

Life in an extreme environment: a historical perspective on the influence of temperature on the ecology and evolution of woodrats

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The heterogeneous topography of the Great Basin province leads to one of the most climatically variable regions in the Northern Hemisphere. Along the southwestern edge lies Death Valley, an area of even more extreme climate and physiographic relief; Death Valley has the dubious distinction of being the hottest place on earth. Our research investigates the adaptive response of *Neotoma* (woodrats) to temperature fluctuations over the late Quaternary on the valley floor and along a nearby elevational and environmental gradient. By combining fieldwork on extant animals living on the valley floor with historical information from museum specimens and paleomiddens, we reconstruct the evolutionary histories of 2 species (*N. lepida* and *N. cinerea*) differing significantly in size and habitat preferences. Here, at the modern limit of both species' thermal and ecological thresholds, we find fluctuations in body size and range boundaries over the Holocene as climate shifted. Although *N. cinerea* is extirpated on the east side of the valley today, it was ubiquitous throughout the late Quaternary. Moreover, we find fundamental differences in the adaptive response of woodrats related to elevation and local microclimate. Modern work suggests the mechanism is physiological; exposure to consistently high temperatures leads to high mortality. Thus, high temperatures strongly restrict time available for the essential activities of foraging and mating. Our results illustrate the profound influence temperature has on all aspects of woodrat life history, ecology, distribution, and evolution.

Key words: adaptation, body-size evolution, climate change, Furnace Creek, late Pleistocene, Titus Canyon

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Yesterday afternoon I put out 49 rodent traps thru the big mesquites and sand-dunes south of the ranch about 1½ miles. Absolutely the only vegetation in sight for hundreds of yards is the mesquite It would appear that the mesquite foliage and beans, and the insects [that] live on these and in the wood of dead trunks and branches (which are abundantly bored) furnish the prime food supply of all the vertebrates in that tract. Wood rat sign is abundant, consisting of small accumulations of mesquite twigs, pieces of [illegible word] and cow and horse manure Many cut-off twig ends high in the mesquites show that the wood rats climb all over these trees . . .

—Field notes of Joseph Grinnell, 10 April 1917

Archives of the Museum of Vertebrate Zoology, University of California, Berkeley

The Great Basin is a unique and striking region of North America. The basin-and-range topography, which is characterized by literally hundreds of parallel-running mountain ranges interposed with deep valleys, leads to substantial physiographic relief, and not surprisingly, quite variable environmental conditions (Hunt 1967; King 1977; Fiero 1986). At the southwestern edge of the geological province lies Death Valley, an extreme region in this already heterogeneous landscape. Death Valley is an ~250-km basin located between 2 major block-faulted mountain ranges, the Amargosa on the east side and the Panamint on the west side. It contains the greatest physiographic relief in the contiguous United States; the gradient from Badwater (–86 m) to Telescope Peak (3,392 m) rises some 3,479 m within a scant 24 km (Fig. 1). Because



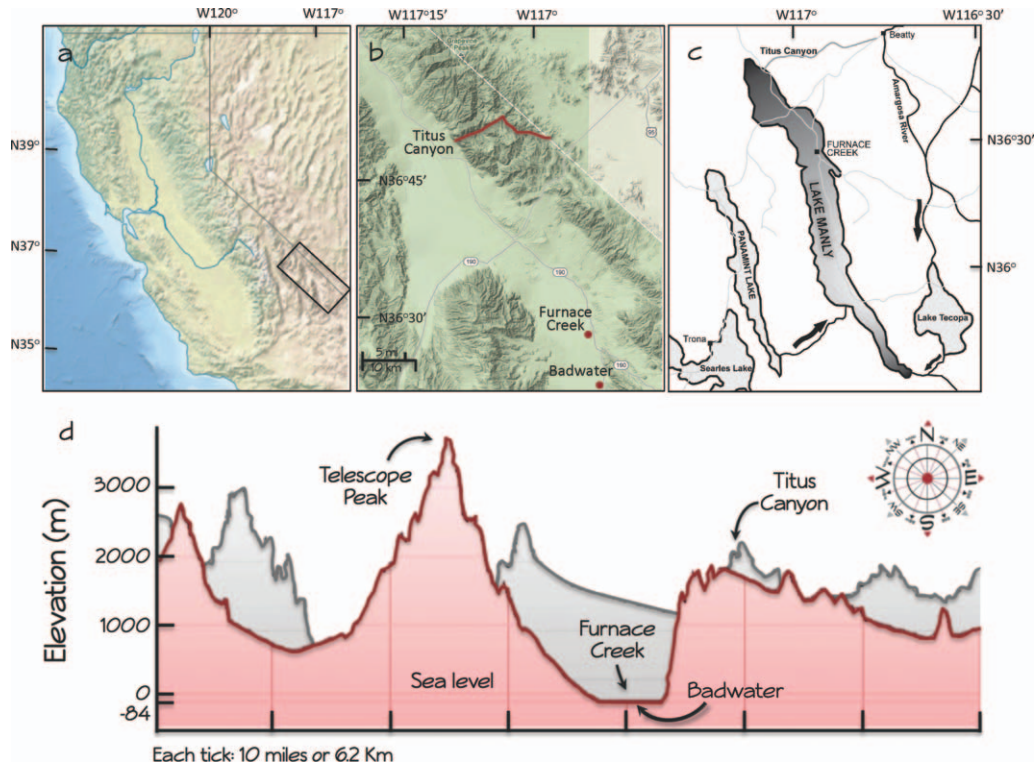


FIG. 1.—Location of study sites. a) Death Valley National Park, California. The park is situated in the southwestern edge of the Great Basin geological province and lies between the Panamint Mountains on the west, and the Amargosa Range on the east. b) Location of 2 study sites within the valley. Paleomiddens were collected during 2006, 2007, and 2009 along a 1,500-m elevational transect following Titus Canyon; livetrapping was conducted during 2003–2008 in mesquite thickets at Furnace Creek. c) Reconstruction of the Lake Manly lake system as it would have appeared during the Last Glacial Maximum (~21,000 years ago). Selected roads (lines) and towns (dots) are shown for context; arrows indicate direction of water flow. Note the location of the Furnace Creek and Titus Canyon study sites. Redrawn after United States Geological Survey image from Wikipedia Commons (http://en.wikipedia.org/wiki/File:Lake_Manly_system.png; National Park Service 2013). d) A composite elevational profile for 2 parallel due-west geographical transects. The transect in pink bisected the highpoint of the Panamint Mountains, Telescope Peak, as well as the low point in Death Valley, Badwater Basin (−86 m). The gray transect bisects just north of Titus Canyon. Elevational profiles were constructed using due-west paths created in Google Earth and were standardized for distance and elevational gain. The extreme topography leads to significant heterogeneity in habitats as well as climate.

of the extreme topography, Death Valley lies in a severe rain shadow, which coupled with below-sea-level elevation, contributes to a hyperarid climate. Indeed, Death Valley has the dubious distinction of being the hottest place on earth (El Fadli et al. 2013), with maximum temperatures regularly exceeding 50°C during the summer months (Western Regional Climate Center 2013).

Living in the hottest place on earth poses significant challenges to animals (Fig. 2). The intense heat is coupled with highly irregular annual precipitation averaging only 4.8 cm/year (Western Regional Climate Center 2012; Fig. 2). It is not just the extreme heat—temperatures of up to 57°C (134°F) have been recorded in the shade (Roof and Callagan 2003)—but also the duration of heat episodes. In 2001, for example, Death Valley experienced 154 consecutive days with temperatures at or above 38°C (100°F—Western Regional Climate Center 2012). Such severe climatic occurrences are likely to become more common over the next few decades. The recent report by the Intergovernmental Panel on Climate Change (2012) on extreme events concluded: “Models project

substantial warming in temperature extremes by the end of the 21st century. It is virtually certain that increases in the frequency and magnitude of warm daily temperature extremes and decreases in cold extremes will occur in the 21st century at the global scale. It is very likely that the length, frequency, and/or intensity of warm spells or heat waves will increase over most land areas. Based on the A1B and A2 emissions scenarios, a 1-in-20 year hottest day is likely to become a 1-in-2 year event by the end of the 21st century in most regions.” In short, Death Valley is likely to become even more thermally challenging in upcoming decades.

