foraging patches (giving-up density, GUD; Brown 1988) and calculated the estimated quantity of seeds in the patches at the beginning of each hour. (6) We statistically tested how energy and water costs, as well as predation risk and resource availability, affect foraging decisions. (7) We used our predicted metabolic costs

during foraging and our GUD data to calculate energetic and water quitting-harvest rates.

The Study System

The golden spiny mouse (*Acomys russatus*) is distributed across the Middle East, in hot and arid rocky deserts. Studies carried out in past decades in the rocky Judean Desert of Israel have produced much insight into the ecology and physiology of this species. Unlike most desert rodents, the golden spiny mouse is diurnal and has evolved behavioral and physiological adaptations to cope with the dry desert environment. They have low water requirements, owing to their ability to reduce fecal water loss (Kam and Degen 1993) and to produce highly concentrated urine (Shkolnik 1966; Shkolnik and Borut 1969). Moreover, to avoid extremely hot conditions, this species uses behavioral thermoregulation during activity, switching from a unimodal activity pattern during winter to a bimodal activity pattern during summer, thereby reducing midday activity (Shkolnik 1971; Kronfeld-Schor et al. 2001a). Furthermore, most of the summer foraging takes place in sheltered and shaded microhabitats under and between large boulders (Jones et al. 2001). Interestingly, golden spiny mice have adapted to diurnal activity, to the extent that diurnality in their natural environment is optimal for energy conservation (Levy et al. 2012).

Ecological factors in this system such as resource availability and predation risk have been found to vary between seasons, moon phases, and microhabitats and to affect golden spiny mouse foraging. In a controlled cafeteria experiment, the species showed a strong preference for arthropods in its diet (Kronfeld-Schor and Dayan 1999). During summer, when arthropods are plentiful at the study site (Vonshak et al. 2009) and green vegetation is scarce, they constitute the main source of energy and water in spiny mouse diets. In winter, however, when insects are scarce (Vonshak et al. 2009) and green vegetation is readily available, the percentage of arthropods in spiny mouse diets is relatively low (Kronfeld-Schor and Dayan 1999). Arthropod availability also differs between habitats: during three of four seasons, arthropods are more abundant in the boulder habitat than in the open habitat; in summer, arthropods become more abundant in the open habitat (Vonshak et al. 2009). Predation risk also differs between seasons in this system. During summer, predation risk from the saw-scaled viper (*Echis coloratus*) is higher at the study site, primarily under boulders, where these sit-and-wait predators rest curled up (Mendelssohn and Yom-Tov 1987; Tsairi and Bouskila 2004). Golden spiny mice reduced foraging in sheltered microhabitats and shifted into more open microhabitats in summer (Jones et al. 2001). Thus, response to predation risk by vipers counters the response to physio-

logical stress. Although the species is largely diurnal, moon phase affects the perceived risk of predation (Gutman et al. 2011), as has been demonstrated for nocturnal desert rodents (e.g., Price et al. 1984; Brown 1988) including common spiny mice, *Acomys cahirinus* (Mandelik et al. 2003). This behavior reflects a legacy of the species' past as a nocturnal rodent (see also Kronfeld-Schor et al. 2000, 2001b; Levy et al. 2007; Cohen et al. 2010). The evolutionary significance of predation in this system is also evident in the spines on spiny mouse rumps and a histological mechanism for tail loss (Shargal et al. 1999).

Field Study

Study Site. The field study took place in Israel, at the Ein Gedi nature reserve near the Dead Sea (35°21'E, 31°27'N; ~300 m below sea level). Two major habitats are found in the area: a boulder habitat, comprising jumbled rocks up to 2 m in diameter where most spiny mouse foraging takes place, and open habitat, characterized by small rocks (pebbles) that offer no refuge. We began trapping and marking golden spiny mice 3 months before data collection in an 80 × 300 m area. Captured mice were individually marked with passive integrated transponder (PIT) tags (Destron-Fearing, South St. Paul, MN).

Foraging Measurements. Since preliminary observations showed that mice rarely forage in the open habitat, we excluded this habitat from our study and measured foraging at two boulder microhabitats: an "under-boulders" (UB) microhabitat (on a rock terrace with overhead shelter) and a more open "between-boulders" (BB) microhabitat (on the terrace surrounded by large stones but no overhead cover). These two microhabitats constitute a gradient in the degree of shelter from predation, with UB the safest from avian predators and BB the least protected. Moreover, climatic conditions differ between the two microhabitats since the BB microhabitat is exposed to the sky and, hence, offers less protection from solar radiation during the day and less thermal cover during the night (detailed description of microhabitats in Gutman and Dayan 2005).

We placed an automonitored foraging patch in each microhabitat, comprising a plastic tray (25 cm diameter), in which 2 L of local soil were mixed with 2 g of cracked sunflower seeds. Food patches were protected from foraging birds by heavy wire frames and fine filament fish netting. Mice reached the trays easily by biting through one strand in the net. Foraging patches were replenished at dawn. We sieved the soil to retrieve all remaining seed particles and weighed them as a measure of GUD. We positioned food patches in four stations, 60 m from one another. Each station contained two food patches, one in each microhabitat. Individual foraging activity was recorded using transceivers

(2001F-ISO; Destron, South St. Paul, MN), with the antennae of each placed under each food patch. When a marked mouse entered a patch, its PIT tag identification code was logged with the exact time of entry. If the mouse stayed in the patch, a new log was recorded every 10 s.

We approximated the quantity of seeds consumed from the foraging patches by fitting a harvest rate curve to the foraging activity (see "Constructing a Harvest Rate Curve to the Foraging Activity" in the appendix, available online, for further details). Our model estimated an attack rate (a) of 6×10^{-4} (s^{-1}) and handling time (h) of 8.6 (s/g), with no significant variation between microhabitats (a : $p = .34$, h : $p = .98$) and moon phases (a : $p = .46$, h : $p = .95$), in which antipredatory behavior may affect GUDs (Jones et al. 2001; Gutman and Dayan 2005; Gutman et al. 2011). Using the harvest curve, we were able to model the quantity of seeds consumed from a patch as a function of exploitation time and, hence, to calculate the quantity of seeds left at a foraging patch after each foraging event.

