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The influence of climate change on the body mass of woodrats *Neotoma* in an arid region of New Mexico, USA

Felisa A. Smith, Hillary Browning and Ursula L. Shepherd

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Earth system scientists have recently concluded that anthropogenic induced climate change is detectable. Because many aspects of an organism's ecology and evolution are influenced by environmental temperature, this suggests temperature mediated changes may be already occurring in natural ecosystems. Using archived mammal trapping and meteorological data, we investigated local changes in climate over the past 8 yr at the Sevilleta National Wildlife Refuge in an arid region of New Mexico to determine i) if environmental conditions had altered, ii) if mean body mass of woodrats had changed over this time period, and iii) if the answers to i) and ii) were positive, were the results correlated? Body mass was chosen because it is highly sensitive to temperature and many crucial ecological and evolutionary parameters are affected by it. Our results indicate that winter temperature measures (average cold and minimum), and maximum summer temperature have changed significantly over the past 8 yr. Summer and winter temperatures have both increased by ca 2.5 to 3°C. When compared to long-term means, all years have had significantly warmer than average minimum temperatures. Mean body mass of woodrat populations has also changed significantly over the past 8 yr, and the changes are negatively correlated with both winter and summer temperatures. We predict that additional climatic warming will lead to further decreases in the mean body mass of woodrats at the Sevilleta NWR. Since many important ecological parameters are tightly linked with body mass (e.g. fecundity, dietary strategy, home range, extinction rates, energetic requirements, predation risk, etc.), our results suggest that further climate change may lead to profound alterations in woodrat life history, and indirectly, on the dynamics and structure of the entire community. This is in addition to any direct effect temperature may have on other plants and animals.

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In December 1995, the Intergovernmental Panel on Climate Change (IPCC) published a report, which concluded that global mean temperature has increased by between 0.3 and 0.6°C over the past 100 yr; a change that is unlikely to be entirely natural in origin (Houghton et al. 1996, Watson et al. 1996). These conclusions have been independently substantiated by other researchers (e.g. Santer et al. 1996, Tett et al. 1996). Regional temperature changes are likely to differ

substantially from the global mean value, and it has been suggested that arid regions in particular are likely to become more extreme (Tett et al. 1996, Watson et al. 1996). With few exceptions, deserts are projected to become hotter but not significantly wetter and “temperature increases could be a threat to organisms that exist near their heat tolerance limits ...” (Watson et al. 1996).

Ecologists are aware that climate change is likely to produce dramatic changes in the abundance and distri-

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bution of organisms (Dawson 1992, Tracy 1992, Vitousek 1992, Murphy and Weiss 1992, Smith and Budemeier 1992, Webb and Bartlein 1992, Field et al. 1992). To the extent that organisms have differing physiological tolerances to temperature or precipitation alterations, climate change may even decouple entire ecosystems. One well known effect of temperature on mammalian populations is Bergmann's Rule; a positive relationship between body mass and latitude. Bergmann's Rule is generally attributed to the increase in heat conservation that arises with a reduced surface to volume ratio, or conversely, with an increased ability to dissipate heat at smaller body masses (Rameaux and Sarrus 1838, Bergmann 1847, Mayr 1956, 1963). It has been well documented for numerous mammalian species (e.g. Brown 1968, Brown and Lee 1969, Panteleyev and Terekhina 1980, Ralls and Harvey 1985), and has even been demonstrated to operate over temporal scales (Smith et al. 1995). Because any number of fundamental physiological and ecological factors scale with body mass, including fecundity, energetic requirements, diet, territory and home range size, longevity and even extinction rates (e.g. Peters 1983, Calder 1984, Schmidt-Nielsen 1984), environmental changes may profoundly affect the basic ecology and life history strategies of organisms.

Here we address the issue of climate change on a local scale. Utilizing an archived 8 yr data set from the Sevilleta National Wildlife Refuge in an arid region of New Mexico, we address the following three questions: i) has detectable climatic change occurred at the Sevilleta over the past 8 yr? ii) have detectable changes occurred in mean body mass of woodrats *Neotoma* over the past 8 yr? iii) are any size changes that may have occurred correlated with changing environmental conditions? We have chosen to work with woodrats, because previous work has demonstrated that body mass in the genus is extremely sensitive to temperature (e.g. Lee 1963, Brown 1968, Brown and Lee 1969, Smith et al. 1995).