Despite such harsh conditions, a number of vertebrates live on the valley floor, some 84 m below sea level. One of these is the desert woodrat (*Neotoma lepida*). This is surprising because, despite the species’ common name, desert woodrats are not especially well adapted for desert life. Not only is *N. lepida* highly sensitive to environmental temperature with relatively low lethal upper temperatures of 38–41°C (Lee 1963; Brown 1968; Brown and Lee 1969; Smith et al. 1995; Smith and Charnov 2001), but it lacks specialized physiological



FIG. 2.—Death Valley. *Looking across desert toward mountains, Death Valley National Monument, California*, image taken by famed photographer Ansel Adams around 1941. This image was part of a series of photographs commissioned by the National Park Service in 1941. Ansel Adams was tasked with creating a photo mural for the headquarters of the Department of the Interior in Washington, D.C. The theme was “nature as exemplified and protected in the U.S. National Parks.” Sadly, World War II intervened and the project was never completed. Photograph courtesy of the National Archives and Records Administration. Note the unusual presence of water on the valley floor; both 1940 and 1941 (particularly the latter) were exceptional wet years with some of the highest recorded precipitation in the 100-year record. Rainfall was more than ~50–75% above the long-term average (Western Regional Climate Center 2012).

adaptations to heat common in other desert-dwelling mammals. These include the inability to produce highly concentrated urine or estivate during unfavorable conditions as well as the lack of a countercurrent water recovery system in the nasal cavity (Schmidt-Nielsen and Schmidt-Nielsen 1950; MacMillen 1964; Tracy and Walsberg 2002). Moreover, woodrats depend on green vegetation for water (Schmidt-Nielsen 1964). Like humans, the survival of *N. lepida* in desert habitats is entirely dependent on its ability to construct “houses.” All species of woodrats build these—complex structures of locally gathered debris that can exceed several meters in height and diameter. Houses serve as important thermal refuges, ameliorating air temperature by as much as 9°C (Brown 1968); they also provide significant protection against predators (Vorhies 1945; Lee 1963; Brown 1968; Smith 1995). Yet, woodrats need to leave their homes to forage and mate and, consequently, are still exposed to above-lethal temperatures for months on end. Thus, the question remains—how and why did woodrats come to inhabit such an extreme environment?

Part of the answer lies in past history: Death Valley wasn’t always such an inhospitable place. During the late Quaternary, pluvial Lake Manly covered much of the valley floor and contributed to a much more moderate climate (Fig. 1c). Even at the beginning of the Holocene (~10,000 years ago), the lake

was 90 m deep (Li et al. 1996; Lowenstein et al. 1999). Many vertebrates colonized when the climate was milder, wetter, and more hospitable; both fossil and molecular evidence suggest that *N. lepida* on the valley floor dispersed into this region from southern California some 50,000–100,000 years ago (Patton and Álvarez-Castañeda 2005; Patton et al. 2008). Analysis of paleomidden data suggests that summers during the late Pleistocene were probably about 8–14°C cooler (Woodcock 1986; Koehler et al. 2005; Smith et al. 2009) and that juniper woodlands extended much lower in elevation than today. The immigration of the flora characteristic of the valley today (e.g., mesquite, creosote, and burrobrush) only occurred after deglaciation at the terminal Pleistocene (12,000–10,000 years ago). With the evaporation of Lake Manly in the Holocene came dramatic shifts in temperature, aridity, and vegetation. Thus, the shift from the pluvial woodlands and cool semidesert to the modern hyperarid ecosystem is relatively recent; it was likely established only during the mid-Holocene (Wells and Woodcock 1985; Woodcock 1986; Spaulding et al. 1990).

Here we report on research investigating the trade-offs associated with living in the hottest place on Earth. Our work employs temporal windows of varying size and resolution and focuses on *Neotoma*, which are extant today in the area and also have a detailed historic record. By utilizing fieldwork,

museum specimens, and paleomiddens, we are able to integrate modern and historical perspectives to investigate the adaptive response of woodrats to temperature. Specifically, we address 2 main questions. First, how do desert woodrats on the valley floor cope with consistently lethal temperatures? What life-history or ecological trade-offs make such an existence possible? We address these questions with a series of field studies conducted from 2003 to 2008. Second, how did the climate shifts of the late Quaternary, which resulted in the establishment of the modern habitat, influence the distribution and evolution of woodrats in this region? To address this question, we employ a chronosequence of paleomiddens produced by 2 woodrat species differing in their habitat and physiological tolerances: desert woodrats (*N. lepida*) and bushy-tailed woodrats (*N. cinerea*). Paleomiddens were collected during 2006, 2007, and 2009 along an elevational transect in Titus Canyon, and they provide a highly resolved historical record extending some 32,000 years.

MATERIALS AND METHODS

Study Animals

Our work focuses on 2 species of woodrats: *N. lepida*, the desert woodrat, and *N. cinerea*, the bushy-tailed woodrat. Although both are found in Death Valley National Park, they differ significantly in body size and habitat preferences. *N. cinerea* is a large, montane-adapted species found on the west side of the valley in the Panamint Range at elevations of ~1,800 m to above tree line (Grinnell 1937; Smith 1997). *N. lepida* is a much smaller animal inhabiting desert and semidesert environments from the valley floor to ~1,800-m elevation on the mountain ranges surrounding the basin (Grinnell 1937; Verts and Carraway 2002). Areas of potential sympatry are restricted because of the marked differences in body size and habitat requirements; today sympatry is confined to a narrow band at ~1,800- to 2,000-m elevation on the west side of Death Valley (Smith et al. 2009; Fig. 1). Although *N. cinerea* is completely absent from mountainous regions on the east side of Death Valley today, earlier work confirmed its widespread occurrence down to about 1,000 m during the full glacial (Smith et al. 2009).

Woodrats are the poster child for Bergmann's rule, the ecogeographic principle relating body size and environmental temperature (Bergmann 1847; Mayr 1956; Brown and Lee 1969). Numerous studies have illustrated that the body mass of populations of woodrats closely tracks environmental temperatures over both time and space, although the response varies by species (Brown 1968; Brown and Lee 1969; Smith et al. 1995, 1998; Smith and Charnov 2001; Smith and Betancourt 2003, 2006). The underlying mechanism is likely primarily physiological; lethal temperature scales inversely with animal body mass (Brown 1968; Smith et al. 1995; Smith and Charnov 2001). Because body mass is highly heritable, much of this response is probably genetically based (Smith and Betancourt 2006).

Woodrats also are remarkable because of the historical record they archive. All species construct houses or dens of varying complexity containing 1 or more middens, or debris piles. Middens consist largely of plant fragments, copious fecal pellets, and other materials picked up by the animals, leading to their other common name, "packrat." Because the animals urinate on the piles, in the arid desert southwest, materials quickly become embedded in desiccated, crystallized urine, which is often referred to as "amberat" because it has some of the same preservative qualities as amber. The documentary quality is high because the amberat leads to long-term preservation of organic materials, including DNA. Middens constructed in open habitat are generally not preserved because of exposure to climatic conditions. However, if sheltered in caves or deep rock crevices, deposits may persist for thousands of years; age can readily be determined by radiocarbon dating. Such paleomiddens provide valuable historical insights into ecology and evolutionary history. For example, examination of plant macrofossils has allowed reconstruction of the vegetation history of the southwestern United States over the late Quaternary (e.g., Wells and Jorgensen 1964; Wells and Berger 1967; Van Devender 1977; Van Devender and Spaulding 1979; Betancourt and Van Devender 1981; Betancourt et al. 1990, and references therein). Middens constructed by the 2 study species can be readily distinguished both by the large and nonoverlapping difference in fecal pellet size (Smith and Betancourt 2006) and by microscopic identification of the molars frequently incorporated within the samples.

The fossilized fecal pellets also yield valuable information. In earlier work, we established that a robust relationship exists between pellet width and woodrat body mass (Smith et al. 1995; Smith and Betancourt 2006). Because caves and mountain ranges may contain many distinct paleomiddens, each of which contains hundreds to thousands of fecal pellets, we can examine patterns of woodrat population body mass change over time (Smith et al. 1995; Smith and Betancourt 1998, 2003, 2006). Our most resolved chronosequences contain > 10–40 radiocarbon-dated middens extending from the full glacial to present.

