QUATERNARY RESEARCH **50,** 1–11 (1998)
ARTICLE NO. QR981982

Response of Bushy-Tailed Woodrats (*Neotoma cinerea*) to Late Quaternary Climatic Change in the Colorado Plateau

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Temperature profoundly influences the physiology and life history characteristics of organisms, particularly in terms of body size. Because so many critical parameters scale with body mass, long-term temperature fluctuations can have dramatic impacts. We examined the response of a small mammalian herbivore, the bushy-tailed woodrat (*Neotoma cinerea*), to temperature change from 20,000 yr B.P. to present, at five sites within the Colorado Plateau. Our investigations focused on the relationship between temperature, plant composition and abundance, and woodrat size. Body size was estimated by measuring fossil fecal pellets, a technique validated in earlier work. We found significant and highly covariable patterns in body mass over the five locations, suggesting that responses to temperature fluctuations during the late Quaternary have been very similar. Although woodrat mass and the occurrence of several plant species in the fossil record *were* significantly correlated, in virtually all instances changes in woodrat size preceded changes in vegetational composition. These results may be due to the greater sensitivity of woodrats to temperature, or to the shorter generation times of woodrats as compared to most plants. An alternative hypothesis is that winter temperatures increased before summer ones. Woodrats are highly sensitive to warmer winters, whereas little response would be expected from forest/woodland plants growing at their lower limits. Our work suggests that woodrat size is a precise paleothermometer, yielding information about temperature variation over relatively short-term temporal and regional scales.

Key Words: **Bergmann's rule; body mass; temperature fluctuations; Pleistocene/Holocene.**

INTRODUCTION

> *Toute chose étant égale d'ailleurs, des corps de même nature perdent à chaque instant des quantités de chaleur qui sont proportionnelles à l'étendue de leur surface libre . . .* [*roughly translated—''all else being equal, bodies of the same nature lose at each instant quantities of heat which are proportional to the extent of their free surface . . .''*]
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> —Rameaux and Sarrus (1838; p. 1095)

An animal's phenotype results from a balance of opposing selection pressures operating at different spatial and temporal scales. Perhaps the most obvious manifestation of phenotype is size, which may be influenced by such factors as maternal investment, digestive efficiency, fecundity, crypsis, competitive pressures and thermal constraints. Of these, temperature in particular has been demonstrated to operate over large-scale spatial and temporal dimensions (Andrewartha and Birch, 1954; Mayr, 1956, 1963; Birch, 1957; Brown, 1968; Brown and Lee, 1969; Panteleyev and Terekhina, 1980; Tracy, 1992).

Carl Bergmann (1847) is routinely credited with the notion that the heat loss of an organism is proportional to its surface to volume ratio, an observation that led to the ecogeographic rule that bears his name (but see quote above). Bergmann's Rule states that there is a positive relationship between body size and latitude, presumably resulting from the selective advantage of a higher body surface to volume ratio in warm areas, or conversely, to the reduced heat loss that accompanies a lowered surface to volume ratio in higher-latitude climates (e.g., Mayr, 1956, 1963; Brown and Lee, 1969). Recently, Bergmann's rule has been demonstrated to hold for temporal as well as spatial temperature fluctuations (Davis, 1977, 1981; Purdue, 1980; Klein and Scott, 1989; Smith *et al.*, 1995; Smith *et al.*, 1988; but see Dayan *et al.*, 1991), reinforcing the importance of temperature as a critical selective pressure (Dawson, 1992).

Increasingly, paleobiologists consider the evolutionary and biological effects of global temperature fluctuations at different frequencies. Redistribution of land masses and mountain uplift drives large-scale changes in global climate on scales of 10^6 yr, while changes in the earth's orbital parameters (Milankovitch forcing) pace changes on scales of 10^4 and 10^5 yr, including glacial-interglacial cycles. At the scale of 10^3 yr, the Greenland ice-core record documents more than 20 abrupt, millennial-scale warming events during the last glaciation, referred to as ''Dansgaard-Oeschger interstades'' (Dansgaard *et al.*, 1993). Warming apparently occurred within decades, followed by gradual return to gla-

0033-5894/98 $25.00

cial conditions over hundreds of years. These 2000- to 3000-yr oscillations occur in series (referred to as Bond cycles), in which the amplitude increases until an unusually cold phase, or Heinrich event, is succeeded by unusual warmth (Bond and Lotti, 1995). From the so-called ‘‘hothouse’’ climates of the Eocene to the Dansgaard-Oeschger events of the Pleistocene, global temperature fluctuations no doubt have exerted substantial selection pressures on organisms, as evidenced by the fossil record for expansion and contraction of the world’s major biomes throughout the Neogene (Huntley and Webb, 1988).

Here, we examine the influence of temperature fluctuations over the past 20,000 years on the body size of woodrats (*Neotoma*) in the Colorado Plateau. Woodrats, small herbivorous rodents, have been demonstrated to be particularly sensitive to temperature (e.g., Lee, 1963; Brown, 1968; Brown and Lee, 1969; Smith *et al.*, 1995; Smith *et al.*, 1988). We focus on five sites that span a relatively restricted geographic region, and compare the response of woodrats both within and between locations. Body mass is estimated from fossil fecal pellets taken from woodrat paleomiddens; dates were determined by radiocarbon dating. Relatively long chronosequences from each site permit the evaluation of woodrat response from what is presumably a single population, as well as investigation of the possible covariation between plant occurrence and woodrat size change.