Materials and methods

Study sites

The Sevilleta National Wildlife Refuge is one of the National Science Foundation Long-term Ecological Research (LTER) sites in a transition zone between Chihuahuan Desert, Great Basin Shrub Steppe, and Great Plains Grassland. It is situated at ca 34° 30' N, 107° 30' W, in Socorro County, New Mexico, USA (Fig. 1). Three study areas were used within the Sevilleta: Two-22, Rio Salado grassland, and Rio Salado *Larrea* (Fig. 1). Two-22 is primarily juniper woodland (*Juniperus* spp.), located at 1825 m a.s.l. in the Great Basin Shrub Steppe near the base of the Ladrone

Mountain range. The topography is rocky and uneven. The Rio Salado study sites (ca 1500 m a.s.l.) are both located in Chihuahuan Desert habitat, and despite their close proximity contain fairly different vegetation types. The Rio Salado grassland is dominated by grasses (*Bouteloua eriopoda*, *Scleropogon brevifolius*, *Sporobolus cryptandrus*) widely interspersed with creosote (*Larrea tridentata*) and mesquite (*Prosopis glandulosa*), while Rio Salado *Larrea* tends to be dominated by creosote interspersed with snakeweed (*Gutierrezia sarothrae*) and some grass. Both locations are relatively flat. Meteorological records were available from two stations; Red Tank, located near Two-22, and Rio Salado, located within the Rio Salado study area.

Meteorological data

We obtained meteorological records for the years 1989–1996 from data archived at the Sevilleta LTER. Additional weather and precipitation records were available from the Historical Climatology Network (HCN) for most years between 1849 and 1992 for the city of Socorro, ca 30 km due south of the refuge (Fig. 1). The Socorro climatic data permitted comparisons of temperature over the past decade with long-term weather patterns for the region. From these weather records we calculated four temperature measures: i) MinCold – the average of the minimum temperatures for the three coldest months preceding capture, December, January and February; ii) AveCold – the average of the mean temperatures for these same three months; iii) MaxHot – the average of the maximum temperature for the three hottest months in the year preceding capture, July, August and September; and iv) AveHot – the average of the mean temperature for these same three months. Additionally, annual precipitation was tabulated, with a year defined as the twelve months prior to the date of mammal trapping (e.g. from June of the previous year to May of the capture year).

Mammal data

Mammal trapping has been conducted by LTER staff twice a year (late spring and late summer) on each of the study sites since 1989. To avoid confounding body mass changes with ontogeny, we used data from only the first trapping session in late spring. Each of the three study areas contain five trapping “webs”, with twelve transects radiating from a central stake (Parmenter et al. 1989, Friggins pers. comm.). The central stake is surrounded by four Sherman Live-Traps set perpendicular to each other, and each transect contains 12 additional Sherman live-traps, for a total of 148 per web. Two of the five webs at each location are designed as removals, with animals archived at the