Study Sites

Here we discuss 2 parallel studies: a paleomidden project conducted in the mountain ranges surrounding Death Valley and a mark–recapture project conducted on the valley floor. The paleomiddens discussed here were all collected from Titus Canyon (36°49'N, 117°08'W), a deep, narrow gorge cut into the steep face of the Grapevine Mountains (Amargosa Range) on the east side of Death Valley (Figs. 1b and 1d). Much of lower Titus Canyon is composed of Cambrian limestone deposited when Death Valley was submerged beneath tropical seas in the Paleozoic (Collier 1990). The canyon is quite narrow and the lower portions are composed of massive beds of dolomite and limestone with some tightly cemented limestone–dolomite breccia. The upper canyon (> 1,200–1,400 m) tends to be characterized by massive cliffs of olive-colored conglomerate and tuffaceous sandstone. Paleomiddens

were collected in 2006, 2007, and 2009, mostly from dolomite or limestone caves or crevices, and many had visible juniper on the surface indicating probable Pleistocene age. Modern vegetation in this area consists of Mormon tea (*Ephedra viridis*), creosote (*Larrea tridentata*), blackbrush (*Coleogyne ramosissima*), and other arid-adapted plants.

Our field site was located on the valley floor at an elevation of -77 m (Figs. 1b and 1d). It was an ~ 10 -ha plot of scattered honey mesquite (*Prosopis glandulosa*), located ~ 2 km northwest of the Furnace Creek Ranger Station ($36^{\circ}28'N$, $116^{\circ}52'W$). The site is located between the base of a large alluvial fan extending from the Funeral Mountains to the east and a salt pan occupying ~ 520 km² on the valley floor (Hunt et al. 1966). The extremely arid conditions lead to a complete lack of an herbaceous understory; *P. glandulosa* is almost the only vegetation ever present in the study area. The mesquite grows in long, linear "rows," tracking the relatively shallow subsurface water. The mesquite is able to exist in this environment because of a massive central taproot, which can extend up to 53 m below the surface (Phillips 1963; Wilson et al. 2001). Desert woodrats (*N. lepida*) build their dens at the bases of the mesquite and rely solely on it for shelter, food, and water.

Furnace Creek Protocols

Animal trapping.—We identified 40 large mesquite "complexes" on our main site that were trapped approximately monthly from 2003 to 2008. We characterized these as complexes because the dense and almost impenetrable brush, coupled with the multitrunked mesquite, often made it difficult to determine how many individual plants or woodrat dens were in each. In each complex, we permanently wired 3–12 Sherman live traps (H. B. Sherman Traps, Inc., Tallahassee, Florida) to branches located 2–4 m up in the mesquite canopy. The number of traps was proportional to the complex size. The orientation of traps was necessitated by high coyote activity, which led to the swift loss of traps placed on the ground or lower in the branches of the mesquite. Runways and clipped vegetation clearly indicated that desert woodrats were using branches as transport and feeding locations. The site was visited monthly and trapped for 3 consecutive nights for a total of ~ 500 trap nights/month, or 19,500 trap nights over the duration of the study. Traps were baited with apple and during cooler months both oatmeal and insulating polyester batting were included. The extreme conditions required some modification to our trapping protocol during the summer months. From late May until September traps were not opened until 2220 h because of high temperature and traps were checked every 60 min or less; animals began dying from hyperthermia if forced to remain outside the den for longer periods.

Upon initial capture, we individually marked animals with numbered fingerling tags clipped onto each ear (model 1005-1; National Band and Tag Company, Newport, Kentucky). At each subsequent capture, we recorded mass, sex, and reproductive status, and assessed body condition or injuries.

We worked under supervision of the Animal Care and Use Committee of the University of New Mexico, and followed appropriate guidelines of the American Society of Mammalogists as outlined by Sikes et al. 2011 (protocol 08UNM073-TR-100489; National Park Service permit DEVA-2004-SCI-0031).

Characterization of activity.—To examine the influence of temperature on activity patterns, we attached miniature temperature data-loggers (Thermochron i-Buttons, model DS1921G; Dallas Semiconductor, San Jose, California) on a subset of adult *N. lepida* ($n = 56$) in both 2006 and 2007. The i-Buttons were set to record at 15-min intervals and could record temperature for ~ 22 days before reaching storage capacity. The use of i-Buttons allowed us to passively record activity patterns of naturally behaving desert woodrats over extended periods of time. Because for most of the year the thermal environment outside the den was so much warmer than inside, we were able to determine where animals were by recorded temperature. Hence, we were able to characterize the onset and duration of foraging and other movements. Here, we focus on the activity patterns for the summer months. We computed the time spent outside the den and the number of activity bouts for each rat as a function of temperature. For further details of i-Button methodology, analysis, and results, see Murray and Smith (2012).

Historical Records

Death Valley has long been a source of interest to naturalists. C. Hart Merriam, Albert K. Fisher, and Vernon Bailey were all members of the Death Valley expedition of 1891, which spent almost 6 months exploring the region (Palmer 1891). They were followed by mammalogists such as Joseph Grinnell and Alden Miller, who trapped extensively along the basin and in the surrounding mountains (Grinnell 1937; Miller 1946; Fig. 2). We examined the adult desert woodrat specimens collected by these earlier naturalists and recorded measurements of body size (length exclusive of tail, and body mass, if provided). Specimens were stored at the National Museum of Natural History (Smithsonian), Museum of Vertebrate Zoology (University of California Berkeley), and the Museum of Southwestern Biology (University of New Mexico). Because of the steep environmental gradient, we restricted our analysis to *N. lepida* trapped at Badwater (-86 m), Furnace Creek (-77 m), or Triangle Springs (-13 m); the collection date spanned January 1891 to present. Body mass in woodrats is normally distributed and moreover, woodrats are sexually dimorphic. Thus, to obtain a reasonable approximation of population size, we further restricted our analysis to years where 9 or more specimens were recovered from a location (sample size varied between 9 and 46) and the sex ratio was approximately equivalent. We use length for the analyses presented here because it was reported for all animals. Length is significantly related to mammal body mass, with a 1% increase in length corresponding to an $\sim 3\%$ increase in mass (McMahon 1973; Smith 1992).

Paleomidden Analysis

Some 94 paleomiddens were collected in close proximity in 2006, 2007, and 2009 along a 1,500-m elevational transect spanning the mouth of Titus Canyon (~200 m) to just below the ghost town of Leadville (~1,700 m) through the Grapevine Mountains within the Amargosa Range (Fig. 1b). Details of the 72 paleomiddens we collected in 2006 and 2007 were reported in Smith et al. (2009). Paleomiddens were collected from recessed rock shelters or caves mostly within limestone formations; sites were georeferenced and permanently marked with metal tags. Middens were carefully cleaned in the field to remove surface contamination and to ensure that they represented a cohesive temporal sample. Most were produced by *N. cinerea*, although some younger Holocene middens were constructed by *N. lepida*.

In the laboratory, samples were cleaned further as necessary, weighed, and vouchers removed for pollen analyses and archival purposes. In general, processing followed the well-established methods of Spaulding et al. (1990). The bulk sample was disassociated by soaking in 14-liter buckets for 2–14 days, and then power washed and wet-sieved to remove nonorganic debris. The remaining damp organic matter was dried at ~60°C in a forced-draft oven for 1–2 days and then dry sieved through a series of standard 1-mm (No. 10) and 2-mm (No. 18) stainless steel mesh geological sieves. Each fraction was subsequently hand-sorted to remove fossil pellets from plant macrofossils and other matrix materials. A series of 32 middens was selected for radiocarbon dating based on their integrity, size, elevation, and visible surface macrofossils. Dates were determined on fecal pellets using a tandem accelerator mass spectrometer at the University of Arizona National Science Foundation Accelerator Facility. Radiocarbon ages were converted to calendar years (years before 1950) using the Fairbanks0107' calibration curve (Fairbanks et al. 2005).

After processing, we measured the width of all intact fossil pellets greater than 4 mm (equivalent to an ~90-g animal) to the nearest 0.1 mm using digital calipers. Sample sizes were typically in the hundreds or thousands of pellets. The mean of the largest 20 was computed and body mass was estimated from this value. For further details on midden processing or validation studies see Smith and Betancourt (2006) or Smith et al. (2009).

Climatic Records

We used 2 sources to characterize temperature for the Furnace Creek study site. First, we empirically recorded temperatures at a variety of heights within the mesquite canopy. We placed i-Buttons at 0.3 m and 2.0 m from the ground within several mesquite trees. These heights are biologically relevant because they represent the height of woodrat dens and the foraging trails of the rats, respectively. Second, we employed climate information both from the Western Regional Climate Center (2012) and a data set compiled by Roof and Callagan (2003). From these sources we

developed a record of daily and monthly maximum, minimum, and mean temperatures for the site.