MATERIALS AND METHODS

Study Sites

The study sites were located in a region bounded by the Colorado Plateau, and all were within the modern distribution of the bushy-tailed woodrat, *Neotoma cinerea* (Fig. 1; Hall, 1981). During full-glacial time *N. cinerea* may have ranged as far south as northern Mexico (Harris, 1984, 1985, 1993). As in many boreal animals, southern distributional limits were shifted northward and to higher elevations as climate warmed. The modern distribution of several other woodrat species (*N. lepida,* the desert woodrat; *N. albigula,* the white-throated woodrat; *N. mexicana,* the Mexican woodrat) overlap that of *N. cinerea* in the southern portion of the Colorado Plateau. There are clear habitat preference differences among each of these different species, however, and the others are not only much smaller but are primarily restricted to low-elevation, xeric sites (Finley, 1958; Smith, 1997). Because *N. cinerea* is the largest and behaviorally dominant woodrat in the Southwest, as well as the only mesic or montane adapted species (Finley, 1958; Brown and Lee, 1969; Smith, 1997), microhabitats that are currently occupied by this species are unlikely to have been inhabitated by other species in the past. Exceptions may have occurred in the southern part of their distribution during the middle Holocene (8000–4000 yr B.P.), when environmental conditions may have been considerably more xeric. The sampling design was able to detect possible species replacements, however, and fossil evidence was used when available to verify species identification independently.

On the Colorado Plateau, most middens were located in recessed rock shelters within sandstone or limestone cliffs. Sites were chosen that had yielded relatively long chronosequences (*N* ranged from 3 to 17, although not all middens from a location were available), in some instances spanning 20,000 years or more. Most middens already had been radiocarbon dated; for these samples all measurements were conducted before the dates were obtained. Modern temperatures for each site were extracted from the Historical Climatology Network (HCN) and generally represented a 70- to 100-yr average. Temperature records were adjusted for elevational differences as necessary, using a warm-month lapse rate of 8.78 ± 0.80°C/km ($r = -0.964$, $p < 0.001$), and cold-month lapse rate of 6.9 ± 1.8°C/km ($r = -0.789$, $p < 0.004$) for Southwestern Colorado (Meyer, 1992).

Midden Processing and Pellet Measurements

Indurated middens were disassociated by soaking in water for several days (e.g., Spaulding *et al.,* 1990). After drying, the materials were sieved and the fecal pellets segregated from the other materials. Pellets were subsequently sorted on the basis of size. The width of the largest ~200 pellets (or ~20% of those available, whatever was greater) was measured to the nearest 0.1 mm, using digital calipers. Previous work had determined that pellet width is significantly related to body mass ($r^2 = 0.69$; $p < 0.0001$); the relationship is not appreciably affected by diet, gender or species (Smith *et al.,* 1995). Previous work had also indicated that measuring 10–20% of the sample is sufficient to characterize the largest pellets; above this threshold maximum size does not vary with sample size. When fewer than 200 pellets were present, all were measured. Pellets with widths less than 4.0 mm (~90 grams) were discarded because of a large increase in measurement error that arose at these size classes (Smith *et al.,* 1995), and because of the difficulty in excluding juvenile woodrats or even large deer mice (*Peromyscus* spp.). The mean, standard deviation, and 95% confidence interval of the 10, 20, and 50 largest pellets, respectively, were calculated, as was the grand mean. The mean of the 20 largest (hereafter denoted as mean_{20}) was chosen to represent body size rather than the grand mean because it (i) was not sensitive to sample size, (ii) minimized measurement and/or environmental error, (iii) avoided the confounding effects of ontogeny, (iv) excluded pellets from other commensuals (e.g., large bodied *Peromyscus* spp.), and perhaps most importantly, (iv) provided additional verification that middens were constructed by *N. cinerea* (no other woodrat within the region overlaps in maximum body mass, and even subadult *N. cinerea* are usually larger than the largest individuals of