Measurements of Body and Ambient Temperatures. Varying body temperature is a key means of altering energy and water requirements and one of the most sensitive variables in heat and mass transfer models of animals in their environments (McClure and Porter 1983). The data enabled us to determine the regulated body temperature during activity and the ambient temperature in our foraging patches for each hour; both are important factors for the model calculation. A week prior to each field study season, all captured mice (summer, $n = 6$; winter, $n = 8$) were implanted with temperature-sensitive radio transmitters (~3 g; Sirtrack, Havelock North, New Zealand; for surgery protocol, see Levy et al. 2007) and released after 48 h (see "Measuring Body Temperature" in the appendix for more details). We successfully monitored body temperatures of five individuals during summer and six individuals during winter. Ambient temperatures were measured to the nearest 0.5°C every 15 min using eight data-logger thermometers (iButton ds1921 thermochrom, Sunnyvale, CA) placed in the shade within 10 cm of a foraging patch.

Estimating Energy and Water Costs of Foraging

We used the Niche Mapper model system, which contains two submodels: a microclimate model and an endotherm niche model (see below). Both models use numerical methods to solve the heat and mass balance equations for each hour for the environment and the animal of choice. We used the microclimate model in Niche Mapper to estimate climatic conditions (wind velocity, relative humidity, long-wave radiation, and solar radiation at the animal's height) for each microhabitat, UB and BB, during each hour of our study. These predictions were then used, together with

actual body and ambient temperature measurements, by the endotherm niche model to calculate energy and water costs of foraging. These estimated costs would allow the homeothermic animal to maintain its core temperature given the current local available environmental conditions and activity level. The details of the animal energetic model have been described by Porter et al. (1994, 2000, 2002, 2006), Natori and Porter (2007), and Levy et al. (2012). See “Microclimate Model” and “Endotherm Niche Model” in the appendix for further information, parameterization, and validation of the models.

Quitting-Harvest Rates of Energy and Water

We used our biophysical predictions and foraging observations to determine the relative contribution of metabolic costs of foraging and predation risk to quitting-harvest rates. The higher the quitting-harvest rates, the higher the marginal value of the seeds left in the patch. For each season and microhabitat, we followed the assumption in Brown et al. (1994b) in which a forager under predation risk should leave a depletable food patch when

$$\text{QHR} = C + P + \text{MOC}, \quad (1)$$

where QHR is the quitting-harvest rate, C is the metabolic cost of foraging (activity and thermoregulation), P is the cost of predation, and MOC is the missed opportunity costs (positive if fitness-enhancing activities still exist at the end of the day; Brown et al. 1994b). To estimate the terms in equation (1), we first estimated the metabolic costs of foraging in the food patch, C , by averaging our biophysical model calculations for energy (W) and water costs ($\text{mg H}_2\text{O/s}$) during foraging. Second, we converted our measured GUD values and our predictions (see above) of attack rate, a , and handling time, h , to energy and water QHR using Holling’s disc equation (e.g., Brown et al. 1994b):

$$\text{QHR} = Nu \frac{a \cdot \text{GUD}}{1 + a \cdot h \cdot \text{GUD}}, \quad (2)$$

where Nu is either the digestive energetic content (14,220 J/g) or the water content (0.085 mL/g) of sunflower seeds (Salari et al. 2009). Although our Nu assumptions may not be accurate (absorption varies between species and sources of sunflower are different), they should not deviate too much. Finally, we calculated the costs of predation, P , by subtracting C and MOC from QHR. Since mice foraged at food patches during only 23% of available hours, we assumed that mice were probably able to exhaust other foraging and non-foraging activities and to retreat to preferred microhabitats during inactivity. Hence, for simplification, we assumed that MOC is the negative of the animal’s resting metabolic rates ($\sim 5.3 \text{ mW/g}$ individual measured body mass [M_b] for ener-

getic loss rates and $0.4 \mu\text{g H}_2\text{O/s/g } M_b$ for water loss rates; Shkolnik and Borut 1969).

Data Management

We stored all field measurements and model predictions in a Structured Query Language database (MySQL, ver. 5.1). For each microhabitat, foraging station, mouse, time of day (i.e., hour), and date, we calculated hourly mean values of ambient temperatures, body temperatures, the estimated quantity of seeds left in the foraging patches at the beginning of the hour, and the amount of time the mouse spent in the foraging patches.

For hours when body temperature measurements for a certain individual were not received by the RX-900 scanner receiver, we concluded that the mouse was not located near our foraging patches ($\sim 60 \text{ m}$ from our antennas) and removed the hour from the data analysis. We added the estimated energy and water requirements for homeothermy for each hour by querying the database by time of day, individual’s mass, ambient temperature, body temperature, microhabitat, and season. The final table used in our analysis is deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.1fg41> (Levy et al. 2016).

Statistical Analysis

We modeled the foraging behavior using a two-part modeling approach (reviewed in Martin et al. 2005), where each part of the model describes a different aspect of foraging decision that depends on a set of covariates (Cameron and Trivedi 1998): (1) an individual decides whether to forage (i.e., foraging occurrence) and (2) for how long to proceed with foraging (i.e., foraging duration), if it occurs. We modeled foraging occurrence as a binary outcome model of foraging probabilities with a logit link function and Bernoulli distribution; for hours when foraging occurred, we modeled foraging duration as a truncated count model of foraging duration using a Poisson-gamma distribution to account for the overdispersion in our data (Zuur et al. 2009).

We tested the effect of season, microhabitat, and moon phase as categorical factors and quantity of seeds, energy requirements, and water requirements as continuous covariates, as well as all possible two-way interactions of quantity of seeds, energy, and water requirements among season, microhabitat, and moon phase responses. Microhabitat and moon phase constitute changes in predation risk, while seasonal changes may represent different reproductive states, energetic states, population densities, and so on. In addition to the linear responses, we used a change-point analysis, to test whether a threshold behavior occurred by energy and water requirements. This behavior is observed when a gradual change in a process causes a disproportionate response once a critical threshold is reached (reviewed in

Beckage et al. 2007). To identify the set of significant variables and interactions that affect foraging decisions, we performed a Gibbs variable-selection analysis (Dellaportas et al. 2002; table 1). We included individuals and foraging stations as a nested random effect to each part of the model and accounted for possible hourly temporal autocorrelation. The model was implemented using the Bayesian approach. For more details, see “Statistical Models of Foraging Behavior” and “Bayesian Models” in the appendix. Parameter estimations are presented in decimal percentages (i.e., the relative change in the odds of foraging or in foraging duration for a unit change in the predictor), calculated as e^{xk} , where x is the predictor and k is the estimated parameter (Ntzoufras 2009).

For GUD analysis, we fitted a gamma linear mixed-effects model to test whether GUD values differ between seasons, microhabitats, and moon phases using the lme4 R package (lmer function; Bates et al. 2012). To account for the variation between foraging stations, we included for-

aging stations as a random effect in the model. Based on the Akaike information criterion (Burnham and Anderson 1998), which measures goodness of fit and model complexity, our final model included all main affects but no interactions (tests not shown).

