Estimating the influence of the thermal environment on activity patterns of the desert woodrat (*Neotoma lepida*) using temperature chronologies

Ian W. Murray and Felisa A. Smith

Abstract: Environmental temperature influences the ecology and life history of animals. In habitats near the thermal range boundary, fluctuations in temperature may influence the ability of species to persist. Desert woodrats (*Neotoma lepida* Thomas, 1893) occupy one of the hottest and most extreme environments in the western hemisphere, Death Valley, California, despite limited adaptations for water conservation or efficient heat dissipation. Moreover, *N. lepida* have a relatively low tolerance for high temperature. Thus, we hypothesized temperature might influence both the timing and the duration of activity. To test this idea, we attached iButton sensors to 56 animals over a 2-year period and recorded activity. Each sensor was set to record at 5 or 15 min intervals and stored approximately 2000 records before retrieval. We found a strong relationship between ambient temperature and onset and duration of activity, influenced by both body size and gender. *Neotoma lepida* did not emerge until air temperature fell below 42 °C. As daily high temperatures increased, both sexes had fewer nightly activity bouts of shorter duration. Our results suggest that activity of *N. lepida* is constrained during the climatically intense summer months. Animals face a trade-off between remaining in the thermal safety of the den vs. emerging to obtain resources.

Key words: Death Valley, iButton, temperature, thermal biology, desert woodrat, *Neotoma lepida*.

Résumé : La température du milieu influence l'écologie et le cycle biologique des animaux. Dans les habitats situés près des limites de l'intervalle thermique d'une espèce, les fluctuations de température peuvent avoir une incidence sur la persistance de cette espèce. Les néotomas du désert (*Neotoma lepida* (Thomas, 1893)) occupent un des milieux les plus chauds et les plus extrêmes de l'hémisphère occidental, la vallée de la Mort, en Californie, malgré le fait qu'ils présentent peu d'adaptations à la conservation d'eau et à la dissipation efficace de la chaleur. En outre, *N. lepida* tolèrent assez mal les températures élevées. Nous avons donc émis l'hypothèse que la température pourrait influencer tant le moment que la durée de leur activité. Pour vérifier cette hypothèse, nous avons fixé des capteurs iButton sur 56 animaux pendant une période de deux ans et enregistré leur activité. Chaque capteur était réglé pour enregistrer à des intervalles de 5 ou 15 min et stockait environ 2000 enregistrements avant que ces derniers soient récupérés. Nous avons constaté un fort lien entre la température ambiante et le début et la durée de l'activité, influencée par la taille corporelle et le sexe des animaux. *Neotoma lepida* n'émergeaient pas tant que la température de l'air n'était pas sous les 42 °C. Quand les températures journalières augmentaient, le nombre et la durée des épisodes d'activité nocturnes des deux sexes diminuaient. Nos résultats suggèrent que l'activité des *N. lepida* est restreinte durant les mois estivaux caractérisés par des conditions climatiques intenses. Les animaux sont confrontés à un compromis entre le fait de demeurer en sécurité thermique dans le terrier et celui d'en émerger pour obtenir des ressources.

Mots-clés : vallée de la Mort, iButton, température, biologie thermique, néotoma du désert, *Neotoma lepida*.

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Introduction

Deserts are arguably one of the most extreme and seemingly inhospitable terrestrial environments on Earth. Shaded air temperatures in excess of 45 °C are routine and surface temperatures may exceed 85 °C (Hunt et al. 1966). Yet these regions are populated by their own distinctive biota, whose ecologies are largely shaped by their thermal environments.

Animals living in deserts face numerous problems that are all ultimately related to the need to maintain homeostasis in a harsh environment (Nagy 1994). These problems can be especially severe for mammals that typically maintain core temperatures that are significantly cooler than ambient temperature and that may not have abundant access to water for evaporative cooling (Walsberg 2000; Bozinovic and Gallardo 2006). Satisfying the basic and constant requirements for

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food and water are also difficult when primary productivity is unpredictable and sporadic, as is common in deserts. Although species in deserts are necessarily adapted to the harsh environment, nonetheless, at times they may be close to their thermal limits (Goldstein 1984; Tieleman and Williams 2002). For example, unusually severe heat waves have contributed to massive bird and fruit bat die-offs in western and southeastern Australia (Serventy 1971; Wolf 2000; Welbergen et al. 2008; McKechnie and Wolf 2010). Hence, warming temperatures in deserts over the next decades may influence animals in deserts more than in other habitats. An important area of study is how desert animals will fare in the face of anthropogenic warming and drying trends.

Woodrats (*Neotoma* Say and Ord, 1825) are a genus of medium-bodied herbivorous, murid rodents. Several species are found in the southwestern deserts, including the desert woodrat (*Neotoma lepida* Thomas, 1893). This is somewhat surprising because *N. lepida* have a relatively low tolerance for high temperatures (Brown 1968; Smith et al. 1995; Smith and Betancourt 1998). Moreover, *N. lepida* lack the physiological adaptations common in other desert-dwelling mammals, such as the ability to produce highly concentrated urine, a counter-current water recovery system in the nasal cavity, or estivation during unfavorable conditions (Schmidt-Nielsen and Schmidt-Nielsen 1950; MacMillen 1964; Tracy and Walsberg 2002). Indeed, the name "desert woodrat" is a bit of a misnomer; the species originated in coastal California and it only expanded into the Mojave Desert during the late Pleistocene (Patton et al. 2008).

Neotoma lepida are able to survive in desert habitats because of their ability to construct houses. All species build complex structures of locally gathered debris that can reach several metres in height and diameter. These houses or dens typically contain several entrances and multiple food and nest chambers (Stones and Hayward 1968). They are important thermal refugia, ameliorating air temperature by as much as 3–9 °C (Vorhies 1945; Lee 1963; Brown 1968). Dens also provide significant protection against predators (Lee 1963; Brown 1968; Stones and Hayward 1968; Cameron and Rainey 1972; Smith 1995*a*).