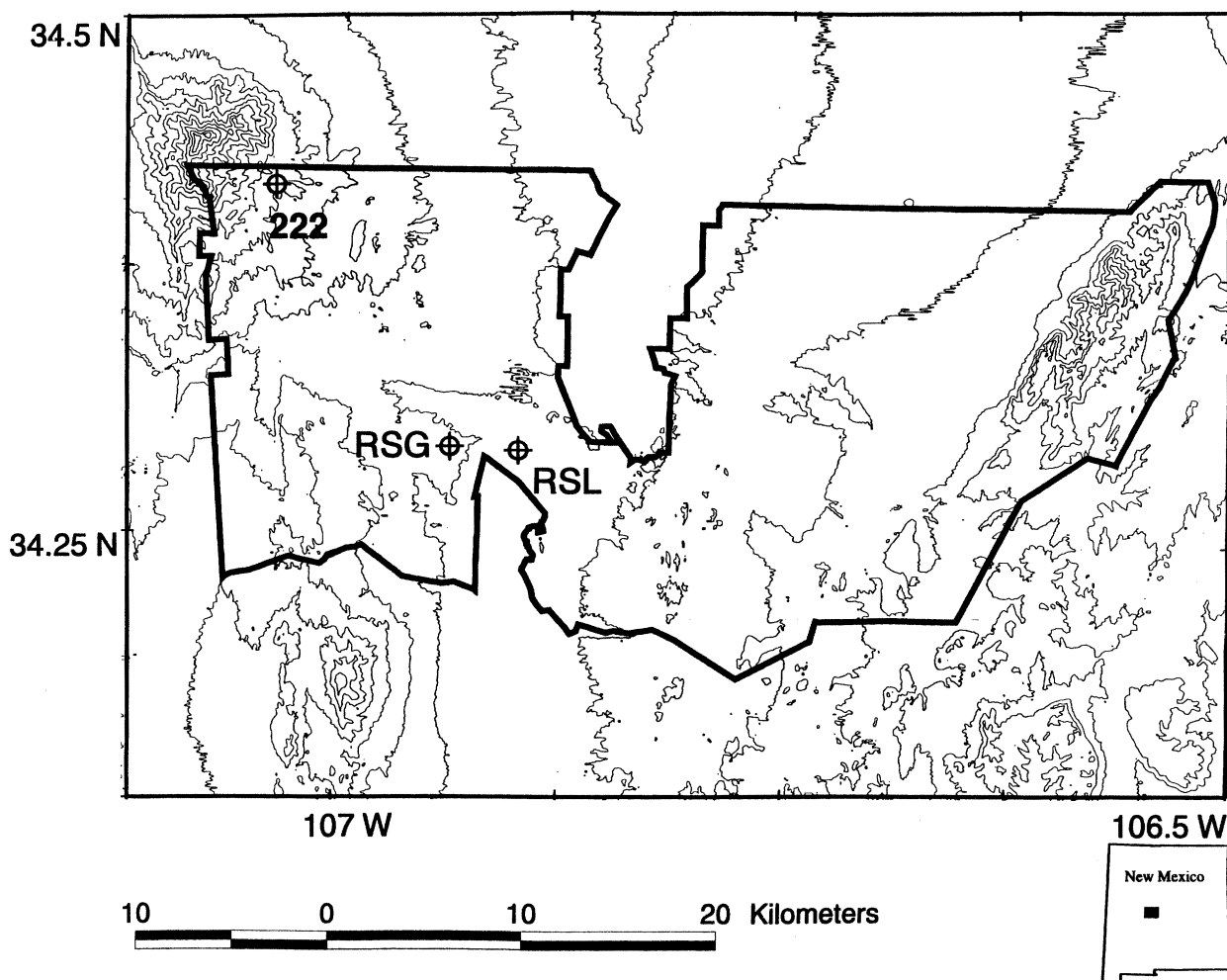


Fig. 1. Location of Sevilleta National Wildlife Refuge in New Mexico, USA. The figure was compiled by the Sevilleta LTER Center at the Univ. of New Mexico and is based on USGS Quadrangles and GPS Survey Data. The town of Socorro is located ca 30 km due south of the reserve. Legend: 222 – Two-22 Juniper woodland, RSG – Rio Salado grassland, and RSL – Rio Salado *Larrea*.

Museum of Southwestern Biology housed at the Univ. of New Mexico; the remainder are mark-recapture, with all animals released at the site. Detailed discussion of the web trapping protocol and implications can be obtained from Anderson et al. (1983) and Parmenter et al. (1989). Traps are baited with rolled oats and set for three consecutive nights, for a total of 2220 trap-nights per session per site. Thus, some 53 280 trap-nights of data were available for this study.

We restricted our data analysis to adult (>115 g) white-throated woodrats *Neotoma albigula*; a species adapted to arid environments. Several other woodrats *N. mexicana*, *N. micropus* occur at the Sevilleta NWR, but at extremely low densities. *Neotoma* are sexually dimorphic in body mass, with males ca 10% heavier than females. Consequently, mean body mass was calculated separately for each sex and then weighted by

the sex ratio. Statistics were conducted for each sex, as well as for the overall weighted average.

Results

Meteorological changes

Significant changes in temperature have occurred over the past decade at the Sevilleta NWR (Fig. 2, Table 1). Winters have become milder, with minimum temperatures averaging ca 2–3°C warmer in 1996 than in 1990 (Fig. 2a, Table 2). Although average maximum temperatures (AveHot) were not significantly different over this time period (Table 2), maximum temperatures rose ca 2–3°C (Fig. 2b, Tables 2 and 3). To determine if the temporal changes were part of the normal fluctuation in

temperature for the region, we compared these data with longer-term climatic records (1849–1992) from the Historical Climatic Network (HCN) for the town of Socorro, New Mexico (Fig. 1). To adjust for site differences between Socorro and the Sevilleta, regressions were conducted for the years for which overlapping data existed (1989–1992, Fig. 3). The regressions were highly significant in all cases, with $R^2 > 0.95$ (Table 2). Although the slopes did not significantly differ from one, the intercepts were not equal to zero, suggesting that consistent differences did exist in climatic regimes between Socorro and the Sevilleta (Fig. 3). Accordingly, the long-term mean from Socorro was corrected, and the deviation from the corrected long-term average was computed for each climatic variable at the Sevilleta (Fig. 4). A one-tailed Wilcoxon's signed-ranks test confirmed that each year from 1989 to 1996 was significantly warmer than the long-term minimum average (Fig. 4a, $N = 12$, $p < 0.005$ for all years but 1992, $p < 0.0461$ for 1992). Further, with the exception of November, December and January, all individual months have experienced significantly warmer minimum temperatures as well (one-tailed Wilcoxon's signed-ranks test, $N = 8$,

$p < 0.019$ or less). A significant increase in maximum temperature is demonstrated for 1989 and for all years from 1993 to 1996 (one-tailed Wilcoxon's signed-ranks test, $N = 8$, $p < 0.005$ for 1989, 1993–1995, $p < 0.0156$ for 1996); temperatures were not significantly different from the long-term mean in 1990, 1991 and 1992 (one-tailed Wilcoxon's signed-ranks test, $N = 8$, $p > 0.05$). The pattern for individual months was less clear; January, February, April and October were the only months that deviated significantly in maximum temperature over the 8 yr (one-tailed Wilcoxon's signed-ranks test, $N = 8$, $p < 0.027$ or less).