We estimated the exchange rate between daily means of evaporative water loss rates during foraging and quitting-harvest rates for energy using a gamma linear mixed-effects model. We included seasons, microhabitats, and moon phases as fixed effects and foraging stations as a random effect. After removing nonsignificant terms (tests not shown), our final model for exchange rates included the quitting-harvest rates and microhabitats, without interaction terms. Using the same model structure, we estimated how daily quitting-harvest rates for energy and amount of water loss changed with the amount of foraging time at each patch. The final models included foraging time and microhabitats. The models were implemented using the Bayesian approach (see “Bayesian Models” in the appendix). Hours are time of day in Greenwich Mean Time + 3.

Table 1: Inclusion probability (%) of each parameter at the foraging occurrence and foraging duration models

Parameter	Occurrence	Duration
Season (winter)	1.0	31.4
Microhabitat (UB)	1.5	98.6
Moon (new)	1.0	1.4
Evaporative water loss (L)	79.0	19.0
Evaporative water loss (L) × season	21.6	5.4
Evaporative water loss (L) × microhabitat	1.8	5.1
Evaporative water loss (L) × moon	.8	1.9
Evaporative water loss (T)	36.9	84.4
Evaporative water loss (T) × season	19.8	31.8
Evaporative water loss (T) × microhabitat	22.1	24.6
Evaporative water loss (T) × moon	6.6	7.6
Energy expenditure (L)	1.2	3.0
Energy expenditure (L) × season	.3	1.1
Energy expenditure (L) × microhabitat	2.0	6.5
Energy expenditure (L) × moon	.6	1.3
Energy expenditure (T)	.6	9.0
Energy expenditure (T) × season	.4	4.1
Energy expenditure (T) × microhabitat	98.2	23.9
Energy expenditure (T) × moon	1.7	15.1
Seeds (L)	8.7	43.4
Seeds (L) × season	1.4	15.9
Season (L) × microhabitat	.7	53.2
Seeds (L) × moon	.7	.6

Note: Parameters were estimated using the Gibbs variable-selection procedure. Parameters with inclusion probability higher than 40% (in boldface) were considered biologically significant, as well as their corresponding main effect, if applicable. UB = under boulders; T = threshold effect; L = linear effect.

Results

Daily Rhythms in Body Temperature, Climatic Parameters, and Foraging Metabolic Costs

Body temperatures of active mice vary slightly throughout the day (between 36° and 37°C; summer: 36.6° ± 0.4°C, winter: 36.7° ± 0.2°C, mean ± SD), especially during early morning hours when mouse temperatures were lower after nightly torpor (Levy et al. 2011a, 2011b). The measured ambient temperatures and other hourly climate variables estimated by the microclimate model showed high daily, seasonal, and spatial variation (fig. 1B). Similarly, the hourly estimated energy expenditure and evaporative water loss also changed throughout the day, between seasons, and between microhabitats (fig. 1C, 1D).

In the BB microhabitat during summer, minimal energy expenditure was reached at 7 h (8.05 ± 0.02, mW/g M_b ± SD) and maximal energy expenditure at 5 h (11.11 ± 1.41, mW/g M_b ± SD). During winter, minimal energy expenditure in the BB microhabitat was reached at 12 h (8.53 ± 0.79, mW/g M_b ± SD) and maximal energy expenditure at 7 h (20.35 ± 1.89, mW/g M_b ± SD) and 17 h (20.58 ± 2.67, mW/g M_b ± SD). In the UB microhabitat, the estimated energy expenditure during summer was 8.02 ± 0.01 (mW/g M_b ± SD) during sunrise and remained almost unchanged. In winter, the energy expenditure was higher than in summer; the minimal energy expenditure was reached at 12 h (8.05 ± 0.09, mW/g M_b ± SD) and maximal energy expenditure at 7 h (9.30 ± 0.65, mW/g M_b ± SD).

The predicted evaporative water loss during summer in the UB microhabitat and during winter at both micro-

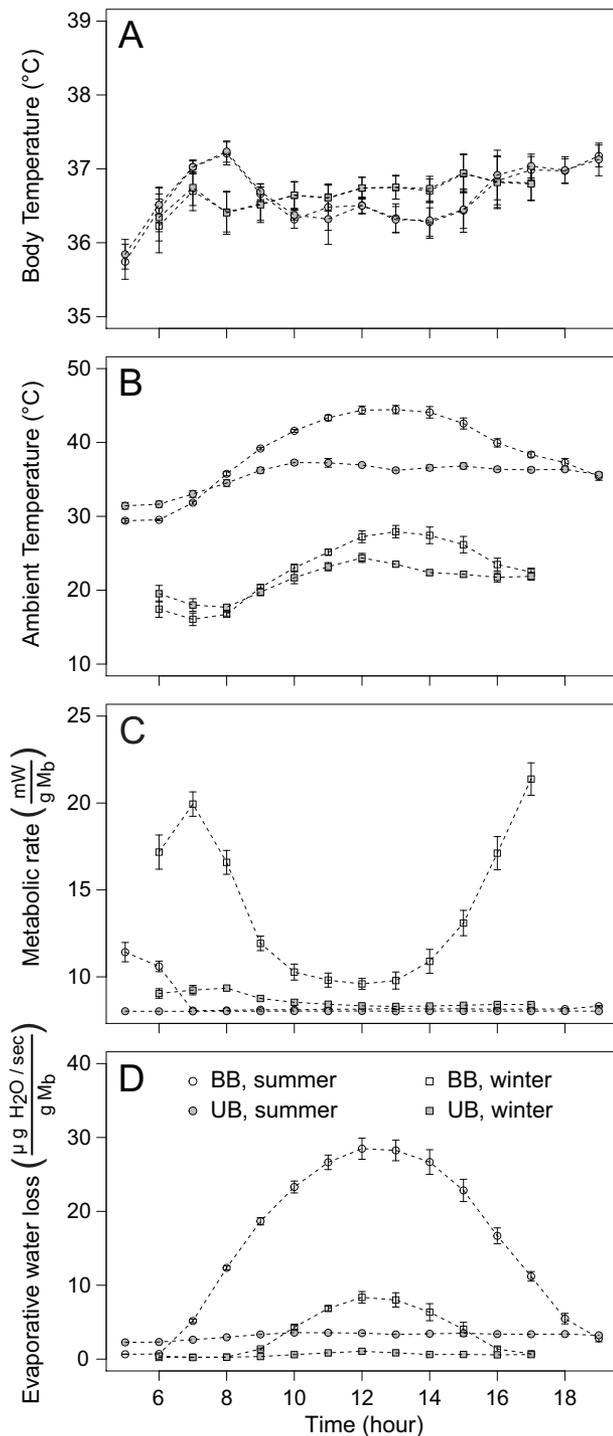


Figure 1: Hourly measured body temperatures (A), ambient temperatures (B), estimated metabolic rate (C), and evaporative water loss rate (D) during the daytime (means \pm SE) in summer (open circles: between-boulders [BB] microhabitat; filled circles: under-boulders [UB] microhabitat) and winter (open squares: BB microhabitat; filled squares: UB microhabitat). We used the body and ambient temperature data to estimate the costs of thermoregulation during activity on our foraging patches.

habitats changed little during the day. However, during summer in the BB microhabitat, evaporative water loss increased from 7 h to 18 h, reaching a maximum of 28.1 ± 0.3 ($\mu\text{g H}_2\text{O/s/g M}_b \pm \text{SD}$) at 13 h.