Here we describe the influence of temperature on the movements and daily activity patterns of *N. lepida* in Death Valley, California, USA. This is one of the hottest and driest environments in the western hemisphere and one that poses significant challenges to animals. Because of the extreme topography, Death Valley lies in a severe rain shadow, which coupled with below sea-level elevation, contribute to a hyper-arid climate. Maximum daily temperatures regularly exceed 50 °C during the summer; much higher than the upper lethal temperature for *N. lepida* of approximately 41 °C, although different investigators have found this figure to vary slightly in either direction (38–40 °C: Lee 1963; 41.4 °C: Brown and Lee 1969; 43 °C: Nelson and Yousef 1979). Moreover, temperature is projected to increase between 2.0 and 5.0 °C within the next 100 years (Cayan et al. 2009). Because *N. lepida* are highly sensitive to high temperatures (Smith et al. 1995; Smith and Betancourt 1998; Smith et al. 1998), we suspected that the thermal environment might constrain the duration and onset of foraging and other activities. *Neotoma lepida* are highly sedentary and display high site fidelity. Indeed, in this habitat, most animals limit nightly activity

to the confines of the mesquite hosting the home den (personal observation (I.W. Murray) of radio-collared individuals). Although the den ameliorates environmental temperature to some degree, *N. lepida* must leave their dens to forage and to search for mates. Thus, temperature may directly impact fitness by modulating activity levels. Here, we address the following questions: (1) Is the onset of foraging and other activities correlated with ambient temperature? (2) Is the duration of activity correlated with temperature? (3) Do gender and body mass influence the onset and duration of activity?
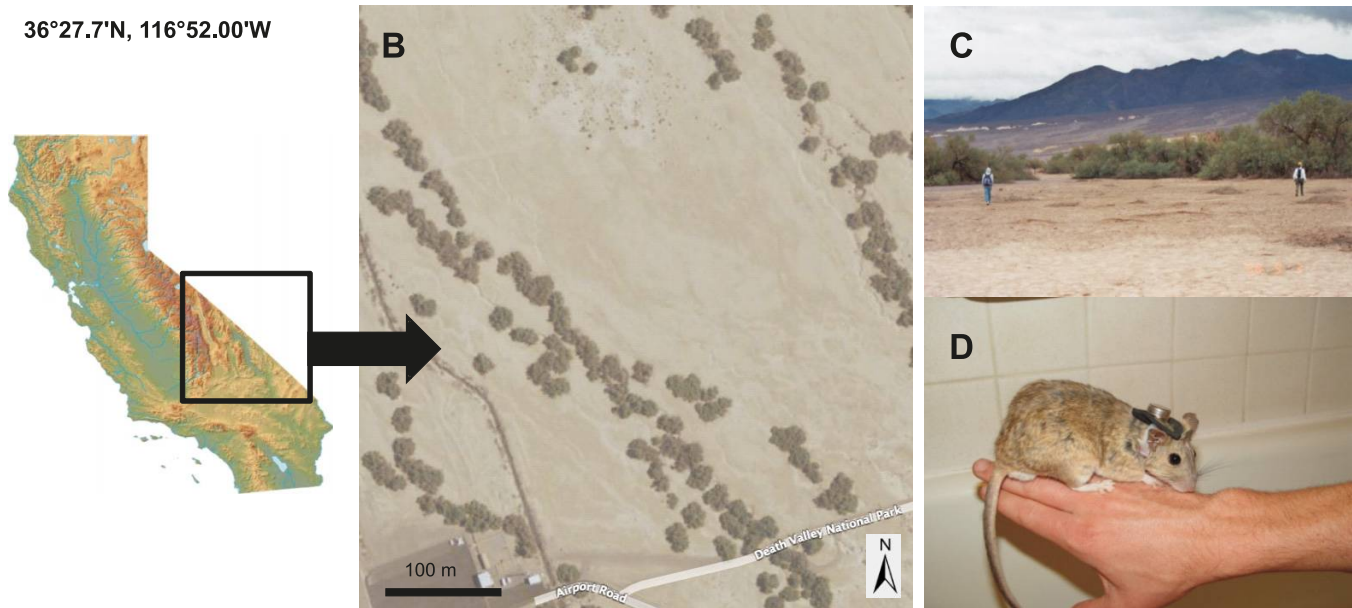
Materials and methods

Study area

Our study site lies on an approximately 10 ha plot of scattered honey mesquite (*Prosopis glandulosa* Torr.) about 2 km northwest of the Furnace Creek Ranger Station at Furnace Creek, Death Valley (36°27.7′N, 116° 52.00′W) at an elevation of –77 m (Fig. 1A). The site is situated between the base of a large alluvial fan extending from the Funeral Mountains to the east and the salt pan occupying approximately 520 km^2 on the valley floor (Hunt et al. 1966). It is in this area of relatively shallow subsurface water that *P. glandulosa* grows, often in continuous linear formations, tracking available groundwater (Fig. 1B). Temperatures here are among the hottest in the world (Roof and Callagan 2003). The intense heat is coupled with irregular annual precipitation that averages 4.8 cm/year. There is a complete lack of an herbaceous understory or other vegetation, tying the *N. lepida*, and its need for succulent vegetation, solely to the honey mesquite. *Neotoma lepida* build their dens at the bases of the mesquite at this site.

Trapping protocol

We live-trapped *N. lepida* on a monthly basis from 2003 to 2008. We permanently placed Sherman live-traps in each of 40 individually marked mesquite clumps, or complexes (Fig. 1B). The site was visited monthly and trapped for three consecutive nights for a total of approximately 500 trap-nights/month, or 19 500 trap-nights over the duration of the study. Traps were baited with apple and during the cooler months both oatmeal and insulating polyester batting were included. Upon initial capture, we individually marked animals with numbered fingerling tags clipped onto each ear (National Band and Tag Co., model #1005-1). At each subsequent capture, we recorded mass, sex, reproductive status, and qualitatively assessed body condition as good vs. poor. We worked under supervision of the Animal Care and Use Committee of the University of New Mexico (protocol No. 08UNM073-TR-100489) and followed appropriate guidelines as outlined by Gannon et al. (2007).