Woodrat body size

The design of the mammal webs was not optimized for capture of *Neotoma*, who tend to be heterogeneously dispersed across the landscape. Consequently, despite over 53 200 trap nights, <1% resulted in the capture of a white-throated woodrat (466 individuals, Table 1). More animals were trapped on the Rio Salado habitats ($N = 339$) than on the Two-22 site ($N = 127$), even when corrected for the greater number of webs located there. The number of juveniles present was not significantly influenced by location (ANOCOVA, $p > 0.748$, $DF = 1$) nor year ($p > 0.117$). Overall, slightly more animals were captured on the two removal plots at each location (46%) than expected (2/5 webs = 40%), but this difference was not significant (ANOVA, $p > 0.455$, $DF = 4$).

There was no effect of location or habitat type on mean adult body mass (ANOCOVA, $p > 0.355$, $DF = 2$), although year was highly significant in this and all subsequent analyses ($p < 0.02$ or less). As expected, adult body mass was significantly influenced by gender (ANOCOVA, $p < 0.002$, $DF = 1$), but there were no interactions between gender and year or between gender and location (two-way ANOCOVA, $p > 0.622$, $DF = 1$). Mean body mass of adult males across the Sevilleta was 174.1 g ($\sigma = 36.72$, range 116–247 g, $N = 106$) vs 160.0 g for females ($\sigma = 27.24$, range 116–267 g, $N = 151$). Because there was no effect of location on mean body mass, we pooled the data across the Sevilleta NWR to increase sample sizes. The grand mean for each year was adjusted for differences in the sex ratio of the population by taking the average of the separately computed means for adult males and females.

The ANOCOVA results suggested that body mass of the adult woodrat population had varied significantly with year. The result was confirmed when we regressed the weighted population mean across the Sevilleta against year (Fig. 5). Because more females were captured than males (Table 1), we reran the analysis using only the average body mass of adult females (which allowed us to use the data for 1991) and obtained virtually the same regression ($y = -3.298x + 6730.5$,

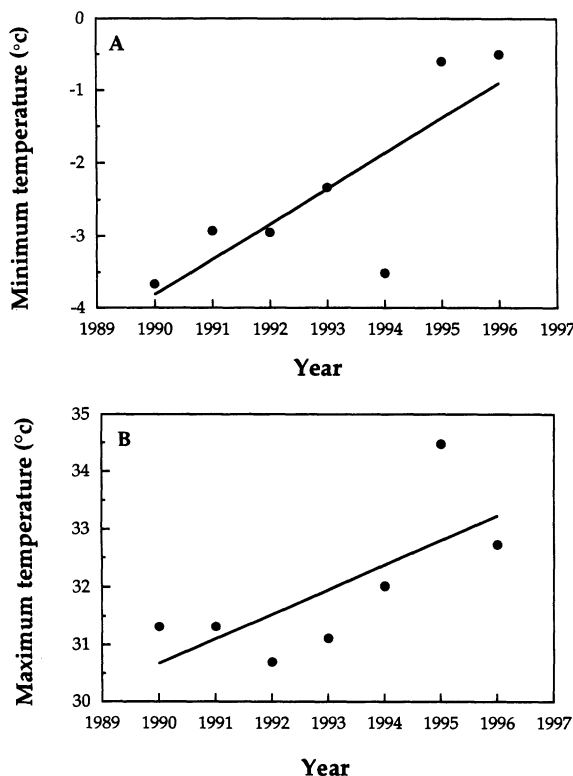


Fig. 2. Temperature changes over the past 8 yr at the Sevilleta NWR. A) Minimum temperature [MinCold = the average minimum for the months of December, January and February]; B) Maximum temperature [MaxHot = the average maximum for the months of July, August and September]. Regression equations are included in Table 2. Both relationships are best fit by a linear model.

Table 1. Summary of trapping and meteorological data for the Sevilleta NWR in 1989–1996. Terms are as follows: Mean adult body mass (MBM), standard deviation (SD), sample size (N), precipitation (Ppt), minimum cold temperature (MinCold), average cold temperature (AveCold), maximum hot temperature (MaxHot), average maximum hot temperatures (AveHot), percent female (% Female). Body mass data for an additional 32 animals were listed as > 100 g.