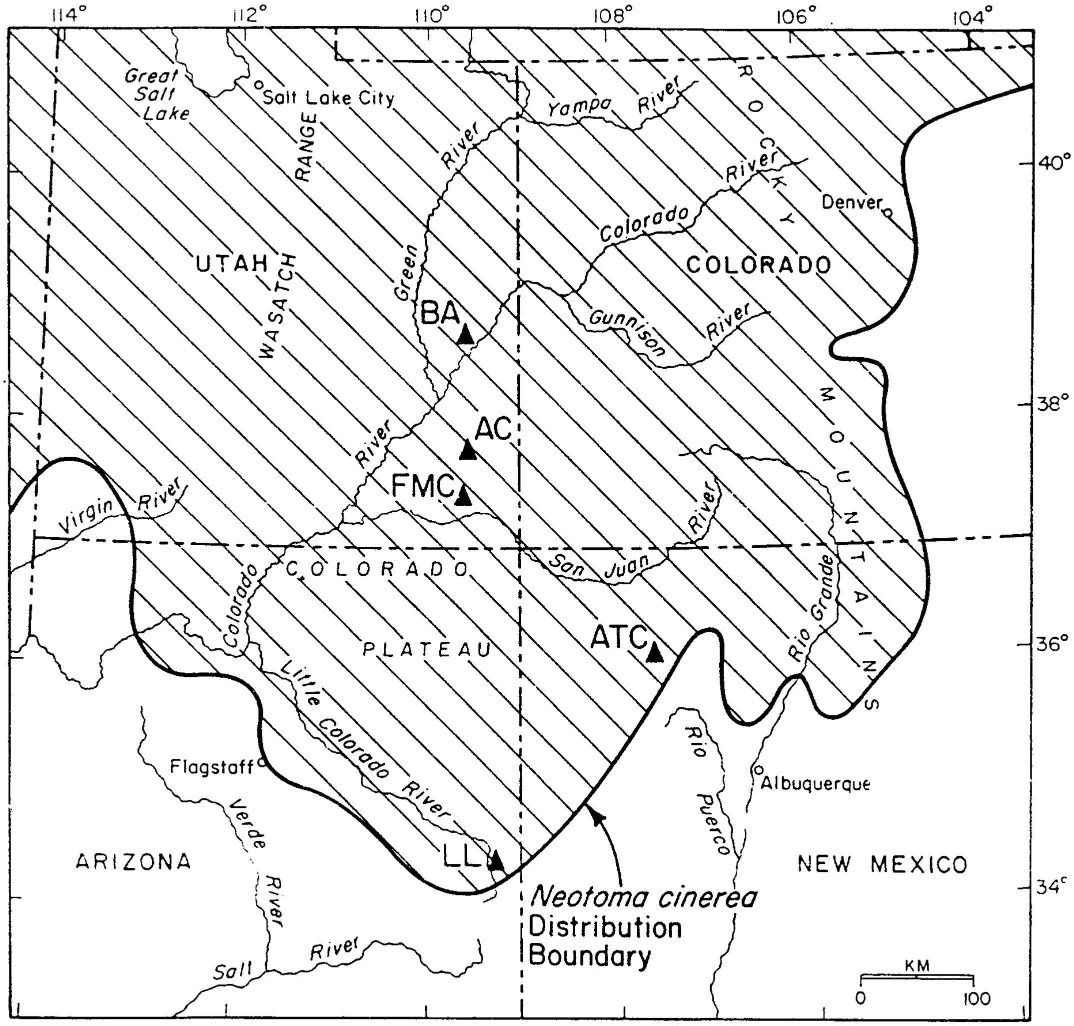

FIG. 1. Map showing location of midden sites within the Colorado Plateau, Southwestern United States. Legend (and collectors): AC = Allen Canyon Cave (J. L. Betancourt), ATC = Atlatl Cave (J. L. Betancourt), BA = Bison Alcove (S. Sharpe), FMC = Fishmouth Cave (J. L. Betancourt), LL = Lyman Lake (P. Koehler).

other coexisting species). Results were qualitatively similar, however, regardless of the number of pellets chosen.

Most middens had been previously radiocarbon dated on plant macrofossils. With the exception of Bison Alcove, middens dated with pellets were not used because of possible bias introduced by removal of the radiocarbon sample. Although Bison Alcove middens *were* dated on pellets prior to measurement, it is unlikely that removal of a small aliquot of pellets from the several thousand contained in these samples materially biased our measurements. We tested this assumption by comparing the rank order of pellet sizes calculated with the inclusion or exclusion of the designated radiocarbon aliquot for several undated middens from Bison Alcove. Results of this analysis confirmed our supposition (t-test, $p > 0.05$, $df = 1$). We found absolutely no difference among overall rank order, mean_{20}, standard deviation, or any other statistic. In other instances, however, samples sizes were not great enough to rule out the potential of introduced bias, so middens radiocarbon-dated on pellets were *not* utilized. Measurements were conducted on Lyman Lake samples prior to radiocarbon dating.

Histograms were plotted for each midden sample to examine the shape of the pellet width distributions. If two distinct climatic regimes (or a species replacement) had occurred within a deposition interval, we anticipated that the histograms might exhibit a skewed or bimodal shape. As expected, for most samples the histograms approximated a left-truncated normal distribution. The two or three Lyman Lake middens with samples sizes below 100 were more difficult to characterize, but no paleomiddens demonstrated a strikingly skewed or bimodal distribution. The shapes of the histograms did not suggest that two