Because of high activity of coyotes (*Canis latrans* Say, 1823), our traps were wired to branches located 2–4 m up in the mesquite canopy, instead of on the ground. An additional modification to our trapping protocol was necessary because of the extreme temperature regimes. During May–September, traps were not set until 22:20 because of the high nighttime temperatures. Even with this modification, traps had to be checked and processed within an hour, as *N. lepida* began dying from hyperthermia if forced to remain outside the den

Fig. 1. Study site at Furnace Creek, Death Valley, California, for desert woodrats (*Neotoma lepida*). (A) Approximate location of Death Valley. (B) Aerial image of our trapping location, showing individual clumps of honey mesquite (*Prosopis glandulosa*) where trapping grids are located and the barren nature of the intervening landscape. (C) Ground view of several trapped mesquite "site complexes". (D) *Neotoma lepida* equipped with an iButton.

36°27.7'N, 116°52.00'W

for longer periods. In contrast, nightly lows often dip below 0 °C during the winter months, and despite the addition of polyester batting, hypothermia was a problem, especially with the smaller females. Accordingly, during the winter months, traps were closed by 00:00.

Temperature recording

We used miniature temperature data loggers (Thermochron iButtons, model DS1921G, Dallas Semiconductor, 3.3 g) mounted on collars to study the movements of free-ranging *N. lepida*. Because we are interested in activity patterns, we concentrated on changes in temperature rather than the actual ambient temperature. As the thermal environment outside the den was significantly different than inside, we were able to determine where animals were by the temperatures recorded on the iButtons. Previous studies have validated the accuracy of using temperature changes to estimate activity in secretive and nocturnal mammals (Osgood and Weigl 1972; Weigl and Osgood 1974; Kanda et al. 2005; LaZerte and Kramer 2011). We set the iButtons to record at 15 min intervals. This provided 2048 consecutive readings, or approximately 22 days per usage interval. A subset of animals ($n = 3$) wore collars set to record every 5 min. The small size of this data logger combined with its high-capacity memory allowed us to passively record activity patterns of naturally behaving animals over long periods of time.

Between 2006 and 2007, we outfitted 56 rats (32 males, 24 females) with iButtons. These were mounted on circular foam platforms using metal snaps and placed around the neck of a rat using a cable tie. The cable ties were threaded through a small piece of foam, and a metal snap base was epoxied to this. The opposite end of the snap was glued to the iButton itself, which allowed rapid retrieval and exchange. The total package weighed between 6 and 8 g and did not exceed 10% of animal mass. Upon recapture of the

animal, data were downloaded via a reader connected to a computer interface and a new collar installed.
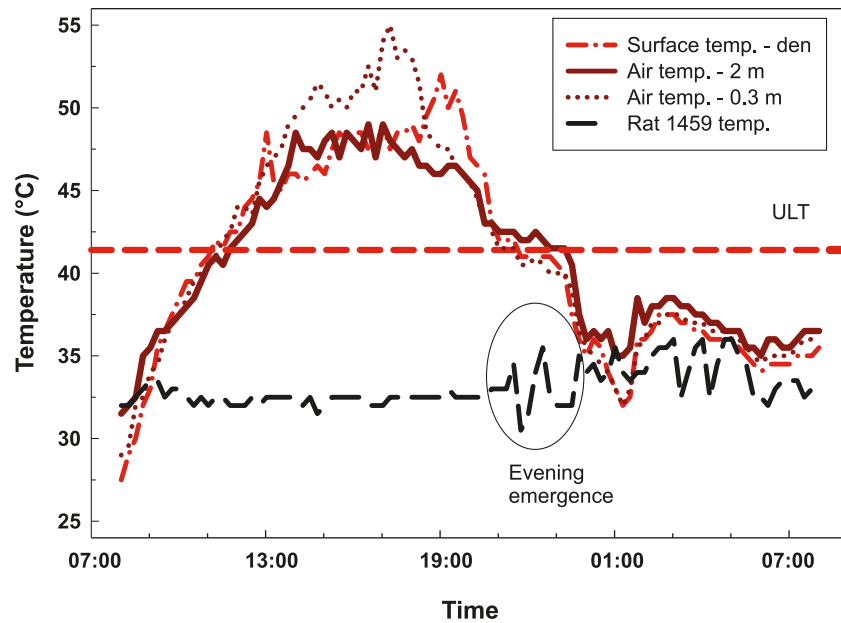
Temperature records

We used two sources to characterize the temperature for the site, which differed in the degree of spatial averaging and duration. First, we empirically recorded temperatures at a variety of heights within the mesquite canopy. The iButtons were placed at 0.3 and 2.0 m within several mesquite trees. These heights are biologically relevant because they represent the height of *N. lepida* dens and the foraging trails of the rats, respectively. Second, we obtained a record of daily temperatures for Furnace Creek, Death Valley, from a weather station situated on the site. From these data, we characterized the historical record of daily maximum and minimum temperatures for the site compared with those from the individual rat collars and the available ambient temperature records (Fig. 2).

Data analysis

Over the course of the study we collected >44 000 individual activity readings of *N. lepida* as inferred from temperature shifts, which complicated the processing of data. To make these data more tractable, we assigned each day to a relative measure of temperature intensity. Daily high temperature is robustly related to nocturnal temperature when we compare diurnal high and nocturnal low temperatures as recorded at a Furnace Creek, Death Valley, weather station ($r_{[363]} = 0.91$, $p = 0.000$). We extracted daily high temperatures and binned them into four measures of thermal stress based on biologically relevant benchmarks: low, medium, high, and severe, representing temperatures below the thermoneutral zone (<31 °C; low), within the thermoneutral zone (31 to 35 °C; medium), above the thermoneutral zone (>35 to <41 °C; high), and above upper lethal temperature

Fig. 2. Twenty-four hour tracing of ambient temperature and iButton temperature on a desert woodrat (*Neotoma lepida*). iButton temperature chronologies illustrating temperature spikes indicative of activity outside of the thermal stability of the den for one *N. lepida* over a 1-day period in June 2007, relative to iButton traces recorded at variable heights within a mesquite (*Prosopis glandulosa*) complex on our study site (30 cm = iButton placed on a wooden stake 30 cm above a den; 2 m = iButton placed on a wooden stake 2 m above the ground in the mesquite canopy; den = iButton placed on the surface of the same *N. lepida* den). Upper lethal temperature (ULT) is given as 41.4 °C.