Climatic data for the museum analysis also were obtained from the Western Regional Climate Center (2012). However, records extending back to the 1800s are rare and the record for Death Valley only extended to 1948. One of the few locations in the western United States that had detailed temperature information spanning > 120 years was St. George, Utah. Because a robust relationship existed between St. George and Death Valley for the ~50 years of overlapping records (slope = 0.912, $P < 0.000$, $r = 0.7$, $df = 45$), we calculated deviations from the long-term mean for each and used the temperature anomalies in our analysis. Data from St. George were only used when anomalies for Death Valley were not available; the use of St. George throughout did not qualitatively change the results of our analysis. Calculated body mass (or length) for Death Valley desert woodrats was compared with mean January and July temperatures; these represent the coolest and warmest months in the Northern Hemisphere, respectively.

Regional paleoclimatic data did not extend far enough back in time, nor were they of sufficient resolution, for us to compare directly with woodrat body mass as calculated from paleomiddens. Thus, we employed several ice core records that estimate temperature from oxygen isotopes trapped within air bubbles. We did not use actual temperatures, but rather anomalies or deviations from modern temperatures at the site. We used both the EPICA (European Project for Ice Coring in Antarctica) and GISP2 (Greenland Ice Sheet Project) records, which are located in the Southern Hemisphere and Northern Hemisphere, respectively (Dahl-Jensen et al. 1998; Jouzel et al. 2007). The EPICA record, in particular, is quite highly resolved and spans some 800,000 years with almost decadal resolution (Jouzel et al. 2007). To determine the mean temperature anomalies during the deposition interval of a midden, we averaged all values falling ± 50 years of the calendar date of the paleomidden. Although use of a global temperature necessarily smooths out important regional fluctuations, it does provide a conservative and long-term record of temperature over the late Quaternary.

Statistical Analyses

We used SPSS version 20 and ProFit version 6.2.8 statistical software (QuantumSoft 2010; IBM Corporation 2011) for all analyses. To examine the influence of temperature on woodrat body size, regressions were conducted using various temperature metrics. For the paleomiddens, we used a 100-year annual anomaly from modern temperature, for the historical records, we used mean January and July temperature anomalies from the long-term average (> 50 years), and for the modern study, we employed mean, mean maximum, and mean minimum January and July temperatures. These represent the coldest and hottest months in the Western Hemisphere, respectively. When possible, analyses were conducted separately for males and females as well as a pooled sample. It is not possible to differentiate between the sexes for paleomiddens. Analyses of variance, linear mixed-effects models, and

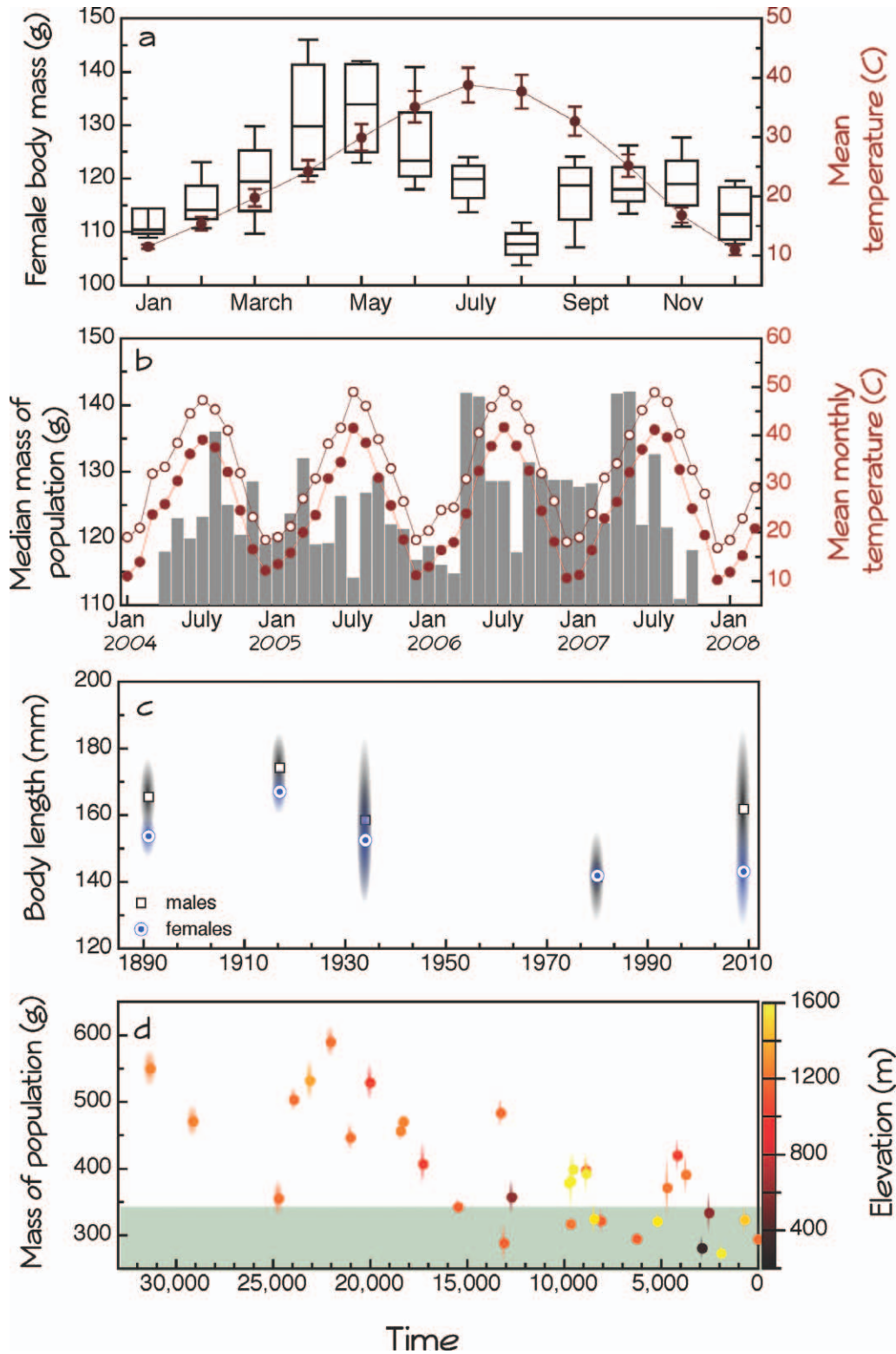


FIG. 3.—Variation in adult woodrat body size over various timescales. a) Box plot of body mass of female woodrats (*Neotoma lepida*) from Furnace Creek (2003–2008); data generally represent a 4-year average. Also plotted is the mean monthly temperature over the period of record. Error bars represent 95% confidence intervals. b) Median mass of the Furnace Creek population from 2003 to 2008 (gray histogram). Also plotted are mean (closed circles) and maximum (open circles) temperature for each month. Note that mean maximum temperature exceeds 41°C for 3–4 months every year. c) Mean body length of museum specimens of *N. lepida* collected at various low-elevation sites on the valley floor from 1891 to 2008. Each datum represents the average of 9 to > 40 individuals; males (open squares) and females (open circles with dots) are plotted separately. Woodrat body mass scales as the cube of length, so fluctuations represent considerable differences in mass. Values are plotted with

