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Evolutionary Ecology Research 3:595-602

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Fitness trade-offs select for semelparous reproduction in an extreme environment

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ABSTRACT

Semelparity (suicidal or one-time reproduction) is generally thought to evolve when selection favours individuals that allocate so much energy towards reproduction that death is inevitable. Among mammals, only males of a few marsupial species are known to exhibit this unusual life-history strategy. Here we report evidence that suggests adaptations to an increasingly harsh environment during the early Holocene favoured a switch from iteroparity (repeated reproduction) to semelparity for a small rodent, *Neotoma lepida*. Our analysis, based on spatial, temporal and physiological relationships between body size and temperature and on calculations using life tables and body size production allometries, highlights a unique way that mammals may adapt to changing environmental conditions.

Keywords: Bergmann's rule, Death Valley, iteroparity, life-history trade-offs, *Neotoma*, temperature, woodrat.

INTRODUCTION

The Valley of Death, Inyo County, California, is the loneliest, the hottest, the most deadly and dangerous spot in the United States . . . It is a pit of horrors – the haunt of all that is grim and ghoulish. Such animal and reptile life as infests this pest-hole is of ghastly shape, rancorous nature, and diabolically ugly. It breeds only noxious and venomous things . . . Its dead do not decompose, but are baked, blistered, and embalmed by the scorching heat through countless ages. It is surely the nearest to a little hell upon earth that the whole wicked world can produce. (Anonymous reporter for the *New York World*, 1894)

Death Valley, California is one of the hottest and driest areas in the Western Hemisphere. Mean maximum July temperature exceeds 46°C and less than 5 cm precipitation falls annually (<http://www.wrcc.dri.edu/cgi-bin/cliMONtmxt.pl?cadeat>). Its maximum recorded temperature, over 56°C, is within a few degrees of the highest temperature ever recorded on the planet (Collier, 1990). The severe rain shadow caused by tall mountain ranges to the west and east is exacerbated by ground subsidence that depressed the valley floor below sea level. The limited and highly variable precipitation, coupled with high evaporation rates, has left much of the valley floor covered with saline pan evaporites and mudflat deposits (Li *et al.*, 1996).

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Despite such harsh conditions, a number of vertebrate species live on the valley floor, some 84 m below sea level. Many colonized during the Quaternary when the climate was milder, wetter and more equable; analysis of palaeomidden data suggests that summers during the late Pleistocene were probably about 8–14°C cooler (Woodcock, 1986). Pluvial lakes during the late Pleistocene occupied much of the valley; these were as deep as 90 m only 10,000 years B.P. (Li *et al.*, 1996; Lowenstein *et al.*, 1999). Between 10,000 and 8000 years B.P., the shift from the pluvial woodlands and cool semi-desert to the modern hyperarid desert was complete (Wells and Woodcock, 1985; Woodcock, 1986). Life in such a harsh environment poses unique challenges to organisms. Here, we show that for one mammalian species (*Neotoma lepida*, the desert woodrat) adaptations to the harsher environment resulted in a major shift in reproductive strategy and survivorship.

With the exception of the males of several Dasyurid species (e.g. Woolley, 1990; Bradley, 1997), mammals are almost exclusively iteroparous (repeated reproducers). Life-history theory predicts that semelparity may be favoured over iteroparity if reproduction can be increased sufficiently in a single bout to overcome the much shortened reproductive life-span (Cole, 1954; Charnov and Schaffer, 1973; Young, 1981, 1990). Such mechanisms assume that death results as an inevitable consequence of the energy expended on reproduction (e.g. Young, 1981, 1990). Here, we propose an alternative mechanism: for large-bodied individuals in the Death Valley woodrat population, seasonal thermal stress leads almost invariably to death and, consequently, the *only* viable reproductive strategy available is semelparity. We show that the large-bodied animals are favoured over the much smaller size that could survive the heat. Our calculations are based on the spatial, temporal and physiological relationships between woodrat body size and temperature and on woodrat life tables and body size production allometries.