(≥41 °C; severe) (Lee 1963; Brown and Lee 1969; Nelson and Yousef 1979). That these benchmarks derived from the literature were relevant for *N. lepida* in Death Valley was evident in the trap mortality records; animals died if they were forced to spend >1 h in temperatures of >40 °C.

We divided data between nocturnal and diurnal periods and defined the onset of activity as a demarcated, abrupt deviation from baseline diurnal den temperature. Because postural adjustments or movements within the den could be reflected in rat temperature profiles, we used the mean standard deviation (SD) for an individual rat's recorded diurnal temperature chronology as the cutoff for separating outside activity from activity within the den. If the difference between two consecutive temperatures was greater or equal to the mean diurnal SD for that given rat, we assumed that activity had taken place, and that that activity was 15 min in length (derived from the period of time between two data points). We summed every rat's activity on a nightly basis to estimate time spent outside of the den. We recorded the number of nightly activity bouts for a rat as the total number of episodes where there was at least 15 min of activity.

Statistical analyses

To study how temperature constrains onset and duration of activity and to examine the influence of body mass and gender on these measures, we fit linear mixed effects models with sex, body condition, and daily high temperature category as fixed factors. Because we had many repeated measurements on a limited number of individuals for largely nonoverlapping periods of time, the utility of tests such as repeated-measures ANOVA is limited. To account for pseudoreplication, we treat rat identity as a random factor in all of our mixed effects models. This allowed us to examine how the factors of interest (i.e., temperature) influenced *N. lepida*,

while accounting for the between rat variance. We set significance at $\alpha = 0.05$, and used SPSS version 19, SigmaPlot version 8.0, and Microsoft Excel for all analyses and figures. All means are followed by the standard errors (SE) reported with the marginal means from the mixed effects models.

Results

Based on monthly trapping ($n = 35 \pm 2.3$ individuals per month), adult body mass of *N. lepida* at Furnace Creek demonstrates a clear annual cycle (Fig. 3). The median body mass of the population declines sharply in the summer months. These changes are not the result of decreases of body mass of individual animals, but rather, reflect higher mortality of larger individuals (F.A. Smith, L.H. Harding, H.M. Lease, J.T. Martin, and I.W. Murray, unpublished data).

Onset of activity

We retrieved 34 of 99 (21 from 32 individuals) iButtons affixed to males and 6 of 41 (7 from 24 individuals) on females. After accounting for equipment malfunction, usable data consisted of 468 *N. lepida* nights from 14 individuals (10 males and 4 females) with over 44 000 individual readings. The mean monthly ambient temperature at the initiation of nightly activity of *N. lepida* closely tracks mean monthly daily high temperatures. During the summer months of June through August where mean daily maximum temperature was consistently >45 °C, *N. lepida* did not begin nightly foraging activities until ambient temperatures were below 42 °C (Fig. 4). This is a significant correlation, as it represents the empirically derived upper lethal temperature (Lee 1963; Nelson and Yousef 1979). We also observed significant differences in timing of nocturnal emergence between male and female *N. lepida*; females initiated nightly movements con-

Fig. 3. Monthly adult median body mass of the desert woodrat (*Neotoma lepida*) plotted against mean maximum monthly daily temperatures for the previous month. Upper lethal temperature (ULT) is given as 41.4 °C.
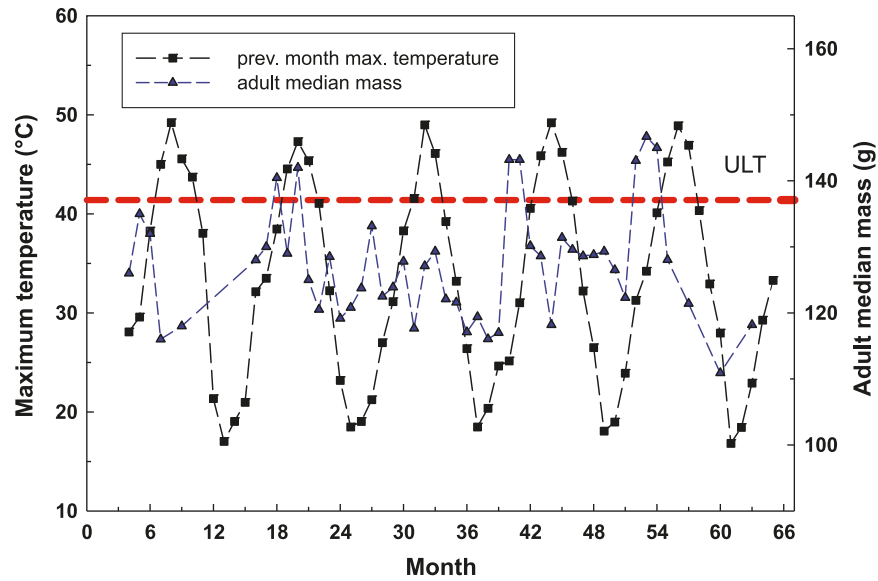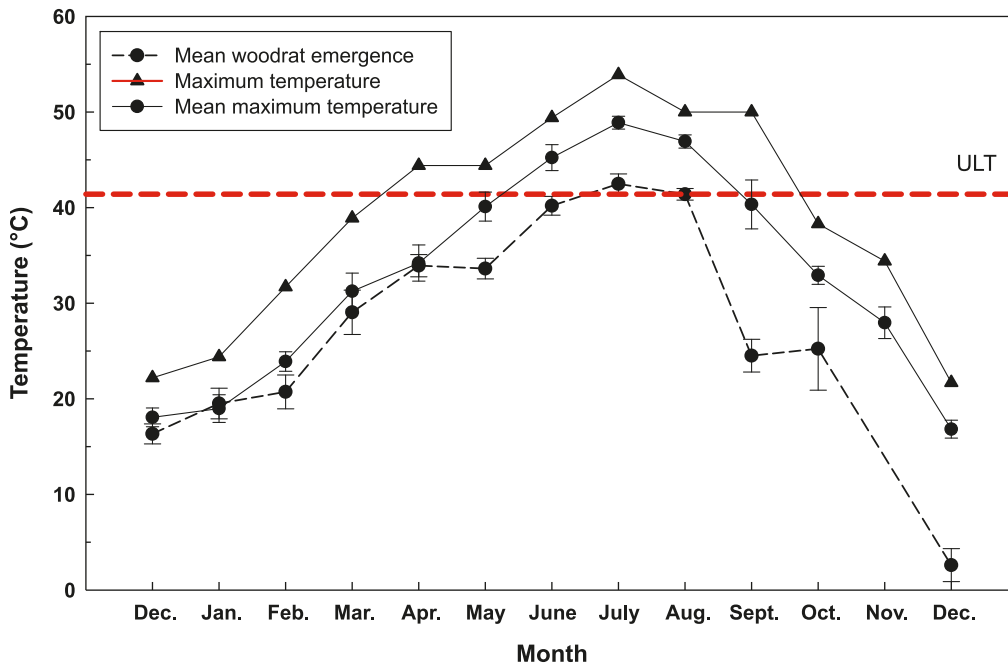