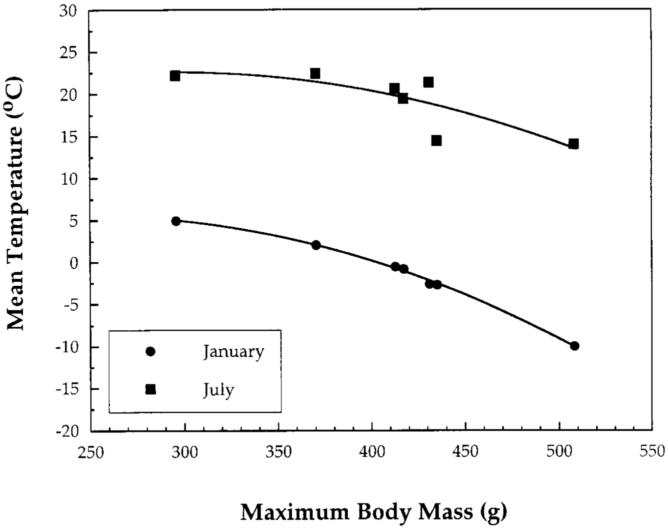

FIG. 2. Mean July and mean January temperature plotted against maximum body mass of contemporary populations of *Neotoma cinerea.* Data were taken from museum specimens housed at the Smithsonian, Museum of Vertebrate Zoology (University of California Berkeley), Museum of Southwest Biology (University of New Mexico) and from unpublished trapping records (M. Smith, unpublished data). Maximum body mass was calculated as the mean of the three largest individuals from each location from a pool of 20–100 adult animals. Weather data represent a minimum of a 50-year average and were obtained from the Historical Climatology Network. Maximum body mass was used rather than the grand mean to ensure that animals had experienced multiple episodes of thermal section (see text). Regression equations: Mean July temperature, $y = 5.632 + 0.115x - 0.0002x^2$, $r^2 = 0.657$, $df = 5$, $p < 0.05$; Mean January temperature, $y = -8.207 + 0.112x - 0.0002x^2$, $r^2 = 0.997$, $df = 5$, $p < 0.001$.

distinctly different climatic regimes were represented within a deposition interval.

Estimating Body Mass and Temperature

Body mass estimates were derived from the mean_{20} using the linear regression equation provided by Smith *et al.* (1995; $y = 0.005x + 3.559$; $r^2 = 0.69$; $p < 0.0001$). Chronosequences for each site were graphed using the mean_{20} versus uncorrected radiocarbon date. Relative size was calculated for each paleomidden by dividing the mean_{20} pellet width by the mean_{20} pellet width for a modern midden from the same location. This permitted the simultaneous comparison of sites spanning different latitudes and elevations, but left some scatter representing geographic variation in the timing and magnitude of various paleoclimatic events.

Mean July and January temperatures were estimated for each paleomidden, using regression equations derived from the relationship with spatial variation seen among contemporary bushy-tailed woodrats (Fig. 2; July temperature, $y = 5.632 + 0.115x - 0.0002x^2$, $r^2 = 0.657$, $df = 5$, $p < 0.05$; January temperature, $y = -8.207 + 0.112x - 0.0002x^2$, $r^2 = 0.997$, $df = 5$, $p < 0.01$). Maximum (asymptotic) body mass of contemporary populations was chosen so that results could be compared directly with the paleomidden data, and because other work suggested that mean body mass of a population underestimated the effect of temperature on woodrats (F. A. Smith, unpublished data), Estimates of mean body mass generally incorporate subadult animals that have attained body masses within the range of mature individuals, but have not yet successfully overwintered. By utilizing maximum mass, we ensured that animals had experienced multiple episodes of thermal (both hot and cold) selection. Relative temperature for each paleomidden was calculated by dividing the temperature estimated from the paleodata by the estimated modern temperature from a modern midden at the same location. We were unable to calculate relative temperature for Allen Canyon Cave because we did not have a modern midden from this location.

Plant Analyses

Plant macrofossils lists were obtained from the collectors and/or literature for Bison Alcove, Fishmouth and Allen Canyon Caves, Lyman Lake, and Atlatl Cave in Chaco Canyon (Betancourt *et al.,* 1983; Betancourt, 1984, 1990; Sharpe, 1991; P. Koehler, written communication, 1995). Abundances classified as ‘‘none’’ or ‘‘trace’’ (0 or 1, respectively on a relative scale) were considered to be absent; greater abundance (e.g., 2–5) was considered present. Analysis of variance was conducted to determine the amount of variation that could be explained by presence or absence of particular plant species. For sites with at least one record of a particular plants species, mean relative body size was computed in the absence and presence of each plant species. Additionally, data were examined to determine if body size changes preceded, succeeded or occurred simultaneously with plant disappearance or appearance from the fossil record. At all of the sites forest/woodland plants such as limber pine (*Pinus flexilis*), Douglas fir (*Pseudotsuga menziesii*), Rocky Mountain juniper (*Juniperus scopulorum*), and blue spruce (*Picea pungens*) would have been growing at or near their lower limits during the Pleistocene.

RESULTS

Chronosequences

Results were qualitatively similar at all five sites (Fig. 3; Table 1). Woodrats were larger during the late Pleistocene and declined to near modern sizes by early in the Holocene. There appears to be a latitudinal effect, with body mass of woodrats at the southern sites decreasing earlier than those farther north, but this conclusion is complicated by the incompleteness of the midden record (only a few locations contained paleomiddens dated older than 16,000 ^{14}C yr B.P.). Further, the inverse relationship between elevation and latitude (the southern sites are at considerably higher elevations