WOODRATS AND TEMPERATURE

Woodrats (*Neotoma*) are particularly sensitive to environmental temperature (Lee, 1963; Brown, 1968; Brown and Lee, 1969; Smith *et al.*, 1995, 1998; Smith and Betancourt, 1998). A strong correlation exists between mean adult body mass and ambient temperature across populations in the western United States (Fig. 1a), with smaller adults found in hotter environments. Such relationships are found for all woodrat species studied, and also hold for individual populations across evolutionary time; *Neotoma* were larger during the last glacial maximum and smaller during the Altithermal (Smith *et al.*, 1995; Smith and Betancourt, 1998). The underlying mechanism is probably physiological; lethal temperature is an inverse function of body mass (Fig. 1b; Brown, 1968). The empirically derived upper critical temperature (Fig. 1b) for the smallest woodrat species (*Neotoma lepida*, the desert woodrat) is about 42°C (Lee, 1963; Brown and Lee, 1969), fairly low for a desert animal. This low threshold is at least partially attributable to their inability to concentrate urine; most desert rodents do so to reduce water loss (MacMillen, 1964). *Neotoma* also lacks any other specialized physiological adaptations to heat stress. It cannot estivate or utilize evaporative cooling, for example, and has no specialized nasal passages to conserve water. The elaborate houses woodrats construct around the base of a cactus or shrub allow successful existence under thermally stressful conditions; depending on the substrate, such structures can ameliorate ambient temperature by up to 5°C (Lee, 1963; Brown, 1968) (Table 1).

Table 1. Temperature differential inside versus outside of woodrat den

Species	Dens examined (n)	House or den type	Mean difference between maximum summer temperature and temperature recorded inside den	Reference
<i>N. cinerea</i>	9	Rock crevices (up to 1.5 m deep)	9.1°C	Brown (1968)
<i>N. albigula</i>	11	Under mesquite/juniper/subterranean	4.8°C	Brown (1968)
<i>N. lepida</i>	c. 100	Under rocks/boulders and various plants	2.5°C	Lee (1963)

Note: Rock crevices and caves provide the greatest thermal buffer, but such substrates are not available to woodrats occupying the valley floor at Death Valley.

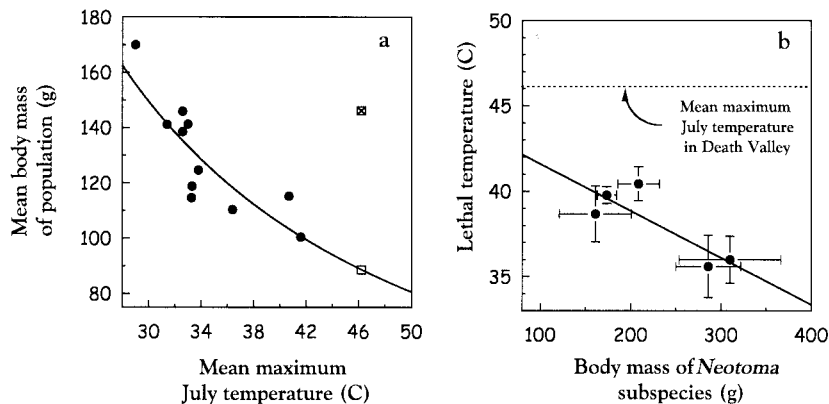


Fig. 1. Scatterplots and regressions showing variation in *Neotoma* body mass as a function of temperature. (a) Relation between mean body mass and mean maximum July temperature in 12 populations of *Neotoma lepida* from western North America. Squares represent Death Valley summer/fall (\square) and spring/winter (\boxtimes). Regressions omit Death Valley data. Data from museum specimens housed at the Museum of Vertebrate Zoology (UC Berkeley), United States Natural History Museum (Smithsonian), Death Valley Natural History Collection (Death Valley National Park) and unpublished field notes. Sample size for each location generally exceeds 20 individuals (range 7–115) and includes approximately equal numbers of males and females. Weather information, from the Western Regional Climate Center (<http://www.wrcc.dri.edu>), generally represents a minimum of a 50 year average. When necessary, a terrestrial lapse rate of -0.5°C per 100 m was used to correct for elevational differences between collection sites and the nearest weather station (Meyer, 1992). Relationship is best fit by a power function: $y = 9163.4x^{1.21}$, d.f. = 9, $r = 0.847$, $P < 0.001$. (b) Relation between mean lethal upper temperature and mean body mass of various woodrat subspecies. Data from unpublished work by J.H. Brown. Error bars represent 95% confidence intervals. Relationship is best fit by a linear model: $y = -0.027x + 44.35$, d.f. = 3, $r = 0.84$, $P < 0.05$.