Fig. 4. Mean ambient temperature upon initiation of nightly activity for desert woodrats (*Neotoma lepida*) relative to monthly mean daily maximum temperature. Error bars represent 95% confidence intervals; *n* = 468 *N. lepida* nights; 10 males and 4 females. The broken horizontal reference line is the upper lethal temperature (ULT; 41.4 °C) for *N. lepida*.

siderably later than males (female emergence after sunset: 95.3 ± 11.3 min vs. male emergence after sunset: 59.5 ± 6.7 min; $F_{[1,9.6]}$ = 7.0, P = 0.025).

Body size is an important determinant of the onset of nightly activity. Larger rats were active less than smaller rats; each approximately 1 g increase in body mass led to an activity reduction by 2.5 min (β = –2.5 ± 0.6; $F_{[1,263]}$ = 18.9, P = 0.000). Moreover, this difference was exacerbated in males; larger individuals emerged over 1 min/g later (min after sunset) than did smaller ones (β = 1.2 ± 0.4; $F_{[1,22.4]}$ = 8.4, P = 0.008). For example, males with body mass of 1 SD greater than the population mean (160 g; male mass =

136.0 ± 23.4 g; *n* = 207) emerged later in the evening (72.0 ± 9.0 vs. 49.0 ± 7.0 min) and were less active overall (246.0 ± 15.0 vs. 311.0 ± 22.0 min) than those smaller than 160 g.
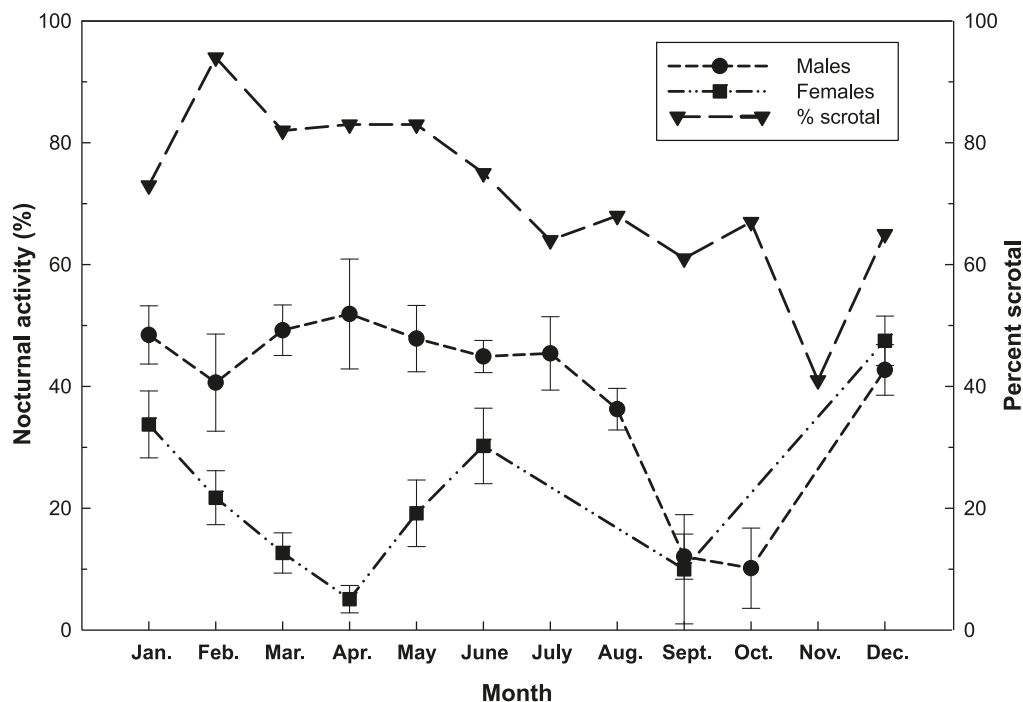
Duration of activity

Neotoma lepida are nocturnal animals. Because of differences in photoperiod, the duration of potential activity time varies seasonally. The decrease in activity observed with increasing daily temperature persisted even after accounting for the proportion of available nocturnal hours utilized ($F_{[3,454.2]}$ = 13.8, P = 0.000; Table 1). The difference in ac-

Table 1. Effect of daily maximum temperature on activity of desert woodrats (*Neotoma lepida*) the following night.