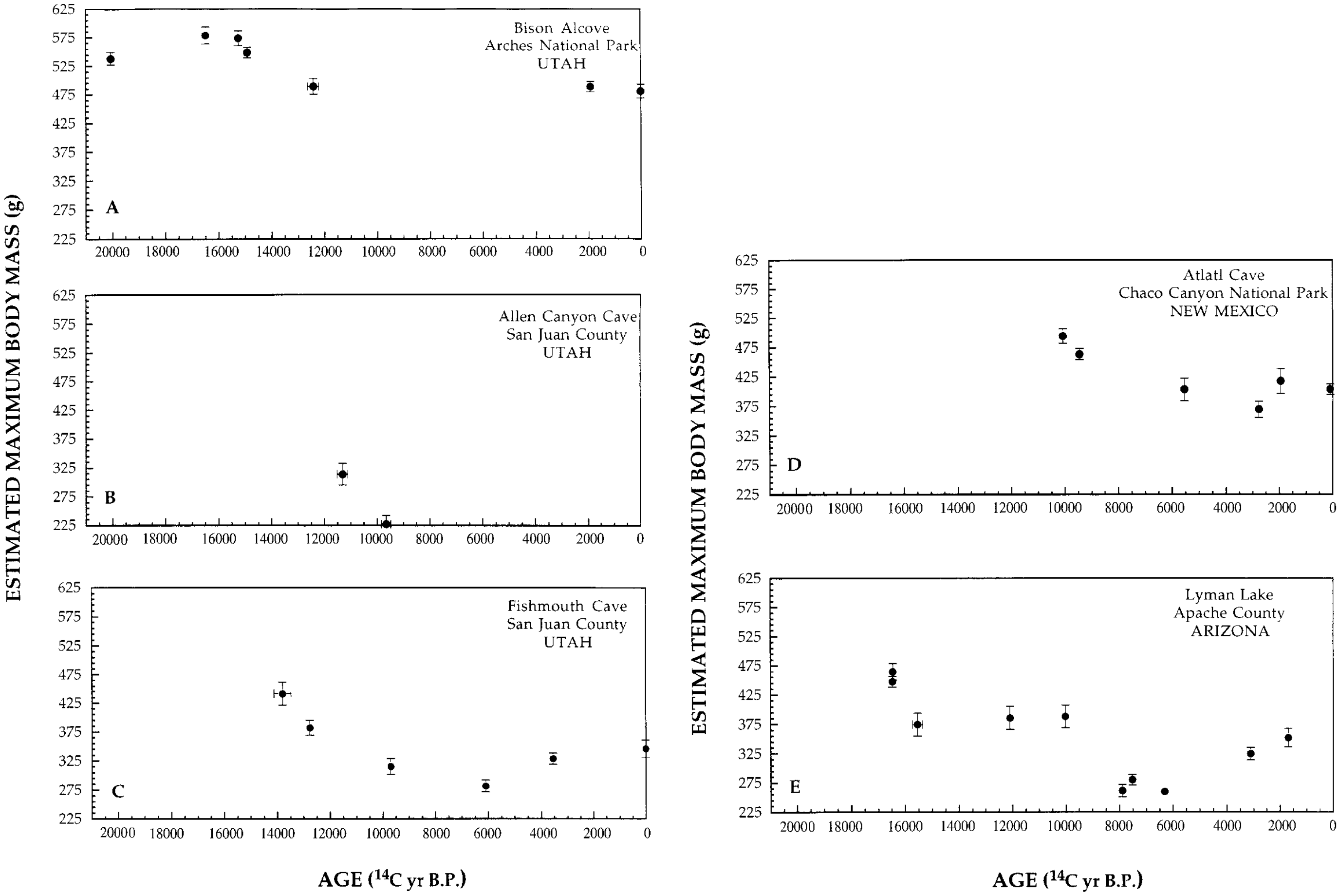

FIG. 3. Chronosequences of body size (mean$_{20}$) from midden sites in the Colorado Plateau: (A) Bison Alcove; (B) Allen Canyon Cave; (C) Fishmouth Cave; (D) Atlatl Cave; (E) Lyman Lake. Results have been plotted as mass estimates rather than the actual measured pellet width for ease of interpretation. Bars around values represent the 95% confidence interval. If no bars are indicated, the uncertainty in the estimate was less than the size of the symbol. Deposition dates were determined by radiocarbon dating the pellets and/or plant macrofossils within the midden, and are uncorrected. Exact locations and details regarding sites are provided in Figure 1 and Table 1.

than the northern ones) may partially obscure such a relationship. Although the decrease in woodrat body size seen at the Pleistocene/Holocene is monotonic for all sites, considerable variation is evident during the mid to late Holocene. During the mid-Holocene, for example, body mass decreases at all sites, but an abrupt increase in body mass is seen at about 2000 ^{14}C yr B.P. (Figs. 3A, 3D, and 3E). These trends are consistent at all sites with paleomiddens of these ages.

The small body mass suggested by the two Allen Canyon Cave paleomiddens was completely unexpected. The estimates for this location, although internally consistent, are discordant with other sites (Table 1). Allen Canyon Cave is located at about 2200 m in a fairly mesic habitat. The shady alcove today supports a grove of Douglas fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), quaking aspen (*Populus tremuloides*), and maple (*Acer grandidentatum*), with pinyon-juniper woodland growing on the exposed ridgetops above the cave. This is classic bushy-tailed woodrat habitat and it seems unlikely that it was replaced by the desert woodrat, *Neotoma lepida,* a xeric-adapted animal that occupies drier, lower-elevation sites nearby. A possible explanation is the poor preservation of larger pellets in the older middens at this relatively wet site.

Estimates of January and July temperature derived from each paleomidden are provided in Table 1. Correspondence between temperature estimated from modern (or the youngest) middens at each location and that taken from weather stations is generally good (Table 2). July values derived from modern middens, for example, differ by an average of only 3.9 (±4.2)°C from the HCN database. When Bison Alcove is excluded, the difference is just 1.5 (±1.2)°C. The underestimate for Bison Alcove is puzzling. The very large body mass of these animals (mean$_{20}$ $>$ 480 g; Table 1) suggests a July temperature estimate of 14.7°C for the modern (undated) midden; an underestimate of 10.9°C. Although Bison Alcove is the highest latitude site, it is also at the lowest elevation (1220 m; Table 2).