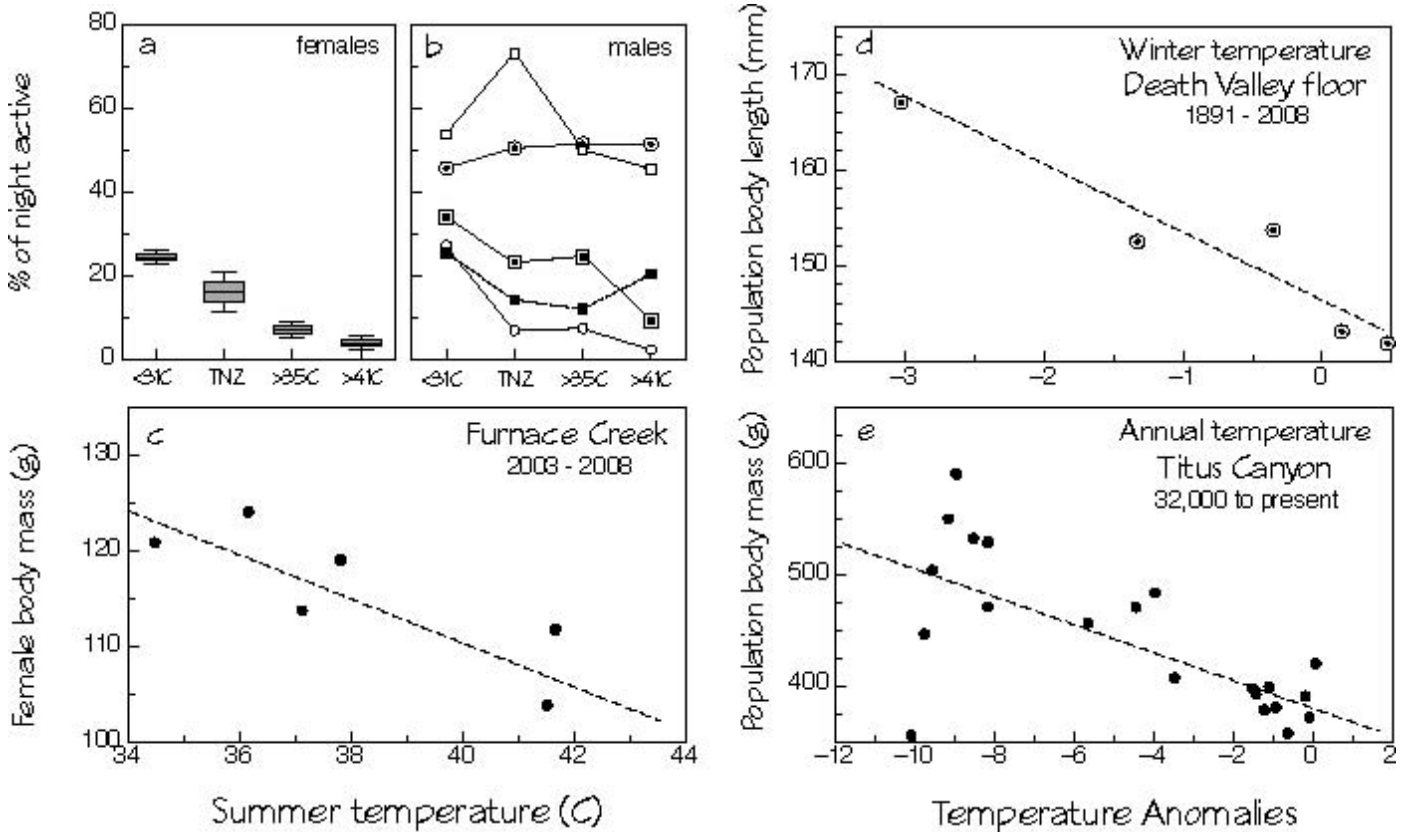


FIG. 4.—Influence of environmental temperature on woodrats at various scales. a) Influence of temperature on activity levels of female desert woodrats (*Neotoma lepida*) at Furnace Creek during the summer. Bins represent biologically relevant temperature thresholds for woodrats; TNZ is the thermal neutral zone (see text for details). b) Influence of temperature on activity levels of male desert woodrats at Furnace Creek during the summer. Because the response is more heterogeneous than for females, data are presented for individual males. c) Median female body mass of woodrats at Furnace Creek during the summer months. Temperature is mean for the previous month. Equation of line (with standard error of the estimate): $y = -2.1 (\pm 0.70)x + 195.2 (\pm 26.62)$; $d.f. = 5, r = 0.832, P < 0.04$. d) Body length of museum specimens of *N. lepida* (Fig. 3b) plotted against winter temperature anomalies. Patterns were stronger for females than for males, and for winter over summer anomalies (Table 1). Anomalies represent deviations from the long-term (> 50 years) record. Equation of line (with standard error): $y = -7.25 (\pm 0.49)x + 144.35 (\pm 0.817)$; $d.f. = 4, r = 0.995, P < 0.005$. e) Body mass of population of *N. cinerea* from Titus Canyon plotted against 100-year averaged temperature anomalies centered on the age of the paleomidden. Equation of line (with standard error of the estimate): $y = -0.01 (\pm 0.002)x + 1.11 (\pm 0.011)$; $d.f. = 33, r = 0.602, P < 0.0001$.

chi-square goodness-of-fit tests were conducted to examine survivorship and activity patterns. Statistical treatment and analysis and results of i-Button records are fully described in Murray and Smith (2012).

RESULTS

At all temporal and spatial scales, we found significant relationships between adult woodrat body mass and environmental temperature (Figs. 3 and 4; Table 1). Below we discuss

these results from a hierarchical framework ranging from a local, short-term perspective to a regional, long-term one.

Furnace Creek

Animal trapping.—Over the course of the study, we trapped 521 desert woodrats at Furnace Creek, 80.8% of which were adults. The sex ratio was approximately equal ($n = 278$ females, $n = 243$ males). Animals exhibited high site fidelity, with the vast majority of adult captures (> 85%) at the same or the adjacent mesquite complex and often even at the same trap (H. M. Lease,

95% confidence interval clouds. d) Chronosequence for paleomiddens recovered from Titus Canyon. Time is shown in calibrated calendar years before present (1950). The record extends some 32,000 years; the Last Glacial Maximum (LGM) was 21,000 calendar years ago. Body mass was estimated from the mean of the 20 largest fossil fecal pellets measured in each midden (see text for details). Values are plotted with 95% confidence interval clouds in both directions; if not visible, error is less than the size of the datum. Elevation of the midden is represented by color. The shaded area represents the range of maximum body mass of desert woodrats (*N. lepida*). Note the extremely large body mass of the population during the LGM.

TABLE 1.—The influence of temperature on woodrats in Death Valley, California.

Location	Species	Age range	Elevational range (m)	Metric	Temperature metrics examined		Comment ^a
					Fossil fecal pellets	Mean annual temperature	
Titus Canyon	<i>Neotoma lepida</i> and <i>Neotoma cinerea</i>	33,000 to modern	298 to > 1,600	Fossil fecal pellets	Mean annual temperature	Most predictive Annual, $r = 0.602$, $P < 0.001$, $d.f. = 33$	Unable to discriminate between males and females, or between winter and summer
Furnace Creek	<i>Neotoma lepida</i>	1891–2007	–54	Body length of museum specimens	Winter and summer temperatures	Winter temperature, $r = 0.995$, $P < 0.005$, $d.f. = 3$ (females); $r = 0.822$, $P > 0.17$, $d.f. = 3$ (males)	Females >>> males Winter > summer
Furnace Creek	<i>Neotoma lepida</i>	2003–2007	–54	Body mass	Winter and summer temperatures	Summer temperature, $r = 0.832$, $P < 0.04$, $d.f. = 5$ (females); winter, $r = 0.657$, $P > 0.15$, $d.f. = 5$	Females >>> males Summer >>> winter
Furnace Creek	<i>Neotoma lepida</i>	Seasonal	–54	Mortality	Winter and summer temperatures	Mortality highest in summer months, $P < 0.000$, $d.f. = 9$ (females); $P < 0.01$, $d.f. = 9$ (males)	Females >>> males Summer >>> winter
Furnace Creek	<i>Neotoma lepida</i>	Daily	–54	Activity	Winter and summer temperatures	~50% reduction in activity of both sexes in summer months; females active ~50% less than males, $F_{1,15,9} = 5.2$, $P < 0.04$	Both sexes reduce activity severely with increasing temperature but female activity impacted >>> male activity

^a Strength of interactions.