WOODRATS IN DEATH VALLEY

The robust relationships between body size and ambient temperature, and between body size and lethal temperature (Fig. 1), independently predict a mean adult body size for the

Death Valley woodrat population of about 80 g. However, the actual mean is 145.4 g (Fig. 1), substantially higher than expected and at odds with the intense thermal constraints faced by animals in Death Valley. Moreover, the largest animals exceed 200 g. Body size this large is characteristic of coastal California populations of *Neotoma lepida*, where maximum July temperatures are typically below 30°C (Fig. 1).

We examined the body size of woodrats in Death Valley as a function of the month in which they were captured. There is a clear seasonal pattern, with mean body mass increasing during fall and early winter and decreasing during the late spring and summer (Fig. 2). These body mass fluctuations are not the result of physiological changes; results are similar when body length is used instead. The pattern is driven by fluctuations in the abundance of the larger body size classes (Fig. 3); minimum size is approximately constant throughout the year. Strikingly, there are *no* large woodrats in the population from late spring until late fall (Figs 2, 3). Moreover, the mean body size for animals collected in Death Valley between June and November is 88.5 g, significantly different than that of animals collected between December and May (146.0 g) and close to the value predicted by the temperature–body size relationships (Fig. 1a, open square).

Other desert woodrat populations display a markedly different seasonal body size pattern from Death Valley (Fig. 3). In general, their body mass is fairly constant over much of the year, although variation increases during the spring and/or fall reproductive period as

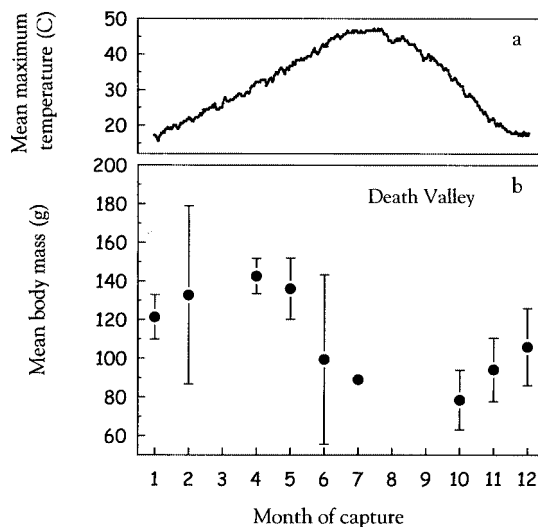


Fig. 2. Seasonal variation in temperature and body mass of woodrats from Death Valley, California, United States. (a) Mean maximum daily temperature at Furnace Creek (–55 m elevation). Data, from the Western Regional Climate Center, represent a 40 year average. Maximum recorded temperature at Furnace Creek is over 56°C, only a few degrees lower than the highest global temperature recorded (Collier, 1990). (b) Mean body mass of woodrats (*Neotoma lepida*) by month. Error bars represent 95% confidence intervals. Data from museum specimens collected between January 1891 and May 2000. A few specimens had no record of body mass; in these instances, we estimated mass from length using a regression derived from Death Valley woodrats for which both measures were provided ($y = 0.014x^2 - 2.98x + 230.6$; $r = 0.86$, d.f. = 54).