TABLE 1
Summary Data for Midden Samples from the Colorado Plateau

Midden ID	*N*	Pellet width (mm)	Standard deviation	Relative size	Body mass (g)	95% confidence interval	Estimated July temperature (C)	Estimated January temperature (C)	Midden age (yr B.P.)	95% confidence interval
LL 1	689	5.63	0.17	1.068	424.4	15.3	18.4	3.3		
LL 2	1000	5.31	0.15	1.008	359.7	13.1	21.1	6.2		
LL 3	318	5.24	0.16	0.994	344.3	14.0	21.5	6.6		
LL 4	300	5.14	0.12	0.975	324.7	10.7	21.9	7.1	3110	60
LL 5	300	5.27	0.17	1	352.1	15.5	21.3	6.4	1690	50
LL 6	271	5.82	0.16	1.104	464.4	14.2	15.9	0.7	16,460	100
LL 7	271	4.82	0.08	0.915	259.6	6.8	22.0	7.4	6310	80
LL 8	236	4.92	0.10	0.934	279.9	9.0	22.2	7.5	7520	60
LL 9	202	4.83	0.11	0.917	261.5	10.3	22.0	7.4	7890	60
LL 10	67	5.14	0.26	0.975	325.3	23.3	21.9	7.1		
LL 11	88	5.38	0.22	1.021	374.6	19.5	20.6	5.7	15,540	190
LL 12	277	5.74	0.11	1.089	447.5	9.5	17.0	1.9	16,480	90
LL 13	167	5.54	0.15	1.051	405.8	13.1	19.4	4.3		
LL 14	101	5.45	0.21	1.034	388.5	19	20.1	5.1	10,020	70
LL 15	70	5.44	0.22	1.032	385.8	19.6	20.2	5.2	12,090	100
ATC M	132	5.53	0.10	1.00	403.5	9.1	19.5	4.4	0	0
ATC 3	350	5.82	0.11	1.052	463.0	9.6	16	0.8	9460	160
ATC 4A	200	5.52	0.21	0.998	403.1	19.1	19.5	4.4	5550	130
ATC 4B	289	5.97	0.14	1.08	493.6	12.5	13.7	−1.7	10,080	140
ATC 5B	217	5.36	0.16	0.969	369.4	14.0	20.8	5.9	2780	120
ATC 6A	289	5.59	0.24	1.011	417.5	21.3	18.8	3.7	1960	120
AC 1	192	4.67	0.17		227.5	15.1	21.4	6.9	10,030	330
AC 7	91	5.09	0.21		314.1	18.8	22.0	7.2	11,310	200
BA M	122	5.90	0.13	1.000	480.9	12.0	14.7	−0.6	0	0
BA 1	198	5.94	0.15	1.007	488.6	15.8	14.1	−1.2	12,420	210
BA 2	236	6.23	0.10	1.056	548.2	8.7	8.6	−6.9	14,910	100
BA 3	226	6.38	0.16	1.081	578.4	14.6	5.2	−10.3	16,490	170
BA 5	206	5.94	0.10	1.007	488.8	9.0	14.1	−1.2	1930	80
BA 9-t	135	5.94	0.14	1.007	487.4	12.6	14.2	−1.1		
BA 9-b	162	5.88	0.12	0.997	476.7	11.2	15.0	−0.3		
BA 11	200	6.01	0.17	1.019	503.5	15.2	12.8	−2.5		
BA 12	235	6.35	0.15	1.076	573.3	13.0	5.8	−9.7		
BA 13	265	6.18	0.12	1.047	538.1	10.8	9.6	−5.9	20,050	160
BA 14	148	5.96	0.27	1.010	492.7	23.9	13.7	−1.6		
BA 16	185	6.09	0.15	1.032	518.6	13.6	11.5	−3.9		
BA 17	200	6.29	0.13	1.066	559.4	11.8	7.4	−8.1		
FMC M	142	5.24	0.07	1.000	345.8	15.3	21.5	6.6	0	0
FMC 1	338	5.42	0.14	1.034	382.4	12.8	20.4	5.4	12,770	140
FMC 4	175	4.93	0.11	0.941	282.1	10.2	22.2	7.5	6100	100
FMC 5	173	5.09	0.16	0.971	315.2	14.0	22.0	7.2	9700	110
FMC 6	397	5.16	0.11	0.985	329.3	9.6	21.8	7.0	3550	60
FMC 12	133	5.71	0.10	1.095	441.3	20.3	18.1	3.0	13,800	320

Note. N was the total number of pellets measured. Pellet width (in mm) represents mean_{20}; relative size is the mean_{20} of a midden divided by that of the modern (or youngest) midden from the locality. Body mass was estimated from mean_{20} pellet width (Smith *et al.* 1995; see text). CI refers to the confidence interval. Estimated July and January temperatures were calculated from mean_{20} using the regression equations presented in Figure 2. Midden ages were determined by tandem mass accelerator and are given in unadjusted radiocarbon years before present. See Figure 1 and legend for midden locations.