Year	MBM (g)	SD	N adult	N juvenile	Ppt (mm)	MinCold (°C)	AveCold (°C)	MaxHot (°C)	AveHot (°C)	% Female
1989	185.9	23.7	12	10						69
1990	162.7	17.4	9	7	203.5	−3.67	3.17	31.32	24.43	46
1991	150.6	17.4	10	10	222.5	−2.93	3.65	31.32	24.55	78
1992	170.9	12.5	59	35	347.2	−2.95	2.96	30.70	23.62	53
1993	169.0	6.91	88	54	244.3	−2.34	3.93	31.12	23.59	61
1994	160.7	8.15	39	16	267.7	−3.52	4.25	32.02	24.75	58
1995	155.7	9.1	32	37	249.1	−0.60	6.29	34.47	25.77	63
1996	153.6	20.46	10	5	120.2	−0.50	6.78	32.73	24.98	60

Table 2. Equations of regressions of climatic data from the Sevilleta NWR vs year, and vs overlapping weather data from Socorro, New Mexico. Regression equations and one-tailed *p* values are given.

	Equation	<i>r</i> ²	<i>p</i>
Sevilleta NWR vs year (1989–1996):			
MinCold	$y = 0.485x - 970.4$	0.642	0.015
AveCold	$y = 0.621x - 1234.1$	0.794	0.004
MaxHot	$y = 0.423x - 811.5$	0.501	0.038
AveHot	$y = 0.186x - 347.0$	0.277	0.113
Precipitation	$y = -9.860x + 19895.9$	0.096	0.249
Sevilleta NWR vs Socorro (1989–1992):			
Minimum temperature	$y = 1.087x + 1.79$	0.956	0.001
Maximum temperature	$y = 1.009x - 2.39$	0.985	0.001

Table 3. Results from linear regressions conducted between the various climatic variables measured at the Sevilleta NWR from 1989 to 1996 (Pearson correlation coefficients are above the diagonal, two-tailed *p* values are given below). Data are pooled across the Sevilleta NWR. Abbreviation of variables, see Table 1.

	MBM	Year	Ppt	MinCold	AveCold	MaxHot	AveHot
MBM	—	−0.820	0.721	−0.641	−0.875	−0.834	−0.916
Year	0.024	—	−0.311	0.801	0.891	0.708	0.527
Ppt	0.106	0.498	—	−0.453	−0.596	−0.323	−0.438
MinCold	0.170	0.030	0.307	—	0.913	0.760	0.566
AveCold	0.022	0.007	0.158	0.004	—	0.860	0.758
MaxHot	0.039	0.075	0.479	0.048	0.013	—	0.921
AveHot	0.010	0.225	0.338	0.185	0.048	0.003	—

$r^2 = 0.583$, two-tailed $p < 0.05$, $DF = 6$). The relationship between body mass and year was relatively robust; results were qualitatively similar when we eliminated years for which small sample sizes existed (e.g. 1991, 1996). Responses of males and females were positively correlated. A regression of male vs female body mass indicated that years when males were larger, females were larger as well ($y = 0.850x + 44.08$, $r^2 = 0.414$). The population was largely post-reproductive; results were not influenced by reproductive status (ANOCOVA, $p > 0.05$).

To determine if woodrat body mass changes were correlated with climatic conditions, we conducted linear regressions against each weather variable (Fig. 6, Table 3). Mean body mass was not significantly correlated with precipitation ($y = 7.78x - 1022.9$, $r^2 =$

0.520, $p > 0.105$, $DF = 6$) or minimum temperature (MinCold, $y = -0.130x + 18.82$, $r^2 = 0.411$, $p > 0.169$, $DF = 6$), but was highly correlated with the other temperature measures (MaxHot, $y = -0.166x + 58.99$, $r^2 = 0.696$, $p < 0.039$, $DF = 6$; AveHot, $y = -0.111x + 42.46$, $r^2 = 0.839$, $p < 0.010$, $DF = 6$; AveCold, $y = -0.203x + 37.42$, $r^2 = 0.766$, $p < 0.022$, $DF = 6$). Because the climatic variables were highly correlated with each other (e.g. Table 3), we did not conduct multivariate regressions on these data. In general, analysis of covariance (e.g. body mass by reproductive condition, location, gender, trap, etc., with each climatic variable) confirmed the earlier results. Precipitation still did not influence body mass ($p > 0.371$), but MinCold yielded significant results ($p < 0.04$).