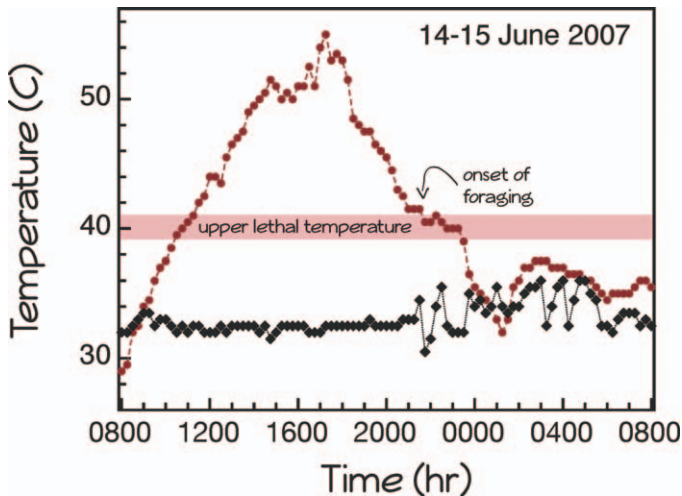


FIG. 5.—Thermal record for a desert woodrat (*Neotoma lepida*) at Furnace Creek in June 2007. The temperature trace represents a 24-h record of ambient temperature (30 cm aboveground in the shade of the mesquite canopy) versus that experienced by a male *N. lepida*. Filled circles represent external temperature; filled diamonds, the woodrat record. Both temperature records were recorded by i-Buttons. The woodrat spent the hot, diurnal period from 0530 to 2130 h in the den within a fairly narrow zone (32–34°C). Once external temperature dropped below upper lethal temperature (~41°C) in the evening, he emerged to begin foraging and other nocturnal activities. This is clearly evident in the abrupt increase in his record at around 2130 h. The well-demarcated temperature shifts during the evening allowed the characterization of nocturnal activity. Note that temperature outside the den in the mesquite canopy reached ~55°C at ~1730 h; this was more than 20°C higher than the temperature to which the male woodrat was exposed.

pers. obs.). The extremely high site fidelity, which was confirmed by radiotelemetry studies indicating little movement between complexes (I. W. Murray, pers. obs.), allowed us to quantify persistence and survivorship based on trapping records. Because animals did not move, individuals not trapped for 2 consecutive months were presumed dead. Survivorship of adult woodrats was highly skewed and not significantly different between females and males ($\bar{X} \pm SD$: 146.8 \pm 187.9 days, $n = 274$; versus 117.4 \pm 171.9 days, $n = 238$, respectively). Mortality was significantly skewed throughout the year for both adult males and females, with survivorship lowest in the warm summer months (chi-square goodness-of-fit test: females, $P < 0.000$, $d.f. = 9$; males, $P < 0.01$, $d.f. = 11$). Some 25.9% of females and 27.5% of males died during July and August; these values increased to 38.2% and 33.6%, respectively, if June also was included. Juveniles entered the population from March to September, with the vast majority in April and May. Survivorship of juveniles could not be quantified because natal dispersal off the 10-ha site could not be disentangled from mortality.

We found consistent relationships in all years between body mass and temperature (Figs. 3 and 4). The mass of the adults in the population fluctuated over the course of the year, with smaller animals present in the summer and larger animals in the winter and spring (Figs. 3a and 3b). Although part of the

pattern reflected the increased mass accompanying reproductive activity, much of it reflected actual turnover of individuals within the population. The influence of summer temperature extremes was particularly striking; there was a dramatic decrease in body size of the adult population every year in the trapping session after temperatures approaching lethal (~41°C) had been experienced (Fig. 3b). The influence of temperature on body mass was especially strong for females (Fig. 4), whose smaller body mass and greater energetic requirements required daily foraging.

Dens ameliorate temperature much more than previously reported (Vorhies 1945; Lee 1963; Brown 1968). Earlier work had suggested a maximum thermal buffering of about 9.1°C for dens located deep within rock crevices and only 4.8°C for those located within mesquite or juniper (Brown 1968). At Furnace Creek we found as much as a 15–20°C differential between the den and ambient temperature within the mesquite thicket (Fig. 5). Because the National Park Service was unwilling to allow us to deconstruct dens on the archeologically sensitive site, we were unable to characterize the internal structure or the extent of subterranean chambers. However, the large trunk diameter and overall massive size of the honey mesquite at Furnace Creek indicated that they clearly were very old; studies suggest that mesquite can live up to 200 years (Wilson et al. 2001). They were likely the same trees trapped by mammalogists in the late 1800s–early 1900s (Palmer 1891; Grinnell 1937). Moreover, the dens were quite large, suggesting ongoing construction and use by sequential generations of woodrats.

Characterization of activity.—As reported in Murray and Smith (2012), the i-Buttons yielded 468 individual 24-h records from 14 adult desert woodrats (10 males and 4 females), for a total of > 44,000 individual readings. Each was assigned to a relative measure of daytime temperature intensity, which reflected degree of thermal stress based on biologically relevant benchmarks for woodrats (Lee 1963; Brown 1968; Nelson and Yousef 1979). These were: low (below the thermal neutral zone, < 31°C), medium (within the thermal neutral zone, 31–35°C), high (above the thermal neutral zone, > 35°C < 41°C), and severe (above lethal, $\geq 41^\circ\text{C}$). The onset of nocturnal activity was defined as an abrupt deviation from the baseline diurnal den temperature, and was clearly discernible in our records (Fig. 5).

The main results as reported in Murray and Smith (2012) were: 1) woodrats do not begin nightly foraging activities until temperature dropped below lethal (~41°C; Fig. 5); 2) males emerged from the den significantly earlier than did females (59.5 \pm 6.7 min after sunset versus 95.3 \pm SD11.3 min for females); and 3) as daily temperatures increased over the summer, all animals exhibited a precipitous decline in nightly activity with fewer bouts of shorter duration (e.g., 251.4 \pm 29.1 min under low temperatures versus 142.4 \pm 28.4 min under extreme temperatures; Figs. 4a and 4b). The decrease in activity with increasing temperature persisted even after accounting for seasonal differences in day length; 4) the difference in overall activity following low-temperature and severe-temperature days was especially notable (40.1% \pm 5.4% versus 23.9% \pm 5.2%); and 5) at any specific

TABLE 2.—Dated paleomiddens recovered from Titus Canyon, Death Valley, California. ID = identification; CI = confidence interval; CA = California; NA = not applicable.

Midden ID	Cave ID	State	Latitude	Longitude	Elevation (m)	N	¹⁴ C age	Age SD
TiC7 modern	UNM 2	CA	36.51	117.03	1,137	944	0	
TiC1 modern	UNM 31	CA	36.51	117.03	1,200	504	0	
UTiC8 modern	UNM 11	CA	36.49	117.01	1,443	677	0	
UTiC12&3 modern	UNM 10	CA	36.5	117	1,528	409	0	
UTiC9	UNM 12	CA	36.49	117.01	1,447	820	731	34
UTiC3a	UNM 46	CA	36.49	117	1,583	1,295	1,942	35
TiC15b	UNM 39	CA	36.49	117.08	582	1,190	2,427	37
TiC14	UNM 38	CA	36.49	117.1	298	1,774	2,782	37
TiC8a TOP2	UNM 36	CA	36.51	117.04	1,220	817	3,433	37
TiC16	UNM 8	CA	36.5	114.04	1,015	470	3,781	42
TiC8 BOTTOM B	UNM 36	CA	36.51	117.04	1,220	1,205	4,116	39
UTiC12a	UNM 10	CA	36.5	117	1,528	988	4,529	39
TiC11b	UNM 6	CA	36.51	117.04	1,154	1,035	5,434	46
TiC9c-1	UNM 4	CA	36.51	117.03	1,156	1,105	7,253	45
UTiC6	UNM 49	CA	36.49	117.01	1,513	1,180	7,626	55
UTiC2b	UNM 44	CA	36.49	117	1,576	905	7,976	47
TiC11a-1	UNM 6	CA	36.51	117.04	1,154	1,259	7,987	47
UTiC2a	UNM 44	CA	36.49	117	1,576	656	8,543	49
UTiC11a	UNM 45	CA	36.49	117	1,559	1,767	8,642	65
TiC13b	UNM 7	CA	36.51	117.04	1,216	501	8,692	49
UTiC11b	UNM 45	CA	36.49	117	1,559	1,740	8,749	49
TiC15a	UNM 39	CA	36.49	117.08	582	375	10,720	66
TiC11c-2	UNM 6	CA	36.51	117.04	1,154	385	11,191	56
TiC2	UNM 32	CA	36.51	117.03	1,190	1,094	11,406	60
TiC11c-3	UNM 6	CA	36.51	117.04	1,154	434	13,273	73
TiC17-take 2	UNM 41	CA	36.5	117.04	1,030	339	14,013	76
TiC4a	UNM 35	CA	36.51	117.03	1,250	1,308	15,056	84
TiC4c	UNM 35	CA	36.51	117.03	1,250	435	15,331	84
TiC17a&b	UNM 41	CA	36.5	117.04	1,030	456	16,768	96
TiC10a	UNM 3	CA	36.51	117.03	1,200	1,126	17,740	100
TiC6	UNM 5	CA	36.51	117.03	1,200	1,542	18,380	140
UTiC1 Back	UNM 43	CA	36.5	117.03	1,345	588	19,400	120
TiC10c-1	UNM 3	CA	36.51	117.03	1,200	745	20,020	120
TiC10d	UNM 3	CA	36.51	117.03	1,200	710	20,710	160
TiC12 TopE	UNM 37	CA	36.51	117.04	1,249	1,040	24,340	200
TiC12 TopD	UNM 37	CA	36.51	117.04	1,249	1,055	26,080	230

temperature, males initiated activity earlier and were active for significantly longer than females (Fig. 4b). Assessment of reproductive status from our trapping data suggested that males spent time both foraging and searching for mates, whereas female activity was mostly geared toward foraging.