The correspondence with January values is not as close as with July temperature; the mean discrepancy between the four modern middens and their nearest weather stations was 7.0 (±3.1)°C (Table 2). Cold temperatures were consistently underestimated at all locations. It should be noted that ‘‘modern’’ middens were typically loose conglomerations

TABLE 2
Weather Stations Used for Midden Locations

Midden	Elevation (m)	Weather station	Elevation (m)	Years of record	July temperature	Adjusted July temperature	Modern midden	January temperature	Adjusted January temperature	Modern midden
Allen Canyon	2195	Blanding	1886	84	22.9	20.2	—	−2.9	−5.0	—
Atlatl Cave	1910	Aztec Ruins	1737	84	24.0	22.5	19.5	−2.8	−4.0	4.4
Bison Alcove	1317	Moab	1220	102	26.5	25.6	14.7	−1.9	−2.6	−0.6
Fishmouth Cave	1585	Bluff	1328	72	25.4	23.1	21.5	−1.9	−3.7	6.6
Lyman Lake	1880	St. Johns	1782	79	22.2	21.3	21.3	−0.1	−0.7	6.4

Note. Temperatures were adjusted for elevational differences using lapse rates for southwestern Colorado (Meyer, 1992; see text for details).

on the surface or top strata of the cave, that had been identified by the collector on the basis of appearance, location or associated plant fragments as being of modern origin. They were not actually radiocarbon-dated. Thus, it is possible that some or all modern middens may actually be 5–200 yr old.

Because of the statistically indistinguishable slopes between January and July temperatures and woodrat body mass (Fig. 2), relative temperature estimates for the individual paleomiddens yielded almost identical anomalies (Table 1). Consequently, we have presented only relative July temperature here (Fig. 4). The estimates derived from woodrat body mass suggest that July and January temperatures for Bison Alcove were as much as 10°C cooler during the last glacial maximum (LGM) than today (Fig. 4A). Although the LGM is not represented at Fishmouth Cave, estimates from about 13,800 ^{14}C yr B.P. suggest differences of about 4–5°C at this time. The two southern locations (Lyman Lake and Atlatl Cave in Chaco Canyon) suggest differences of in excess of 6°C (Fig. 4b, c). The relative temperature estimates for Fishmouth Cave and nearby Bison Alcove are strikingly consistent (Fig. 4A). Modern temperatures were evident by about 12,000 ^{14}C yr B.P., with a warmer period between 10,000 and 4000 ^{14}C yr B.P., and a slight cooling of ~1°C about 2000 ^{14}C yr B.P.

The onset of the interstade was both earlier and more abrupt at Lyman Lake than at other sites (Fig. 4B), presumably reflecting its more southerly location (Fig. 1). Near-modern temperatures are evident by ~15,000 ^{14}C yr B.P. The cooler period at ~12,000–10,000 ^{14}C yr B.P. (some 1° to 1.5°C) may reflect Younger Dryas cooling. Temperatures were about 1°C warmer during the middle to late Holocene. Temperature estimates for Atlatl Cave are somewhat more difficult to interpret since no middens dated to the last deglaciation. The relatively cool temperature estimates for 10,000–9000 ^{14}C yr B.P. may reflect later warming occurring at this location. Based on HCN weather information, Atlatl Cave is the coolest of the five sites today, with January temperatures averaging −2.8°C (Table 2). Temperature fluctuations are evident in the late Holocene, with estimates varying from 1.5°C warmer than today at about 3000 ^{14}C yr B.P. to 1°C cooler than today at 2000 ^{14}C yr B.P.

Plant Macrofossils

Of the twelve species of plant macrofossils present, only six (*Rhus tribobata*, *Juniperus osteosperma*, *Pinus flexilis*, *Pinus edulis*, *Pinus monosperma* and *Juniperus scopulorum*) were found in sufficient middens (>10) to warrant analysis (Table 3). Four of these yielded significant differences between woodrat body mass and the presence or absence of macrofossils (one-way ANOVA, $p < 0.02$ in all instances, $df = 17–25$; Fig. 5). In several instances of warm-adapted plants (*Rhus tribobata* and *Juniperus osteosperma*), relative body size was *smaller* when the plant macrofossils were present than when they were absent (Fig. 5). Relative body mass was larger when the macrofossils were present for the other plants (*Pinus flexilis*, *Pinus edulis*, *Pinus monosperma*, and *Juniperus scopulorum*). Results were not influenced by the particular paleosite from which the macrofossils were obtained ($p > 0.05$ in two-way ANCOVA). Five of the six comparisons between plant presence/absence and body mass went in the predicted direction (one-tailed Wilcoxon's signed rank test, $p < 0.05$; Fig. 5). The covariation seen between plant presence and woodrat body mass, however, was probably due to a common reaction to temperature fluctuations. Woodrat body-size change preceded (in most instances) or at the very least coincided with the disappearance of cold-adapted plants from the midden record (Table 3). In the case of *Rhus tribobata* and *Juniperus osteosperma,* woodrat body size decreased before the *appearance* of the plants in the midden record (Table 3; Fig. 5). Thus, the presence or absence of particular plant species apparently was not the proximate nor ultimate cause of woodrat body-mass changes.