Activity parameter	Low < TNZ (<31 °C)	Medium TNZ (31 to 35 °C)	High > TNZ < ULT (>35 to <41 °C)	Severe > ULT (≥41 °C)
Activity (min)	251.4±29.1a	190.7±31.2b	177.9±30.3b	142.4±28.4c
Percent night active	40.1±5.4a	31.4±5.5b	29.4±5.4b	23.9±5.2c
Mean activity bout duration (min)	34.5±3.1a	27.1±3.0b	25.3±2.8b,c	22.2±2.6c
No. of activity bouts	11.3±3.9a	9.1±3.9b	8.3±3.9b	6.8±3.9c

Note: Different letters represent significant differences between temperature categories (Tukey's LSD, *P* < 0.05). Marginal mean values are presented with model standard errors. Daily high temperatures are binned into low, medium, high, and severe categories based on the empirically determined thermoneutral zone (TNZ) and upper lethal temperatures (ULT) for *N. lepida*.

Fig. 5. Activity of desert woodrats (*Neotoma lepida*) as a percentage of available nocturnal hours used relative to time of year, sex, and for males, an index of sexual activity, the percentage of reproductive males (any male noted as being scrotal or partially scrotal for a given trapping period) on a monthly basis. We have no November activity data for males and no October–November activity data for females; *n* = 468 *N. lepida* nights; 10 males and 4 females.

tivity (as the percentage of available nocturnal hours utilized) following "low" temperature and "severe" temperature days was striking (40.1% ± 5.4% vs. 23.9% ± 5.2%). As might be expected, time outside the den was intermediate following "medium" and "high" temperature days (31.4% ± 5.5% and 29.4% ± 5.4%, respectively). Interestingly, at each temperature level, animals in good condition were active 6.5% ± 2.3% longer than those in poor condition (34.4% ± 5.3% vs. 27.9% ± 5.3%, respectively; $F_{[1,429.9]}$ = 7.7, *P* = 0.006). It also appeared that individuals occupying larger mesquite complexes engaged in higher levels of activity (β = 0.04 ± 0.01; $F_{[1,17.3]}$ = 8.4, *P* = 0.01).

As daily high temperatures increased over the summer, all *N. lepida* showed a precipitous decline in nightly activity (Table 1), but at any specific temperature, males were active for significantly longer than females. On average, this was 133.3 ± 58.4 min per night ($F_{[1,15.9]}$ = 5.2, *P* = 0.036; mean female activity: 124.0 ± 49.8 min vs. mean male activity: 257.3± 29.2 min; $F_{[1,15.9]}$ = 5.2, *P* = 0.036). This trend was not monotonic, however, and activity closely mapped the actual

diurnal temperature. For example, following "low" temperature days, *N. lepida* were almost 80% more active than after "severe" temperature days (251.4 ± 29.1 vs. 142.4 ± 28.4 min; Tukey's LSD, *P* = 0.000). Although there was a trend for nocturnal activity to be higher after "medium" temperature relative to "high" temperature days (190.7 ± 31.2 vs. 177.9 ± 30.3 min), this was not significant (Tukey's LSD, *P* = 0.44).

As might be expected, activity patterns changed during the winter–spring reproductive season and were different for males and females. Male rats were consistently active for about half the nighttime hours (41%–52%) during the months of January through July, when corrected for changing day length (Tukey's HSD, *P* > 0.05; Fig. 5). When females were no longer receptive, however, there was a significant decline in male activity. In September and October, for example, *N. lepida* were active for only 10%–12.0% of the nighttime hours (Tukey's HSD, *P* < 0.05; Fig. 5). Activity increased markedly just prior to when females once again became sexually receptive (e.g., in December 366 min; 43.0% ± 5.0%).

Although male activity patterns represent both foraging and searching for mates, that of females is largely centered on the search for resources. Females exhibited a steady decline in nighttime activity from a high of 34.0% ± 5.0% (283 min) in January to a low of 5.0% ± 2.0% (32 min) in April (Tukey's HSD, $P < 0.05$). As temperatures warm, females became active for a larger proportion of the night (Fig. 5). We have no data for July–August but note that female rats paralleled the September lull in activity for males (10% ± 9.0%), as well as the marked activity increase in December (47.0% ± 4.0%; Tukey's HSD, $P < 0.05$).

Neotoma lepida made significantly fewer trips outside the den as daily high temperatures rose ($F_{[3,437.4]} = 8.2$, $P = 0.000$; Table 1). Indeed, under "severe" conditions, the number of trips outside the den was cut almost in half (Table 1). There was no significant difference between males and females. Larger *N. lepida* engaged in fewer activity bouts overall ($\beta = -0.06 \pm 0.03$; $F_{[1,459.5]} = 5.2$, $P = 0.024$) and animals inhabiting larger mesquite "complexes" initiated more activity bouts ($\beta = 0.04 \pm 0.01$; $F_{[1,53.0]} = 34.9$, $P = 0.000$). The decrease in activity with rising temperature was quite consistent; *N. lepida* instigated 0.1 fewer activity bouts for each 1 °C increase in daily ambient temperature ($\beta = -0.08 \pm 0.03$; $F_{[3,437.4]} = 8.2$, $P = 0.000$).

Not only did *N. lepida* reduce the number of activity episodes as temperatures increased, but male and female rats spent less time active on a given bout of movement as temperatures increased (34.5 ± 3.1 vs. 22.2 ± 2.6 min after "low" and "severe" temperature days, respectively; Tukey's LSD, $P = 0.000$; Table 1). The mean duration of an activity bout following daily temperature exceeding the upper critical temperature was significantly less than that following days within the thermoneutral zone (Tukey's LSD, $P = 0.045$). This pattern was moderated by animal condition; *N. lepida* in good condition spent 4.4 ± 1.9 min more per activity bout than those in poor shape ($F_{[1,254.6]} = 5.2$, $P = 0.024$). Again, animals living in larger mesquite "complexes" invested more time in each activity bout ($\beta = 0.02 \pm 0.001$; $F_{[1,15.8]} = 9.9$, $P = 0.006$), and less time per activity bout as seasonal night length increased ($\beta = -0.04 \pm 0.01$; $F_{[1,353.8]} = 9.9$, $P = 0.002$).