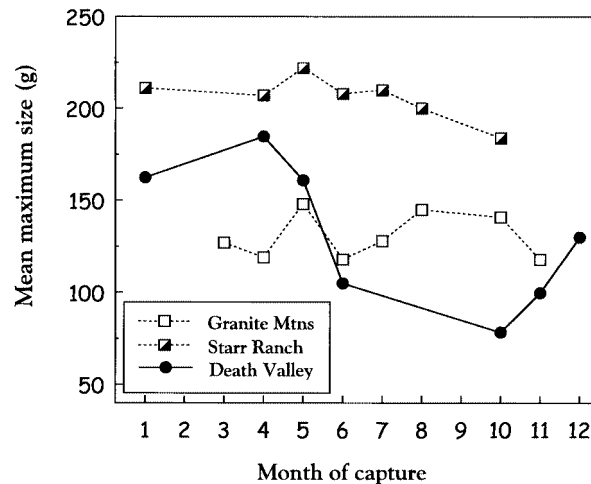


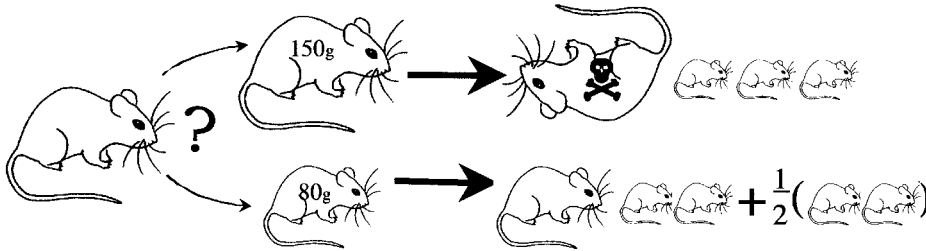
Fig. 3. Maximum body size of three populations of desert woodrats as a function of month of capture. Data for Death Valley animals taken from museum specimens; the other two from field studies of the populations (F.A. Smith, unpublished). Maximum size was calculated by averaging the body masses of the two largest males and females caught in that particular month. \blacksquare , *Neotoma lepida intermedia* from Starr Ranch (an Audubon Society Nature Reserve), Orange County, California; \square , *N. l. lepida* from UC Granite Mountain Reserve, Mojave Desert, San Bernardino County, California; \bullet , *N. l. lepida* from Death Valley, Inyo County, California.

juveniles enter the population. Furthermore, their maximum body mass is roughly constant throughout the year (Fig. 3) and population studies suggest that the largest animals are typically the oldest individuals (Linsdale and Tevis, 1951; Smith, 1996).

We believe that woodrats larger than about 90 g (*c.* 150 mm in length) are absent between June and November because they die of the intense heat (e.g. Fig. 1). On average, maximum daily temperature exceeds 45°C from 25 June until 31 August, a period of over 60 days. Even more extreme temperatures are common. Temperatures exceeding 50°C, for example, have been recorded for 68 different days during the summer (<http://www.wrcc.dri.edu>) and operational ground temperature is usually 50% higher.

We suspect that woodrats in Death Valley grow to an adult body mass of about 135–175 g during fall and winter, reproduce during late winter and spring and, as a consequence of their large size, die during early summer. Given the extreme summer temperatures, the only viable alternative life-history strategy would be to remain as an adult at approximately 80 g, which would probably allow summer survival but limit fecundity. These two alternatives are illustrated in Box 1. Using data from woodrat life tables and body size, we ask if natural selection will favour one or the other life-history strategy. Our calculations of lifetime reproductive output strongly suggest that, if the alternatives are to be iteroparous at 80 g or semelparous at 150 g, semelparity is favoured because of the increased reproductive output of the larger size (Box 1). Indeed, our calculations are conservative in favouring semelparity; 80 g is probably the upper bound for an iteroparous adult, and we have not included the allometric advantages that a larger body gives to a herbivore (increased digestive efficiency, ability to utilize coarser vegetation, etc.).

Box 1. Natural selection and woodrat life histories



Potential life-history strategies for *Neotoma* inhabiting the extreme environment of Death Valley, California. Woodrats can either have a large body size and hence higher fecundity, but die in early summer, or they can remain extremely small, have limited fecundity, but persist to a second reproductive bout. We estimate that woodrats at the Pleistocene/Holocene transition (when climate was about 8–14°C cooler; Woodcock, 1986) would have been about 150 g (Fig. 1a). Each of the two body-size morphs produce an average of three offspring over its adult life.