Historical Records

Despite the limited sample remaining after restricting our historical analysis to eliminate sources of known bias ($n = 5$ temporal periods), we found a significant relationship between the body length of museum specimens of *N. lepida* and various temperature metrics (Figs. 3c and 4d). Interestingly, patterns were stronger for females than for males, and for winter over summer temperature anomalies. Because a sufficiently long-term temperature record was not available for Death Valley, we could not regress body mass directly against absolute temperature. Instead, we employed an approach often used in paleostudies and computed the temperature deviations (anomalies) from the long-term record (> 50 years) at a nearby site that did have such a record (St. George, Utah). Note that

woodrat body mass increases as the cube of length (Smith and Betancourt 2003), so the fluctuations in length (Fig. 3c) represent considerable differences in mass of animals in the population over time.

Paleomidden Analysis

The midden chronosequence recovered from Titus Canyon is one of the most comprehensive obtained to date for a region (Table 2; Fig. 3d). Radiocarbon analysis revealed that the oldest middens were deposited more than 31,000 years ago; moreover, about one-half of the samples were Pleistocene in age.

In general, woodrats responded to late Quaternary climate change as expected; smaller body mass was selected for during warmer periods, and larger body mass was selected for during cooler intervals (Figs. 3d and 4e). In particular, note the extremely large body mass estimated during the late Pleistocene (Table 2) when climate was some 8–14°C cooler (Woodcock 1986; Koehler et al. 2005; Jansen et al. 2007). There was a highly significant relationship between woodrat

TABLE 2.—Extended.

Calendar age	Calendar age <i>SD</i>	Material dated	Average maximum width (mm)	Width <i>SD</i>	95% <i>CI</i>	Mass estimate (g)	Mass 95% <i>CI</i>	Species identified by
0	25	NA	5.00	0.089	0.06	295.2	11.29	Pellets
0	25	NA	4.99	0.147	0.09	293.8	18.67	Pellets
0	25	NA	4.93	0.093	0.06	281.3	11.77	Pellets
0	25	NA	5.03	0.143	0.09	302.4	18.12	Pellets
685	15	Pellets	5.13	0.123	0.08	322.9	15.66	Pellets
1,895	38	Pellets	4.89	0.086	0.05	272.7	10.93	Pellets
2,523	130	Pellets	5.18	0.171	0.11	333.5	21.70	Teeth/pellets
2,883	49	Pellets	4.93	0.101	0.06	280.5	12.77	Pellets
3,713	64	Pellets	5.46	0.164	0.10	390.5	20.85	Pellets
4,150	65	Pellets	5.60	0.137	0.09	419.6	17.45	Teeth/pellets
4,677	102	Pellets	5.37	0.247	0.15	371.2	31.36	Pellets
5,187	95	Pellets	5.12	0.076	0.05	320.6	9.60	Pellets
6,246	37	Pellets	4.99	0.054	0.03	294.4	6.82	Pellets
8,084	59	Pellets	5.12	0.103	0.06	321.2	13.04	Pellets
8,447	51	Pellets	5.14	0.135	0.08	324.1	17.16	Pellets
8,849	104	Pellets	5.47	0.175	0.11	392.3	22.28	Pellets
8,861	98	Pellets	5.49	0.108	0.07	397.1	13.73	Pellets
9,522	22	Pellets	5.50	0.144	0.09	398.5	18.23	Teeth/pellets
9,628	67	Pellets	5.41	0.232	0.14	380.5	29.41	Pellets
9,655	71	Pellets	5.10	0.049	0.03	316.7	6.16	Pellets
9,751	106	Pellets	5.40	0.077	0.05	378.2	9.78	Pellets
12,697	54	Pellets	5.30	0.141	0.09	357.1	17.86	Pellets
13,092	115	Pellets	4.96	0.154	0.10	288.3	19.51	Pellets
13,255	83	Pellets	5.91	0.122	0.08	483.1	15.50	Pellets
15,456	134	Pellets	5.23	0.058	0.04	342.3	7.34	Pellets
17,261	218	Pellets	5.54	0.172	0.11	406.7	21.87	Pellets
18,274	242	Pellets	5.85	0.054	0.03	470.2	6.87	Teeth/pellets
18,413	301	Pellets	5.78	0.092	0.06	456.1	11.68	Teeth/pellets
19,991	298	Pellets	6.14	0.15	0.09	528.6	18.99	Teeth/pellets
21,004	161	Pellets	5.73	0.113	0.07	446.2	14.31	Pellets
22,018	333	Pellets	6.43	0.128	0.08	589.6	16.30	Teeth/pellets
23,092	217	Pellets	6.15	0.165	0.10	531.9	20.92	Pellets
23,919	155	Pellets	6.01	0.095	0.06	503.2	12.08	Teeth/pellets
24,701	253	Pellets	5.29	0.144	0.09	355.1	18.34	Teeth/pellets
29,116	260	Pellets	5.85	0.131	0.08	470.6	16.67	Teeth/pellets
31,318	285	Pellets	6.24	0.151	0.09	549.5	19.22	Teeth/pellets

body mass and independently derived global paleotemperature estimates (Fig. 4e; $df. = 33$, $r = 0.602$, $P < 0.001$). Although there is certainly gene flow up and down Titus Canyon, there is insufficient variation in physiography or environmental conditions in the Amargosa Range to support much of a body-size gradient with elevation. Thus, most if not all of the fluctuations evident over the late Quaternary were due to in situ adaptation, rather than wholesale extirpation and replacement by differentially sized animals (Smith and Betancourt 2006).

Intriguingly, examination of our data clearly indicates that *N. cinerea* was present in Titus Canyon during the Pleistocene and early to middle Holocene (Fig. 3d). This was unexpected given the complete absence of this species from the east side of Death Valley today. Yet, our results were unequivocal; in several instances we obtained body-mass estimates of well over 500 g, equivalent to the maximum sizes of *N. cinerea* from the extreme north of their modern range (Table 2; Smith 1997). Not only was *N. cinerea* extant, but examination of our data suggests it occupied cave sites as low as 1,015 m during the late Pleistocene (Fig. 3d). This raises the possibility that *N. cinerea* was widespread across the entire Grapevine Mountains

and Amargosa Range during the late Quaternary. Note that although body mass is generally considered to be a poor diagnostic characteristic for species identification, in this instance it provides an easy way to distinguish the 2 species; *N. lepida* and *N. cinerea* have virtually nonoverlapping body mass distributions and no overlap at all in the largest size classes (Smith and Betancourt 2006; Smith et al. 2009). Identifications based on mass were confirmed using geometric morphometric analysis of > 100 fossil teeth contained within the middens (Table 2; S. Whiteman, University of New Mexico, pers. comm.).

We found clear evidence of sympatry between *N. lepida* and *N. cinerea* over the late Quaternary (Fig. 3d). Desert woodrats migrated into Titus Canyon at the onset of the Holocene. The 2 species were both present in Titus Canyon for much of the Holocene, although they occupied different regions. Middens with overlapping radiocarbon dates suggest at least an ~300-m elevational displacement within the canyon, with *N. cinerea* occupying the higher cave sites (Fig. 3d; note that elevation of the midden is represented by the color of the datum). As *N. cinerea* retreated to higher elevations during the middle

Holocene and was ultimately extirpated from Titus Canyon (and indeed the entire Amargosa Range), *N. lepida* migrated up the elevational gradient (Fig. 3d). Today, *N. lepida* is found throughout Titus Canyon up to ~1,800–1,900 m.