Discussion

Our results strongly suggest that environmental temperature influences the activity patterns of *N. lepida* at Furnace Creek, and moreover, that the magnitude of the effect depends on gender and body mass. As temperature increased, animals have less time to spend for the essential activities of mating and foraging. Higher temperature leads not only to a reduction of nightly activity bouts, but also limits the duration of each.

Temperatures of over 50 °C can occur anytime during the spring and summer months. Indeed, between April and October, the mean daily maximum temperature at Furnace Creek, Death Valley, never drops below 35 °C. Yet, numerous studies have demonstrated that the maximum temperature in the thermoneutral zone of *N. lepida* is 35 °C and the upper lethal temperature is around 41 °C (Lee 1963; Brown and Lee 1969; Nelson and Yousef 1979).

The ability of *N. lepida* to survive in an environment that has temperatures consistently over lethal is entirely due to the den and the availability of succulent mesquite. However, *N. lepida* are unable to store sufficient forage within the den to meet water demands during the warm summer months; clipped mesquite loses virtually all of its water content within 5 h (J. Martin, personal communication, 2011). Thus, animals are forced to leave the thermal neutrality of their dens to obtain required resources even under the most extreme of conditions. Regardless, *N. lepida* did not commence nightly activities until ambient temperatures were ≤41 °C, which is at the empirically derived upper lethal temperature (Lee 1963; Brown and Lee 1969; Nelson and Yousef 1979; Fig. 3).
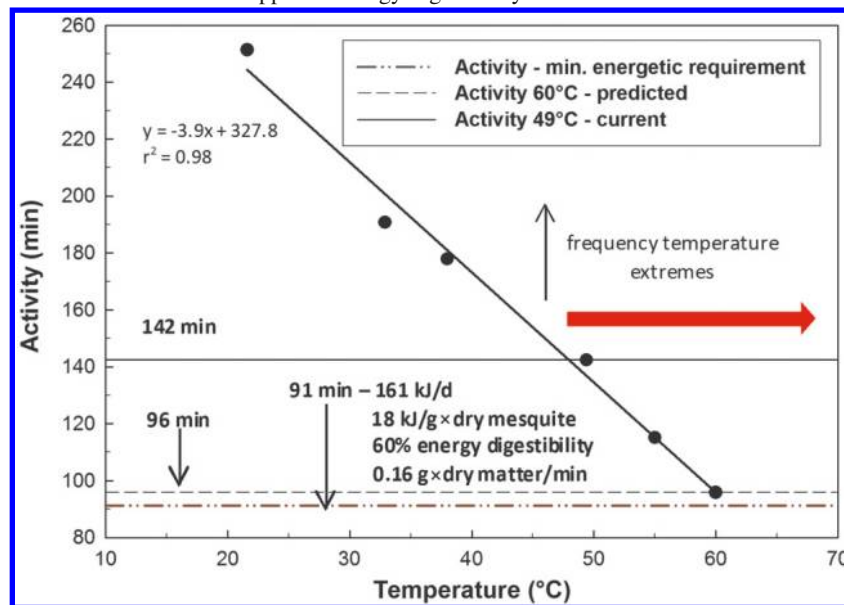
Body mass and gender of *N. lepida* are important determinants of how ambient temperature constrains the initiation and extent of activity outside of the den. Male *N. lepida* at this site are always active longer than females (Fig. 5, Table 1), and larger animals are active less and emerge later than smaller individuals. We suggest that this may be due in part to the demanding energetic requirements sustained by reproducing females. The energetic demands of reproduction are especially high in the lactating female, and one strategy that can be employed to minimize energy costs is to minimize locomotor activities (Sorensen et al. 2005a). Indeed various rodent species limit activity during peak energy requirements associated with reproduction (Slonaker 1925; Richards 1966; Randolph et al. 1977; Wade and Schneider 1992). Additionally, 5 years of trapping data suggest that female *N. lepida* at this site are under more intense thermal selection of body mass following peak summer temperatures, a phenomenon probably intertwined with the intense demands of reproduction (Fig. 3; F.A. Smith, L.E. Harding, H.M. Lease, J.T. Martin, and I.W. Murray, unpublished data), which may compel them to remain within the temperature-buffered den for longer periods of time. Male *N. lepida* are not as constrained by such high costs of reproduction enabling them to invest in behaviors such as mate searching and scent marking while occupying larger home ranges (Cranford 1977; Vaughan and Schwartz 1980; Conditt and Ribble 1997; Henke and Smith 2000; but see MacMillen 1964 and Bleich and Schwartz 1975). Indeed, individual males in this population are more likely than females to engage in long-distance movements culminating in the switching of occupied mesquite trees (H. Lease, personal communication, 2012).

In addition to body mass, body condition and home mesquite complex size were important factors influencing the onset and duration of activity. Lethal temperature scales inversely with body size in the genus *Neotoma* (Smith et al. 1995; Smith and Charnov 2001), thus it is not surprising that the larger *N. lepida* were forced to emerge from their dens later and engaged in less outside activity. For each 1 g increase in body mass, there was a 2.5 min reduction in nocturnal activity. Large males (>160 g) were, on average, active 65 min less each night and emerged 23 min later, relative to small males (<160 g). Furthermore, at a specific temperature, rats in better body condition were active for 40.7 ± 12.7 min longer per night and 5.1 ± 2.0 min per activity bout than those in poor body condition. Rats in poor condition generally had patchy, dull pelage and a thin and bony overall feel to them. Rats in this state may minimize the proportion of their time devoted to intraspecific interactions and (or) re-

Table 2. Hypothetical lost opportunities for energy and water intake associated with reductions in activity of desert woodrats (*Neotoma lepida*).