To evaluate if one life-history strategy would be favoured over the other in Death Valley, we computed a life table based on a woodrat population (*Neotoma lepida lepida*) studied at the University of California Granite Mountain Reserve (Smith, 1996). At this xeric site in the eastern Mojave Desert, animals were uniquely identified and live-trapped monthly or bimonthly for almost 4 years (1988–91). Thus, we were able to calculate survivorship (l_x) estimates. Woodrats typically reproduce first the spring after their birth (c. 11 months), and again in late summer (c. 16 months) if environmental conditions are good. Litter size for a particular female is fairly constant over her lifetime (Egoscue, unpublished data).

Time (x)	Iteroparous 80 g female			Semelparous 150 g female	
	l_x	Std l_x	m_x	l_x	m_x
1	1		0		0
6	0.32		0		0
11	0.09	1	b_1	1	b_2
16	0.05	0.56	b_1	0	0
21	0	0	b_1	0	0

As is typical for rodents, there is high juvenile mortality. However, approximately 56% of adults that reproduced once survived to the second reproductive period (std l_x); almost none survived to a third. Suppose an 80 g female can reproduce b_1 offspring in each of her two litters, while a 150 g female can reproduce b_2 in her single litter. Assuming survivorship (S) to the first reproductive bout is similar in both cases, the lifetime fecundity will be $S \cdot b_2$ for the 150 g female and $S \cdot [b_1 + 0.56b_1]$ for the 80 g female. Semelparous or suicidal reproduction (150 g) is favoured by natural selection if $S \cdot b_2 > S \cdot b_1 \cdot (1.56)$; i.e. $b_2/b_1 > 1.56$. Reproductive output in mammals generally scales with body mass raised to the 0.7 (Charnov, 1993), thus $b_2/b_1 \cong (150/80)^{0.7}$, or 1.55, just reaching the threshold. Indeed, as discussed in the text, this is probably an underestimate of the advantages of the larger body size.

Our evidence for semelparity is admittedly indirect; we have no direct observations of size-based mortality. However, we cannot envision alternative explanations consistent with the observed patterns. Selective migration of larger animals to higher (and cooler) elevations, even if plausible, would entail considerable long-distance movement across inhospitable habitat. Such large-scale movements are highly unlikely for any small rodent, but especially so for woodrats who are both sedentary and territorial (Linsdale and Tevis, 1951; Smith, 1996). Similarly, no evidence exists for novel physiological adaptations; morphologically, *Neotoma* from Death Valley are indistinguishable from other populations (F.A. Smith, personal observation). Furthermore, woodrats cannot estivate because of their high energetic demands (Linsdale and Tevis, 1951; Smith, 1995).

Neotoma lepida have inhabited Death Valley from at least the Quaternary onward (Wells and Woodcock, 1985; Woodcock, 1986). Plant macrofossils identified from woodrat palaeomiddens documented the shift from the pluvial woodlands and cool semi-desert of the full glacial to the modern hyperarid desert (Wells and Woodcock, 1985; Woodcock, 1986). We suspect that the shift from iteroparity to semelparity evolved at some time during the early Holocene (roughly 10,000 to 8000 years B.P.), as climate rapidly warmed. Our findings suggest a novel way that organisms may respond to climate change. The major modes previously postulated have involved the shifting of species distributions or some form of physiological adaptation to altered temperature regimes (see Peters and Lovejoy, 1992; Mooney *et al.*, 1993; Chapin *et al.*, 1995; Harte and Shaw, 1995; and references therein). Here we show that fundamental changes in life-history strategy may result from adapting to changing climatic conditions.

ACKNOWLEDGEMENTS

We thank J.H. Brown for unpublished data and L. Shively for assistance in preparing illustrations. J.H. Brown and T.P. Young provided numerous insightful comments on the manuscript. M. Ernest endured early summer Death Valley temperatures to procure much needed specimens; a hearty thanks somehow seems inadequate.

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