Foraging Behavior

Observed foraging behavior varied throughout the day and between microhabitats and seasons (fig. 2). On average, one peak of activity was observed at ~ 7 h during summer at the UB microhabitat and at ~ 9 h during winter at both microhabitats. A bimodal activity pattern was observed during summer at the BB microhabitat (fig. 2B). Our harvest rate model suggested a gradual decrease in the quantity of seeds throughout the day, with higher giving-up densities found at the BB microhabitat compared to the protected UB microhabitat (fig. 3).

We found a good fit between the foraging models and the data for both the foraging occurrences model (Bayesian $p = .51$) and the foraging duration model (Bayesian $p = .62$). The odds for foraging decreased by $5.4\% \pm 0.9\%$ ($\pm \text{SD}$, $p < .01$, 95% confidence interval [CI]: [3.6, 7.0]) for each increase of $1 \mu\text{g H}_2\text{O/s/g M}_b$ in evaporative water loss (fig. 4A). At the UB microhabitat, an increase by $87.6\% \pm 25.9\%$ ($\pm \text{SD}$, $p < .001$, 95% CI: [48.8, 133.8]) in foraging odds occurred when energy expenditure required more than 8.8 ± 1.5 ($\text{mW/g M}_b \pm \text{SD}$), which occurred at 40% of the hours in our data set (fig. 4B).

When foraging occurred, the duration of foraging was $133.1\% \pm 44.7\%$ ($\pm \text{SD}$, $p < .001$, 95% CI: [66.9, 208.8]) longer at the UB microhabitat. Foraging duration was shorter by $74.5\% \pm 11.3\%$ ($\pm \text{SD}$, $p < .01$, 95% CI: [45.1, 88.9]) when thermoregulation required evaporative water loss of more than 20.4 ± 3.2 ($\mu\text{g H}_2\text{O/s/g M}_b \pm \text{SD}$), which occurred only during 1.5% of the foraging hours (fig. 4C). Foraging was longer by $55.5\% \pm 12.8\%$ ($\pm \text{SD}$, $p < .05$, 95% CI: [21.7, 77.3]) for each increase in 1 g of seeds available in the foraging patches (fig. 4D). The positive effect of seed availability was stronger in the UB microhabitat, with an additional increase of $67.3\% \pm 16.2\%$ in foraging duration ($\pm \text{SD}$, $p < .001$, 95% CI: [24.9, 95.9]).

Giving-Up Densities and Quitting-Harvest Rates

Giving-up densities were $\sim 50\%$ lower in the UB microhabitat ($\beta = -0.69 \pm 0.08$, $t = -8.27$, $p < .001$, log gram $\pm \text{SD}$), with no significant effect of season ($\beta = 0.15 \pm 0.09$, $t = 1.70$, $p = .09$) and moon ($\beta = -0.14 \pm 0.08$, $t = -1.7$, $p = .10$). Similarly, when the GUDs were converted to quitting-harvest rates (W for energy and $\text{mg H}_2\text{O/s}$ for water), quitting-harvest rates were lower in the UB micro-