Discussion

We initially set out to address three questions: i) had detectable climatic change occurred at the Sevilleta over the past 8 yr? ii) had detectable changes occurred in mean body mass of woodrats *Neotoma* over the past 8 yr? iii) were any size changes that may have occurred correlated with changing environmental conditions? The answer to all three questions appears to be "yes". Not only is the Sevilleta NWR ca 2–3°C warmer than it was eight years ago, but each one degree increase in average winter and/or summer temperature has lead to a ca 10 g reduction of the average body mass of the

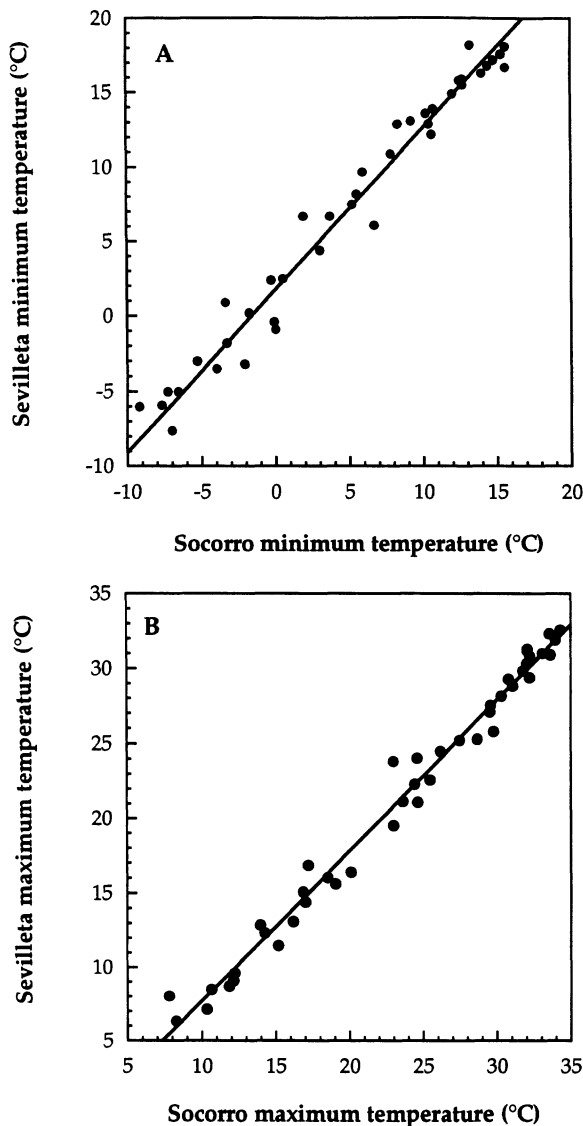


Fig. 3. Site differences between the Sevilleta NWR and the town of Socorro, New Mexico. A) Minimum monthly temperature for the years 1989–1992; B) Maximum monthly temperature for the years 1989–1992. Terms are defined in text and in Fig. 2. Regression equations are included in Table 2.

woodrat population. The response of woodrats has been both stronger and more rapid than we originally anticipated, and appears to be more directly influenced by temperature than habitat type. Overall, there were no significant differences in mass between the study locations (ANCOVA results). In 1994, however, the difference in MinCold between the Two-22 and Rio Salado sites was 1.77°C, almost as great as that occurring during the eight years of the study. In this year, mean body mass for the two sites was significantly different (two-tailed t-test, $p < 0.05$), with animals at Rio Salado larger than those at Two-22.

We cannot rule out the possibility that mass changes in the woodrat population are actually due to some unmeasured factor correlated with the observed climatic fluctuations. We were unable to directly compare body mass changes with plant abundance and/or composition, for example, because quantitative vegetational analyses had not been consistently conducted on each site. It also should be noted that sample sizes for several years are relatively small (Table 1). Although the overall results are not particularly sensitive to those years (e.g. Fig. 5), it does indicate the need for some caution when quantitatively interpreting the data.

Our results are only marginally affected by ontogeny and probably only slightly skewed by age structure. Although mammal trapping is conducted twice a year at the Sevilleta NWR (> 106 400 trap nights were actually available for the 8 yr), we used data only for the first trapping period in late spring (post-reproduction). It is unlikely that young born early in the season could attain an adult body mass of 115 g or greater by June. Thus, our data set largely represented animals that had successfully overwintered. Woodrats typically exhibit a sigmoidal growth curve, with little change in adult mass after maturity (e.g. Linsdale and Tevis 1951, Bleich and Schwartz 1974, Schwartz and Bleich 1975, Smith 1996). Consequently, whether the animals were born the previous spring or summer is unlikely to materially influence body mass. Woodrats were not individually identified from year to year, so it is not possible to estimate what proportion of the data set represented yearly recaptures, nor to estimate survivorship. We suspect recaptures represent a very small fraction. Not only do woodrats have a very steep survivorship curve with mean life expectancy considerably less than one year (e.g. Linsdale and Tevis 1951, Smith 1996), but ca 75% of the population was removed annually (ca 46% of captures occurred on the removal webs, which were trapped twice each year). Thus, we estimate that there was almost complete annual turnover of the population at our study locations.