Activity reduction	Mesquite leaf energy (kJ/g dry matter)	Mesquite leaf water (% water by mass)	Intake per unit time (g dry matter/min)	Intake per meal (g dry matter/meal)	Energy loss (kJ)	Water loss (g)
49 min	18.35	46.3	0.16	—	86.3	6.8
2 activity bouts	18.35	46.3	—	0.36	8.0	1.3

Note: We assume that a single activity bout equates to one meal. Intake rate data are drawn from Sorensen et al. (2005*b*) captive *N. lepida* of 125 g. Energy content of leaves of honey mesquite (*Prosopis glandulosa*) from Baptista and Launchbaugh (2001) and leaf water content is J. Martin (personal communication, 2011).

Fig. 6. Predicted reductions in activity of the desert woodrat (*Neotoma lepida*) under scenarios of increased temperatures, given the observed relationship between ambient temperature and activity. Minimal energetic requirements for a 125 g *N. lepida* are 161 kJ, which necessitates 91 min of feeding given published intake rates and apparent energy digestibility.

quire longer periods of time within the thermally buffered den to maintain homeostasis, which results in reduced activity.

The canopy area of mesquite trees occupied by *N. lepida* was also an important determinant of activity. Individuals living in larger home complexes were active for 0.02 ± 0.007 min per activity bout, initiated 0.04 ± 0.006 more activity bouts, and were 0.2 ± 0.08 min more active per night for each metre increase in home complex area (213–1216 m^2; area measured using Google Earth). Larger complexes presumably offer better predator protection (I.W. Murray, personal observation) and probably have better thermal buffering capacity in the form of older, more established den sites, as well as greater canopy coverage, to buffer against daily high temperatures. Also, larger complexes simply hold more dens. Animals living within "good" complexes such as these probably invest more time making territorial rounds of their home territory and may encounter and engage in more rat–rat interactions as a result of the larger area of mesquite occupied.

Our results suggest the warming climate over the next decades will likely influence the fitness of *N. lepida* in Furnace Creek, Death Valley. Annual temperatures in California are projected to increase up to 5 °C over the next century (Cayan et al. 2009). Mean maximum July temperatures (the hottest month of the year) have already risen almost 1.0 °C over the last 2 decades (Roof and Callagan 2003). Indeed, the mean maximum temperature for every day in July has increased over the past 20 years, relative to the almost 100 year mean maximum temperatures (Roof and Callagan 2003).

Warmer temperatures correlated with decreased time spent outside of the den for both males and females. The reduction in activity we found (Table 1) shortens drastically the time available for meeting energy and water requirements. For example, field and laboratory studies suggest that a typical 125 g adult *N. lepida* requires 161 kJ/day and 5.0 g H$_2$O/day just to maintain body mass (Lee 1963; Karasov 1989; Schmidt-Nielsen 1997). *Neotoma lepida* have dry matter feeding intake rates of 0.16 g/min and 2.89 g·meal^{-1}·kg^{-1} (Sorensen et al. 2005*b*) and an apparent energy digestibility of approximately 60% (Karasov 1982, 1989; Smith 1995*b*). Given that a "severe" temperature day resulted in a reduction of activity by 49 min and 2 activity bouts (Table 1), this corresponds to a potential loss of opportunity to gain 86.3 kJ of energy and 6.8 g of water (for a loss of 49 min; Table 2). This is a substantial amount, representing 54% of the energy and 136% of the total daily water requirements of a 125 g animal (minus losses in feces and urine, and not taking into account metabolic water production). Furthermore, our calculation ignores the potential loss of water and energy required for maintaining homeostasis in the face of foraging in extreme temperature. Clearly, even warmer temperatures could more greatly influence this physiological balance. At

some point, the trade-offs must be great enough that remaining in the den despite a lack of water or forage is preferable. Larger animals are more susceptible to the potentially negative effects of high temperatures, and likely face stiffer trade-offs. Indeed, we found a significant difference in the body mass of animal trap moralities in the summer vs. winter months. Although small individuals were more likely to die in traps during the winter, this pattern was reversed in the summer months (104.8 ± 4.4 vs. 121.7 ± 6.4 g, respectively; Student's t test, $t_{[22]} = 2.07$, $P = 0.04$). Despite our hourly checks of traps, these mortalities could represent animals forced to remain away from the thermal safety of their dens for longer than was physiologically possible given the temperature extremes. Additionally, our monthly trapping data clearly indicates a seasonal pattern of mass with temperature (Fig. 3).

Water in particular may be the driving force behind the continuation of foraging despite extreme temperatures. *Neotoma lepida* in Death Valley meet their relatively high water requirements through a dependence on freshly clipped mesquite (J. Martin, personal communication, 2011). To illustrate these high water requirements, at a temperature of 39 °C, Nelson and Yousef (1979) recorded evaporative water losses over 5.0 mg H_2O/mL O_2 in *N. lepida*. These values are considerably higher than those of other rodent species (Schmidt-Nielsen and Schmidt-Nielsen 1950; Hudson 1962; Tucker 1965; Breyen et al. 1973; Bradley et al. 1975). On multiple occasions at our study site, we observed heat-stressed *N. lepida* profusely coating the anterior portions of their body with saliva. This undoubtedly helps alleviate heat loads, but presumably produces water deficits potentially detrimental to fitness. Any factor, such as increasing ambient temperature, which constrains the time spent outside of the den makes homeostasis more difficult to achieve. Interestingly, larger animals should be better able to withstand water deprivation because of their higher mass (Peters 1983; Calder 1984); this may help explain why animals are so large on this site (Smith and Charnov 2001).

A major emphasis of much of modern science is to understand how organisms will respond to the warmer temperatures, drier conditions, and more frequent extreme weather predicted over coming decades. *Neotoma lepida* at Furnace Creek are already operating at close to their thermal limits. Higher summer temperatures may further restrict activity outside of the den, thus compromising the survivorship and fecundity of animals on the site. For example, activity of *N. lepida* is reduced to 115 min at 55 °C and 96 min at 60 °C, scarcely accommodating the time required to intake the minimal amount of mesquite necessary to meet energetic requirements (Fig. 6). Indeed, our computations suggest that this unique population of rodents may be unable to persist under the most pessimistic of climate change scenarios.

Acknowledgements

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