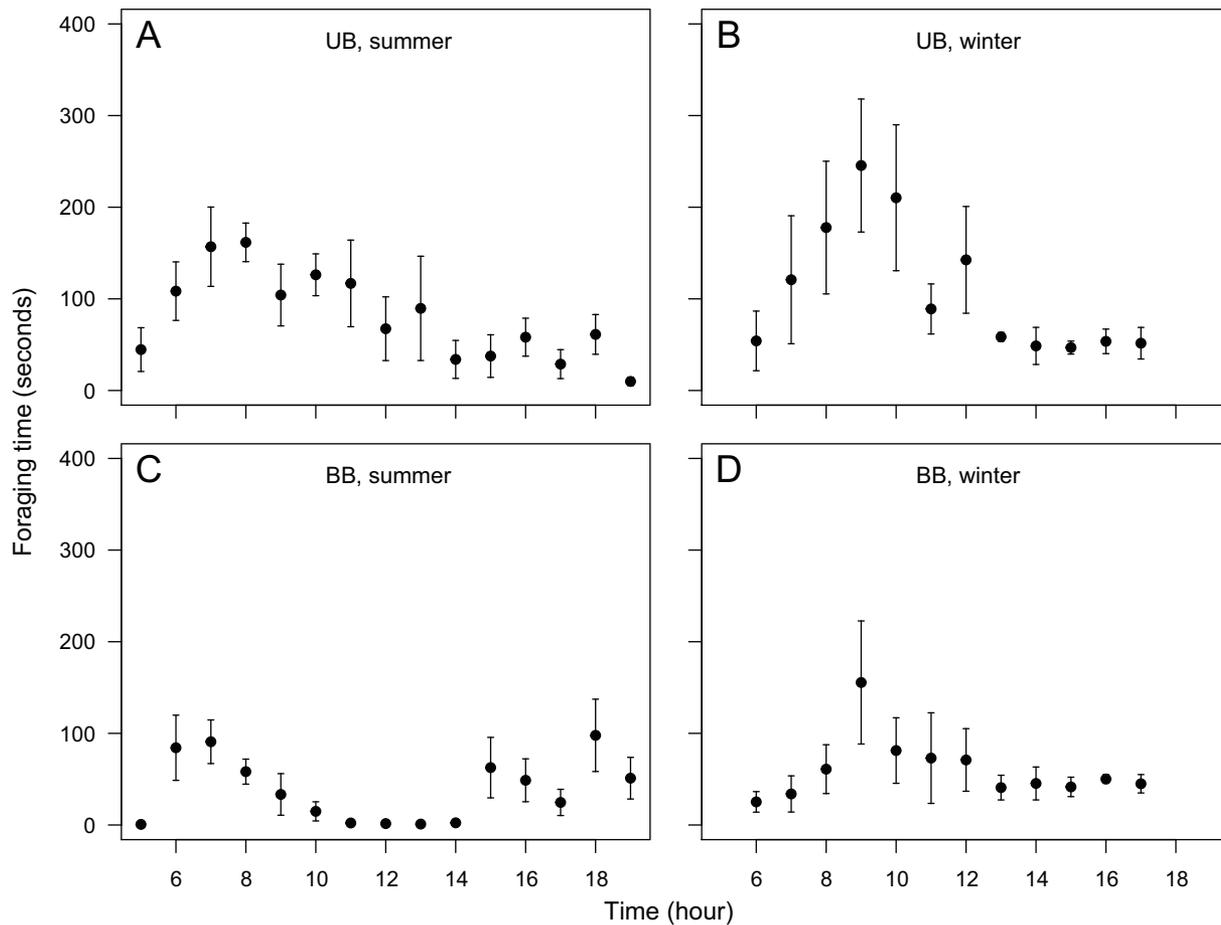


Figure 2: Mice constantly foraged less in the between-boulders (BB) microhabitat, probably due to higher water and predation costs. We show the spiny mice foraging behavior as observed across daytime (mean \pm SE; summer: $n = 5$; winter: $n = 6$) at foraging patches located in the protected, under-boulders (UB) microhabitat (A, summer; B, winter) and at the nonprotected, BB microhabitat (C, summer; D, winter).

habitat (table 2). Quitting-harvest rates reached a low of 3.68 W and 0.022 mg H₂O/s in the UB microhabitat during the summer and as high as 8.53 W and 0.047 mg H₂O/s in the BB microhabitat during winter. Foraging costs, as predicted by the biophysical model, were lower than the quitting-harvest rate for energy but higher than the quitting-harvest rate for water, except during winter at the UB microhabitat (table 2). Hence, we were able to calculate only predation costs for energy, which were higher for the BB microhabitat than in the UB microhabitat (table 2).

Mice lost $4.7\% \pm 1.9\%$ (\pm SD, $p < .05$, 95% CI: [1.1, 8.3]) more water for every 1 W decrease in quitting-harvest rates, with costs lower by $76.7\% \pm 3.7\%$ (\pm SD, $p < .001$, 95% CI: [68.4, 83.2]) in the UB microhabitat (fig. 5A). Quitting-harvest rates decreased by $72.3\% \pm 7.1\%$ (\pm SD, $p < .001$, 95% CI: [69.2, 75.5]), and evaporative water loss increased by $83.3\% \pm 15.1\%$ (\pm SD, $p < .001$, 95% CI: [56.8, 117.2]) with every 1,000 s of daily foraging activity. The positive ef-

fect of foraging time was $70.0\% \pm 7.1\%$ (\pm SD, $p < .001$, 95% CI: [56.9, 84.4]) lower in the UB microhabitat (fig. 5B).

Discussion

Foraging behavior is affected by a variety of abiotic and biotic variables. Elucidating the relative significance of each is crucial for understanding the forces that shape foraging behavior and time budgets. Our study is the first to analyze the effects of climate on foraging at an hourly resolution, while factoring in ecological interactions such as predation risks and resource availability. We combined use of biophysical modeling with use of the experimental approach that measures giving-up density; this combination of approaches allowed us to gain insight into the forces underlying temporal and spatial foraging patterns at the diel scale.

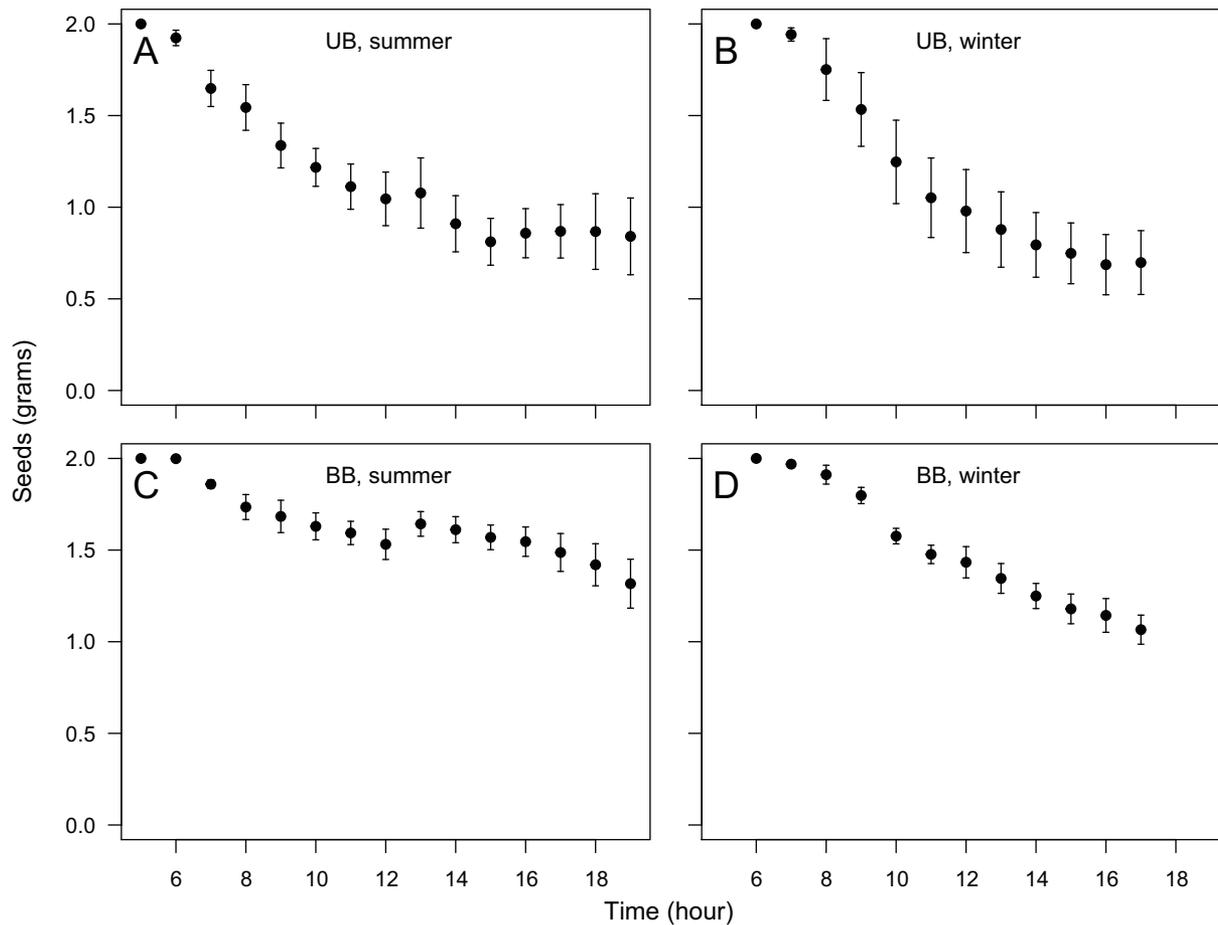


Figure 3: Estimated quantity of seeds in our foraging patches at the beginning of each hour (mean \pm SD; $n = 4$ at each microhabitat), as predicted using the relationship between daily foraging time and the quantity of seeds left in the patch at dawn.