There are a number of likely mechanisms that may explain the robust response of woodrat body size to temperature. One is that greater numbers of smaller bodied individuals are overwintering successfully, shift-

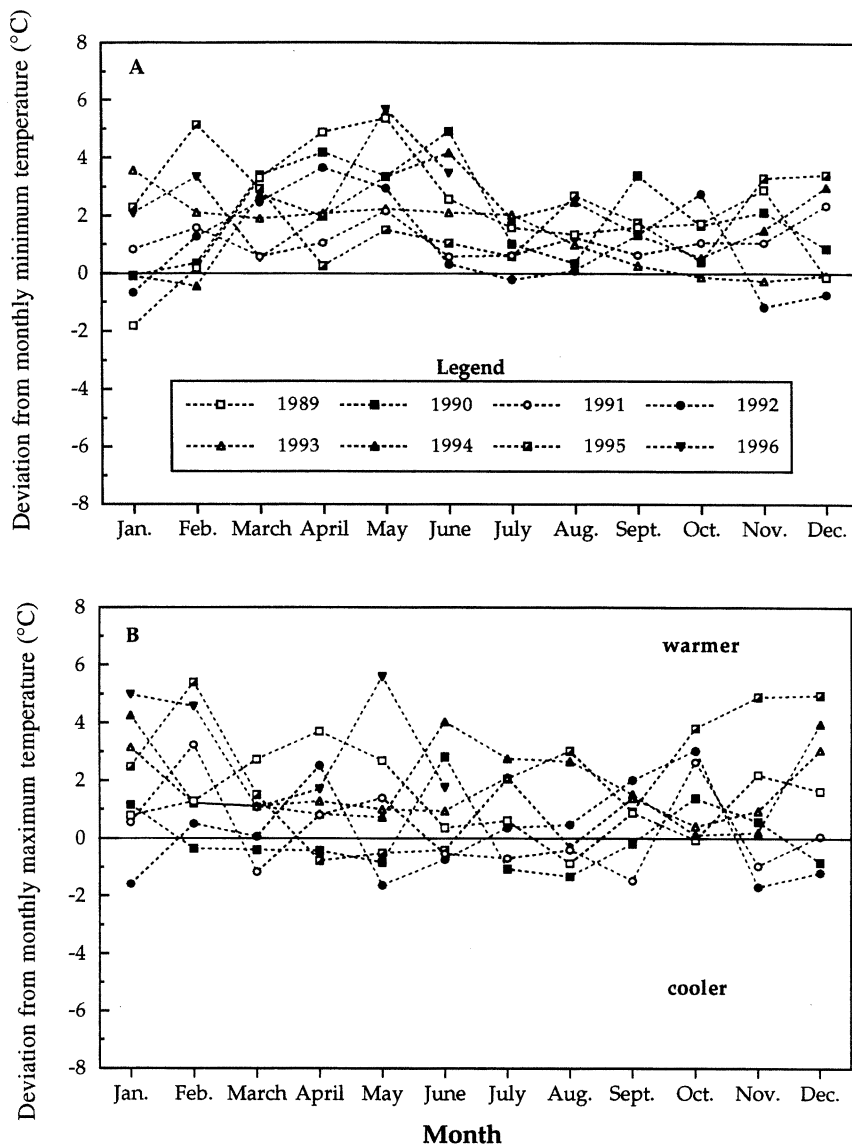


Fig. 4. Deviations from corrected long-term climatic averages versus month. A) Deviations from average minimum temperature for each month from 1989 to 1996; B) Deviations from average maximum temperature for each month from 1989 to 1996. Long-term climatic averages are from a meteorological station at Socorro, New Mexico, and are adjusted for site differences between the Sevilleta NWR and Socorro (see Fig. 3, Table 2).

ing the population mean downward. This may well be a direct physiological result of milder winter temperatures requiring less fat reserves or permitting animals with a higher surface to volume ratio, and consequently a higher heat loss, to survive. The correlation with warm temperature was particularly robust and may also reflect a direct physiological response. White-throated woodrats inhabit an environment where they consistently face summer temperatures only a few degrees below their lethal limits (Brown 1968). Lee (1963) argued that high diurnal temperatures experienced within the den or nest chamber were more important than low temperatures experienced while active at night. Our findings support his theory; while body mass is significantly correlated with both minimum and maximum temperatures (e.g. Table 3, Fig. 6), it is apparently more

responsive to sustained high temperature (AveHot). The temporal response we observed (Fig. 5) cannot be explained by summer temperature alone, however, since neither one of the warm temperature measures (MaxHot, AveHot) was significantly correlated with year (Table 3).