DISCUSSION

Our study clearly indicates the profound influence of temperature on all aspects of woodrat biology (Table 1). At an individual level, ambient temperature determines when animals emerge from their den, how much time they can invest in essential activities such as foraging and mating, and ultimately, their survival (Figs. 3a, 4a, 4b, and 5). At a population level, these constraints lead to highly predictable fluctuations in the body size of both woodrat species that persist though both space and time (Figs. 3b–d, 4c, and 4d). Although earlier work had amply demonstrated the influence of temperature on woodrats (e.g., Lee 1963; Brown 1968; Brown and Lee 1969; Smith et al. 1995; Smith and Charnov 2001), we demonstrate that the effects are much more pronounced at Death Valley. Here, at the limits of these species' thermal and ecological thresholds, even small fluctuations in temperature have profound effects on the ecology and evolution of the animals.

The solution to the conundrum of how desert woodrats on the valley floor cope with consistently lethal temperatures seems to be closely tied to the presence of honey mesquite (*P. glandulosa*). The deep taproots of the mesquite are able to effectively access underground water (Phillips 1963). This ability, coupled with their massive size, affords considerable thermal protection and a predictable source of food and water for animals. Hence, woodrats are able to construct and occupy dens that ameliorate temperature to a previously unappreciated degree (Fig. 5). The large thermal differential (~15–20°C) we observed between the interior and exterior of the den may be unique to Death Valley; earlier studies reported thermal buffering of less than 5°C for mesquite (Brown 1968). Nonetheless, woodrats must still leave the den to forage and reproduce. Given that temperatures above 50°C are likely for more than 3 months of the year (Western Regional Climate Center 2012) with little nocturnal relief, animals consistently face a thermal environment approaching or exceeding their lethal tolerances.

So how do animals cope? One way is by limiting essential activities during stressful thermal conditions (Figs. 4a and 4b). Desert woodrats do not commence nocturnal activity until temperature drops below lethal (41°C; Fig. 5). In practical terms, this means that during the summer they emerge later after sunset than in other seasons. Moreover, as temperature increases, woodrats drastically reduce the number of trips outside the den and spend about one-third less time during each bout. Indeed, we were forced to modify our trapping protocols during the summer because animals died if exposed to high nocturnal temperatures for longer than ~45 min. Because woodrats are dependent on green vegetation for water (Schmidt-Nielsen 1964) and honey mesquite clippings rapidly

lose water (J. Martin, pers. obs.), woodrats cannot rely on cached food supplies, but must forage nightly.

Second, there is strong selection on the body size of female desert woodrats. Larger females experience higher mortality during warmer conditions, leading to a much smaller "characteristic" body size during the summer months (Figs. 3a and 4c). Because upper lethal temperature of woodrats scales negatively with body mass (Smith et al. 1995), this provides some physiological "space" to cope with high temperatures. However, this does not appear to hold for males. We speculate that their much larger size may allow them to withstand greater degrees of water deprivation (Peters 1983) and thus, remain in the relative thermal safety of the den during particularly stressful periods. Why larger females are favored during other seasons is an open question, but is likely related to a positive scaling of size with fecundity (Smith and Charnov 2001).

The evolutionary history of woodrats in the Death Valley region is complex. Both fossil and molecular analyses suggest that desert woodrats originated in southern coastal California; not only do the coastal clades provide a coalescence signature of stable populations, but the base is approximately an order of magnitude deeper than that for desert clades (Patton and Álvarez-Castañeda 2005; Patton et al. 2008). The oldest fossils reliably identifiable to *N. lepida* date to 500,000 years ago from Orange County, California (Jefferson 1991). During the cooler conditions of the late Pleistocene, there was a rapid radiation from this core population into the Mojave Desert. This was a fairly recent event, perhaps some 50,000–100,000 years ago (Patton and Álvarez-Castañeda 2005; Patton et al. 2008). At this time, Death Valley would have been a considerably more hospitable place, with summer temperatures some 8–14°C cooler (Woodcock 1986; Koehler et al. 2005; Smith et al. 2009; Fig. 1c).

It is likely that *N. cinerea* has been in the region for much longer than *N. lepida*. Bushy-tailed woodrats are the oldest extant species of woodrat, with fossils dating at least back to the Pliocene (~3.1 million years ago—Hay 1921). Although their distribution was shifted south during the Pleistocene, the Death Valley region was close to the center of the range (Graham and Lundelius 2010); certainly they were widespread in mountainous regions of the western United States (Harris 1984; Smith 1997). Today, *N. cinerea* is restricted to higher elevations of the Panamint Range on the west side of Death Valley. However, our paleomidden research in Titus Canyon reveals that these woodrats were present on the east side of the valley throughout the late Pleistocene and into the middle Holocene.

How did the climate shifts of the late Quaternary, which resulted in the establishment of the modern habitat, influence the distribution and evolution of woodrats in this region? For much of the late Quaternary, bushy-tail woodrat populations adapted to climate fluctuations by phenotypic changes in body mass, likely coupled with slight movements upslope and downslope (Fig. 3d). These adaptations followed the patterns expected by Bergmann's rule; during colder episodes woodrats

were larger, and during warmer intervals, animals were smaller (Fig. 4e). Note that there is much too little physiographic relief in Titus Canyon for animals to cope with climate shifts by simply moving upslope or downslope. The proximate mechanism was probably physiological, as demonstrated by our field studies (Figs. 4a–c). The cooler and wetter environmental conditions supported a very different vegetative community than found today, dominated by juniper (*Juniperus* sp.) and pinyon pine (*Pinus monophylla*) at higher elevations (Smith et al. 2009). In particular, the widespread distribution of juniper (*Juniperus* sp.) may have facilitated the presence of *N. cinerea*. There was an ~1,000-m downward displacement of juniper in the late Pleistocene in Titus Canyon (Smith et al. 2009).

As climate changed, *N. lepida* expanded its range to include lower-elevation caves within Titus Canyon (Fig. 3d). For this to occur required both warmer environmental conditions and the absence of the larger dominant species (Smith and Betancourt 2003). The middle Holocene was both warmer and drier (Grayson 1993, 2000). Earlier work documents a clear environmental separation between *N. lepida* and *N. cinerea*, with each species responding to different abiotic factors (Grayson 2000; Smith and Betancourt 2003; Smith et al. 2009). Today, *N. lepida* is not found in habitats where mean January temperatures typically drop below freezing. In contrast, the much larger *N. cinerea* can tolerate extremely cold winter temperatures, but is unable to cope with warm summer ones (e.g., mean July temperatures $> \sim 25^{\circ}\text{C}$ —Smith and Betancourt 2003). Both species coexisted for the early part of the Holocene, although *N. cinerea* continued to retreat to higher elevations as climate continued to warm. Eventually *N. cinerea* was extirpated not only from Titus Canyon, but also from the entire eastern side of Death Valley. What led to this is unknown. Perhaps it was an episode of climate change too abrupt or severe for animals to adapt or perhaps it was the combined effects of continued environmental change and small effective population size. Although the Grapevine Mountains do reach over 2,600 m in elevation, there is considerably less available habitat at higher elevational zones (Smith et al. 2009). Such range contractions for *N. cinerea* during the middle Holocene have been seen in other Great Basin habitats (Grayson 2000).

By integrating modern and historic studies, we have been able to obtain a holistic perspective of the influence of temperature on woodrats (Table 1). Paleomiddens, in particular, provide a unique and incomparable historical record. Indeed, within 1 elevational gradient in Death Valley, we were able to observe the entire spectrum of predicted possible responses to anthropogenic climate change: adaptation in situ, range contraction and expansion, and even local extirpation (Fig. 3d). Our results demonstrate both the dynamic nature of distributional boundaries, which clearly responded to even fine-scale climate fluctuations of the late Quaternary, as well as some of the likely proximate causal mechanisms. Temperatures in Death Valley are predicted to increase by 2.0–5.0°C within the next 100 years (Cayan et al. 2009). Leaving aside the potential

influences on mesquite (e.g., lowering of the water table or increased salinity of underground water), such shifts will further constrain the activity and survivorship of animals during the summer and will lead to changes in the body size of the population. Finally, although we have not addressed this issue here, consider that virtually all biological rates and times scale with body size (Peters 1983). Thus, even small changes in body size have profound effects on the ecology of animals and on their role in ecological communities (Smith 2012).

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