We found that water requirements had the strongest effect on the observed foraging decisions. When ambient temperatures increased to a level that demands enhanced water evaporation to avoid hyperthermia, foraging occurred less frequently. Moreover, when the demand for evaporative water loss increased above a threshold level, a sharp decrease in foraging duration occurred. Thus, the influence of water requirements on foraging behavior accounts for the low foraging levels observed during noon hours at the BB microhabitat, when ambient temperatures are highest and the thermoregulatory demand for evaporative water loss rises. These pressures shape the bimodal activity pattern of morning and afternoon foraging in summer described for this species (Shkolnik 1971; Elvert et al. 1999; Kronfeld-Schor et al. 2001a). A similar pattern was observed in other diurnal mammals such as *Psammomys obesus* (Ilan and Yom-Tov 1990), *Octodon degus* (e.g., Bacigalupe et al. 2003), *Xerus inauris* (Aublet et al. 2009), *Capra ibex* (Bennett et al. 1984), and *Spalacopus cyanus* (Rezende

et al. 2003). The substantial decrease in midday activity helps retain a positive water balance in desert habitats, where water and food (the main water source in the desert) availability is scarce and unpredictable. Our quitting-harvest rates suggest that foraging ceases to prevent water loss even when energetic returns would be high. The ecological outcome is that under warm conditions, small mammals may decrease foraging sharply or cease it altogether due to water shortage.

Our findings are consistent with previous studies pointing to the importance of a positive balance between energetic costs and gains (e.g., Bacigalupe et al. 2003), which depends on the relative proportion of the energy gained by foraging and the energy spent for digestion, thermoregulation, growth, reproduction, and other processes (e.g., Karasov 1986). Understanding foraging behavior in arid environments is complex; both energy and water balance are crucial for survival and should be considered to avoid underestimating the forces exerted by climatic conditions, which would consequently overestimate predation risks.

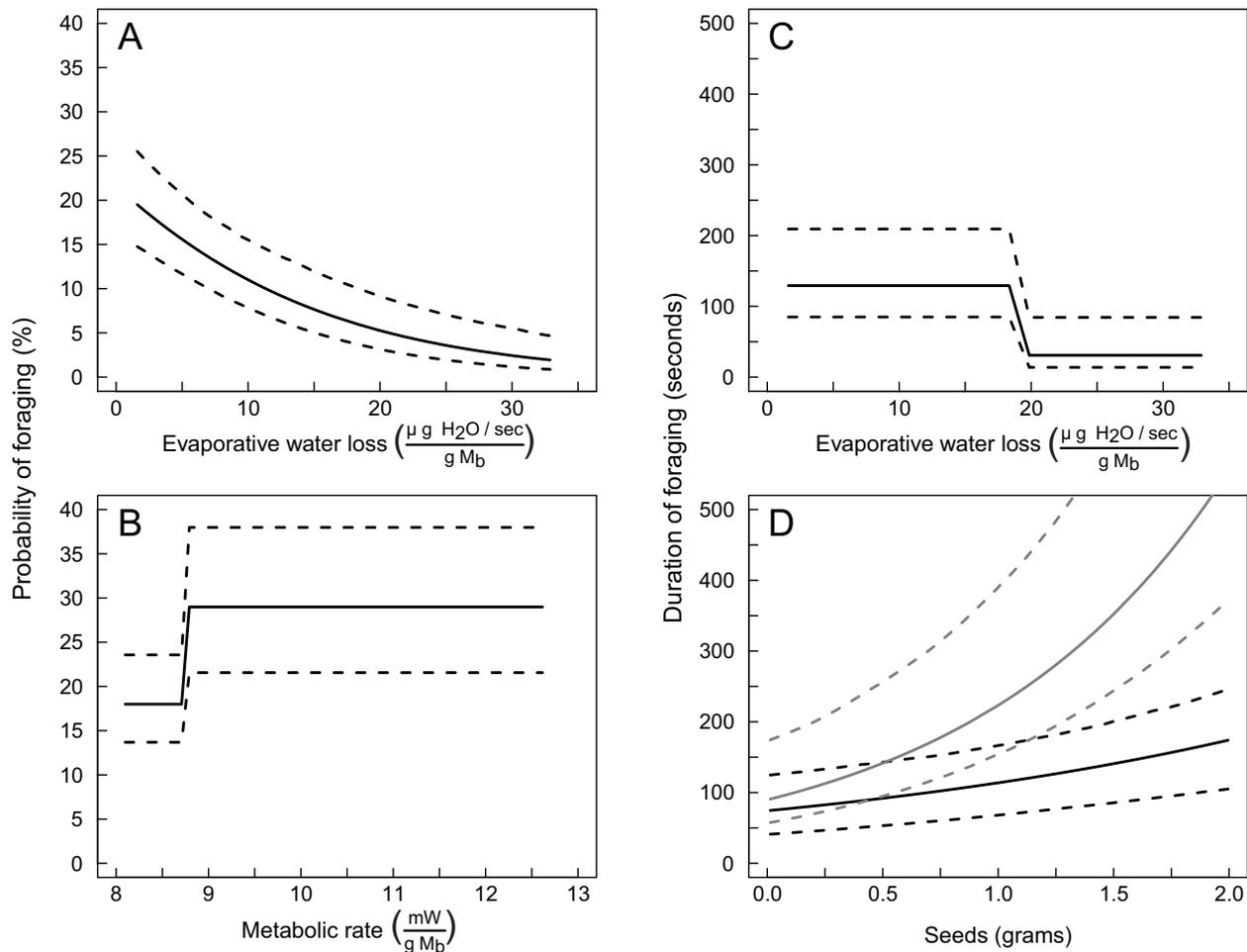


Figure 4: Mice fine-tuned their foraging patterns in response to hourly variations in water and energy costs of foraging and the availability of food in the foraging patches. We show the significant relationships found in our statistical models between evaporative water loss and foraging probability (A), metabolic rate and foraging probability (B), evaporative water loss and the duration of foraging (C), and quantity of seeds in foraging patches and the duration of foraging (D; between-boulders effect: black; under-boulders effect: gray). Solid line = mean slope; dashed line = 95% confidence intervals of slopes.