Do the observed body mass changes result from phenotypic plasticity or genetic changes in the woodrat population? While we cannot directly address this issue, we suspect that both factors may be operating. Previous work has indicated that the heritability of body size in *Neotoma* is very high (Smith et al. 1995, Smith unpubl.), and research with other species within the genus also demonstrates a strong and robust relationship with temperature (Brown 1968, Brown and Lee 1969, Smith et al. 1995). Further, body mass and length are highly

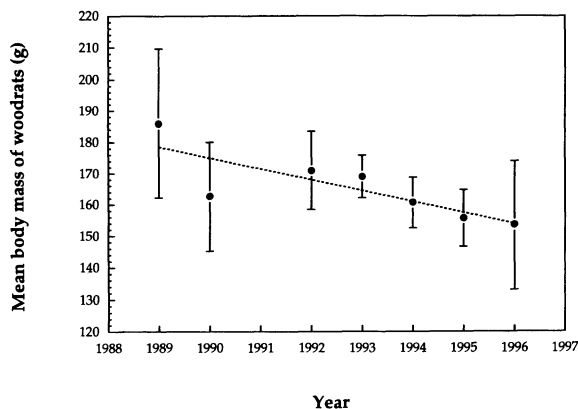


Fig. 5. Mean body mass of woodrats *Neotoma albigula* at Sevilleta NWR over the past 8 yr. Means are weighted to correct for bias due to an unequal sex ratio (see text). Equation of regression is $y = -3.518x + 7175.4$, $r^2 = 0.672$, $p < 0.024$. Data from 1991 are excluded because the number of males captured was extremely low, and so it was not possible to calculate a weighted mean. Values are shown with associated 95% confidence interval.

correlated for *Neotoma* (e.g. Smith 1992), so it is likely that at least some of the mass differences between years reflect real changes in body skeletature, rather than varying fat content.

Our results suggest that further climatic change will have substantial and measurable impacts on the life history and ecology of woodrats at the Sevilleta. Smaller body size directly impacts woodrat foraging and dietary strategy (e.g. Justice and Smith 1992, Smith 1995), for example, forcing smaller animals to depend on higher quality food items. These items are not only less predictable both temporally and spatially, but may also incur higher energetic costs in terms of foraging time and increased competitive pressures from other rodents. We have focused on woodrats because of their robust physiological response to temperature (Brown 1968, Brown and Lee 1969, Smith et al. 1995), which makes them a particularly sensitive indicator species. Our work indicates that aside from the predicted impacts on distribution and abundance (e.g. Vitousek 1992, Murphy and Weiss 1992, Smith and Buddemeier 1992, Webb and Bartlein 1992, Field et al. 1992), climate change is likely to directly influence the life histories of organisms.

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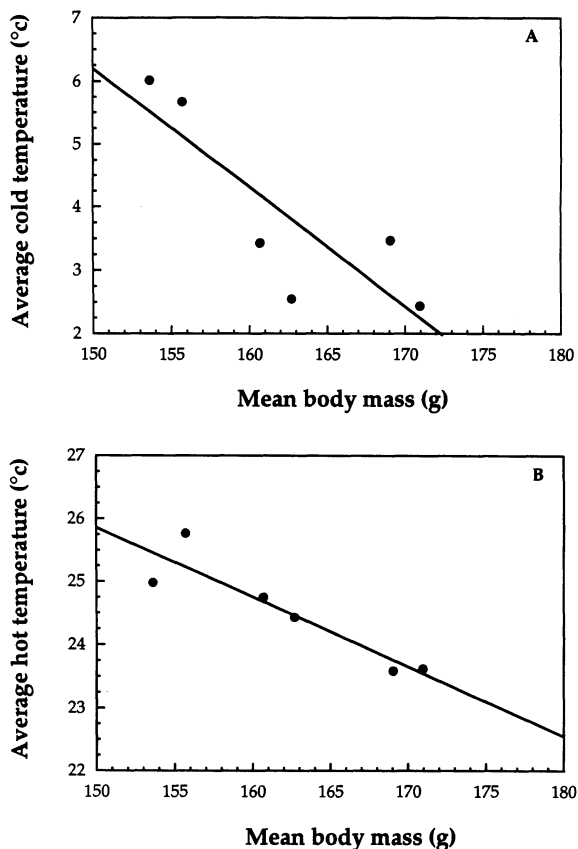


Fig. 6. Climatic variables plotted against mean body mass of woodrats at the Sevilleta NWR. A) Average minimum temperature [AveCold], $y = -0.203x + 37.42$, $r^2 = 0.766$, $p < 0.022$, $DF = 5$; B) Average maximum temperature [Ave-Hot], $y = -0.111x + 42.46$, $r^2 = 0.839$, $p < 0.010$, $DF = 5$.

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