Desert species were found to cease foraging even though patches still contained plenty of food (e.g., 10–20 times higher than energetic costs; Brown et al. 1994b), perhaps to avoid high rates of water loss. In our study, golden spiny mice ceased foraging when the rates of evaporative water loss were higher than the rates of water received from the foraging patches. Previous studies suggest that where food and water are complementary, a forager may be able to resume foraging and, hence, gain more energy from a patch when water is abundant or by foraging for food with high moisture content, as previously shown in other species, such as *Capra nubiana* (ibex; Hochman and Kotler 2006), *Corvus coronoides* (Australian raven; Kotler et al. 1998), and *Capra hircus* (goat; Shrader et al. 2008). Hence, making water available to the golden spiny mice would have led to lower giving-up densities. In contrast, when water avail-

ability is high or when foraging costs of water are low, additional water supply would not increase foraging efficiency (Druce et al. 2009). To complicate matters, animals can compensate for water loss during one activity by exploiting nearby water holes or by gaining water metabolically.

In their arid environment, mice increasingly lost more water as they continued to deplete the energy from the foraging patches (fig. 5). This exchange rate might be even worse for animals in which predation risks increase vigilance. Conceptually, one should be able to calculate how exchange rates between water and energy change between levels of predation risks, as well as to calculate exchange rates between predation and water loss, as researchers have done for energy (Brown 1988; reviewed by Brown and Kotler 2004). Interestingly, in our study, the lack of difference in attack rates and handling times between moon

phases and microhabitats suggests that mice did not increase vigilance under riskier conditions. This might be another strategy by which golden spiny mice avoid water loss, since vigilance would further increase the rates of water loss per energy gain in the riskier and warmer BB microhabitat. Other factors that may affect exchange rates are the energy and water states of the foraging animal. For example, when water availability is high but energy availability is low, animals may forage under higher exchange rates as the marginal value of water becomes lower. Perhaps the large unexplained variance in our exchange rate model ($R^2 = 0.29$) suggests that mice foraged at different energetic and water states throughout the study.

The challenges of keeping a positive water balance are substantially higher in dry regions. Even nocturnal rodents, which are less exposed to climatic extremes, must consume substantial amounts of green vegetation and insects to gain enough water in desert habitats (Reichman 1975; reviewed by Walsberg 2000). Sperry and Weatherhead (2008) found that during periods of drought, small mammals have less vegetation and probably fewer arthropods to eat (Bell 1985), leading to reduced reproduction and increased starvation. Although many species living in arid ecosystems are adapted to short-term droughts, especially where droughts are relatively common, climate change is predicted to bring more intense, longer, and frequent dry and warm conditions, particularly in the Mediterranean, West Africa, central Asia, and Central America (Sheffield and Wood 2008; Trenberth et al. 2014). These changes will be driven primarily by reductions in precipitation with increased evaporation caused by higher temperatures (Sheffield and Wood 2008). In some regions, increases in precipitation are offset by increased evaporation (Sheffield and Wood 2008). The negative responses of ecosystems to recent droughts (e.g., Albright et al. 2010; Oliver et al. 2015) underscore the urgent need to better understand how organisms respond to these conditions.

Seed density and microhabitat type also affected foraging duration in our study. These factors reflect biotic pressures alone, because climatic costs were accounted for by the covariates of energy and water requirements. Time spent foraging significantly decreased with decreasing food density, probably because of diminishing returns. Moreover, mice foraged shorter periods in the more exposed BB microhabitat, even with high seed density. The differences between the microhabitats reflect the differences in predation risk. In the BB microhabitat, energy and water quitting-harvest rates were twice as high, and predation costs (P in eq. [1]) were 3.63 W higher. Hence, mice probably preferred the UB microhabitat not only for its microclimate conditions, which were more comfortable for activity, but also for its refugia from predators such as raptors (Jones et al. 2001; Mandelik et al. 2003; Gutman et al. 2011). Differences in foraging preferences that result from predation risk were

observed previously in golden spiny mice (Jones et al. 2001; Gutman et al. 2011) as well as in other species (e.g., Brown 1988; Lima and Dill 1990; Werner and Peacor 2003; Brown and Kotler 2004), but our study is the first to quantify them energetically. In fact, our preliminary observations revealed that mice almost completely avoided open microhabitats, which were not only exposed to solar radiation like the BB microhabitat but offered no nearby protection from predators.

Our analyses show that climatic and biotic factors influenced foraging behavior differently. Although mice reduced the frequency and duration of foraging as evaporative water loss increased and increased activity under high energy expenditure, only the duration of foraging was affected by seed density. We can explain these patterns by looking at the interplay between quitting-harvest rates and the metabolic and predation costs of foraging. A forager can choose its quitting-harvest rates, based on the costs of foraging, even before entering a foraging patch. However, a forager must first exploit a patch to gauge the harvest rate. For foraging to occur in a patch, its potential (i.e., marginal value) at that time should attract the forager. For example, since seeds are poor water sources, warmer conditions reduce their marginal value (table 2), making foraging for seeds less profitable. In fact, golden spiny mice show a strong preference for arthropods, which constitute their main diet during summer (Kronfeld-Schor and Dayan 1999). Under cold conditions, on the other hand, energy expenditure is high and the marginal value of seeds increases due to their high energetic content, but only at the UB microhabitat, where metabolic and predation costs are lower. Only when foraging

Table 2: Energetic and water quitting-harvest rates (QHR) and costs of foraging in our artificial food patches

Variable, season, microhabitat	QHR	C	MOC	P	QHR/C
Energy (W):					
Winter:					
UB	4.34	.39	-.23	4.18	11.14
BB	8.53	.58	-.23	8.18	14.63
Summer:					
UB	3.68	.34	-.23	3.56	10.75
BB	7.88	.35	-.22	7.75	22.53
Water (mg H ₂ O/s):					
Winter:					
UB	.026	.023	-.018	.021	1.14
BB	.051	.116	-.017	C > QHR	.44
Summer:					
UB	.022	.134	-.017	C > QHR	.16
BB	.047	.369	-.016	C > QHR	.13

Note: Foraging costs were 10.7–22.5 times lower than the QHR for energy but were 2.3–7.7 times higher than the QHR for water, except during winter at the under-boulders (UB) microhabitat. C = energy or water metabolic cost; MOC = missed opportunity cost; P = cost of predation; BB = between boulders.

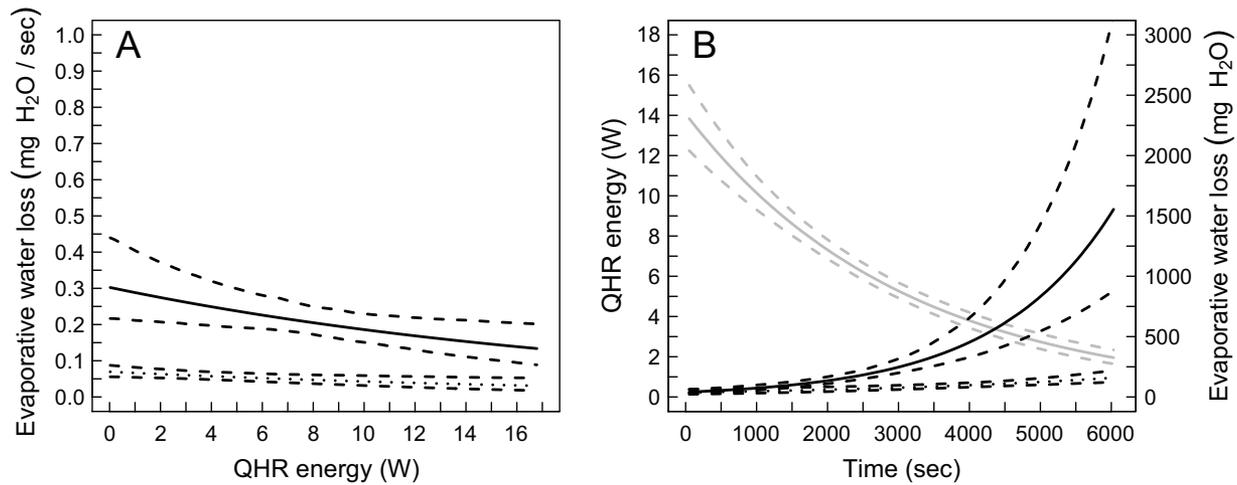


Figure 5: During each day, the mean rates of evaporative water loss increased when mice quit foraging at lower harvest rates of energy (A; between-boulders [BB] effect: solid line; under-boulders [UB] effect: dashed line). As mice spent more time foraging in the patches, they reached lower quitting-harvest rates (B; gray lines) but also lost more water for thermoregulation (B; BB effect: solid line; UB effect: dashed line). Dashed lines represent 95% confidence intervals of slopes. QHR = quitting-harvest rate.

begins can a forager sense the harvest rate of the patch, based on seed density, and then forage until it reaches the quitting-harvest rate.

The implications of ecological thresholds and nonlinear dynamics have attracted attention in recent decades (Ficetola and Denoel 2009). Determining whether ecological thresholds exist, and estimating their values, has been considered a major challenge (e.g., Muradian 2001; Ficetola and Denoel 2009). Most studies to date addressed the minimal area or habitat required to avoid extinction (e.g., With and King 1999; Fahrig 2001), climate-change induced migration (e.g., Collingham and Huntley 2000), or biological invasions (e.g., Dewhurst and Lutscher 2009). Another ecological threshold response is a nonlinear decrease in foraging when prey density falls below a certain threshold (e.g., Harding et al. 2007). In our study, the threshold response to an increase in evaporative water loss may reflect the high priority of keeping a water balance in an arid environment. Moreover, the increase in foraging when energy expenditure reaches a certain threshold may represent the need to search for more energy when energetic demands are high, increasing the marginal value of energy.

In summary, understanding the links between animal behavior, biotic conditions, and climate under natural field conditions is a major challenge. Advances in animal tracking and modeling techniques allow a better understanding of activity patterns and provide insight into optimal foraging. Previously, foraging behavior was mostly studied in the light of predation costs, with some attempts to understand energy considerations (reviewed by Stephens and Krebs 1986; Stephens et al. 2007) but almost no ability to es-

timate water costs and their importance. Here, we were able to highly refine the roles of energy and water to reveal the dominant and dramatic effects of water costs in foraging decisions. We also show that mice fine-tuned their foraging activity to minimize water loss and predation risks at the expense of energy gain. Hence, our results suggest a triad of energetic costs, predation costs, and water loss costs rather than a duality of energetic and predation costs (as well as missed opportunity costs) in golden spiny mice. To better understand this triangular relationship, future studies should explore the role of water costs in risk and time management in species adapted to deserts and less dry environments. Such studies may help us estimate how less adapted species may aim to compensate for water deficit during droughts, a rising challenge under climate change and, on the other hand, how increased water availability due to urban or agricultural water resources may alter the ecological systems of arid regions, by promoting the invasion and spread of nondesert species. Can we use artificial patches of water to mitigate the severity of climate change? Exploring such questions may help us understand the ecological, physiological, and evolutionary challenges of arid environments and future droughts.

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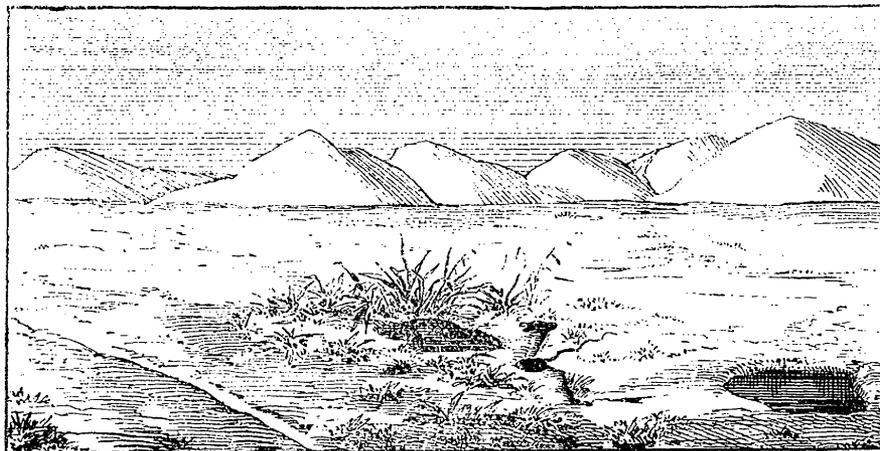
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“Day break the following morning found the party en route to Silver Peak, the next objective point. Silver Peak, a small mining camp, is located near the west side of Clayton Valley, and at the eastern base of the Red Mountain range. Near this place and along the western border of the salt marsh which forms the major part of the basin are the Thermal Springs. . . . Just north of [the first spring] is found a cluster of springs; the largest and most central one is called Saturn [illustrated]. Their temperatures are 69.5° Fahr.” From “The Springs of Southern Nevada” by D. A. Lyle (*The American Naturalist* 1878, 12:18–27).