DISCUSSION

The chronosequences from all locations indicate remarkably similar patterns of temperature fluctuation within the Colorado Plateau from the late Pleistocene to present. All locations with middens dating to 2000 ^{14}C yr B.P., for example, clearly indicate a cooling of about 1°C at this time (Figs. 2 and 3). Further, significant changes in woodrat body size

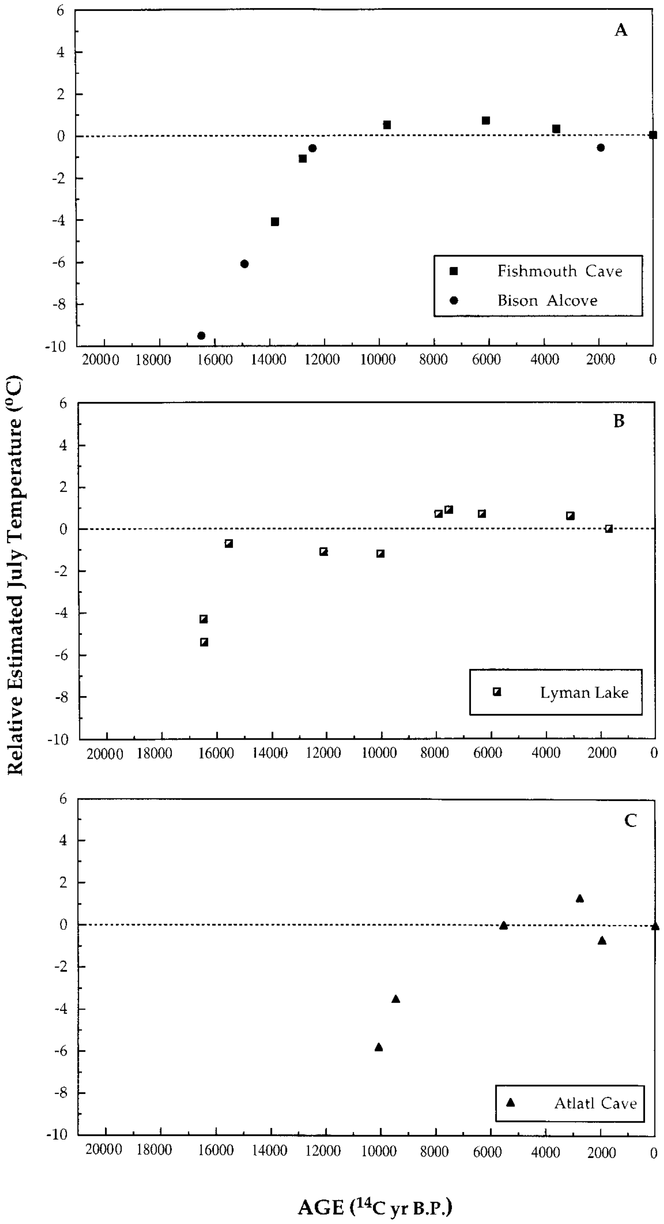

FIG. 4. Relative estimated temperature vs. uncorrected radiocarbon date of paleomidden: (A) Bison Alcove and Fishmouth Cave; (B) Lyman Lake; (C) Atlatl Cave. Relative estimated temperature is calculated by dividing the temperature estimate for each paleomidden (Table 1), by the temperature estimate for a modern midden from the same location.

are seen within relatively short time scales—on the order of 200–1000 yr (Fig. 2)—corroborating suggestions that climate shifts occurred rapidly (e.g., Allen and Anderson, 1993).

Our results correspond well both quantitatively and qualitatively with those of other researchers in this region. Based on insect assemblages, Elias (1996) suggested that regional climates in the Rocky Mountains began warming by 14,000 ^{14}C yr B.P. with most warming occurring by 12,300 ^{14}C yr B.P. Modern temperatures were reached at ~11,300 ^{14}C yr. B.P., and a warming trend occurred over most of the Holocene. We observe the same general trend, although our data indicate more fluctuations within the mid-Holocene and an earlier onset of warming beginning at about 16,000 ^{14}C yr B.P. (Fig. 3; however, several of our midden sites are older than those used by Elias). In addition to concordance with the overall qualitative trend, our quantitative estimates of July temperatures closely approximate those of Elias (1996), suggesting full-glacial values ~9–10°C colder than today (Table 1, Fig. 4). We do vary considerably in our estimation of January temperatures over these time periods. Our data suggest January temperature anomalies of about 4–6°C at about 14,000 ^{14}C yr B.P. (Table 1), values that differ considerably from Elias's (1996) somewhat inexplicable estimate of 26–30°C.

Coupled with the temperature fluctuations of the late Quaternary were shifts in the seasonality, distribution, and abundance of precipitation (Thompson *et al.,* 1993). Although we cannot exclude the possibility that some measure of the changes observed in woodrat body size were in response to alterations in precipitation, this seems unlikely. Among contemporary woodrat populations no relationship has been detected between woodrat body mass and precipitation (Smith *et al.,* 1998).

That changes in woodrat body mass preceded vegetational changes (Fig. 5) is not unexpected, given the generally longer generation (and hence response) time of plants. It does suggest that woodrat body size responded primarily to temperature fluctuations and not to vegetational changes. This is not to say that alterations in plant composition and abundance are unimportant to woodrats. Although perhaps only marginally influencing body mass, vegetational changes directly impact other aspects of the life history and ecology of woodrats. As hindgut herbivores, for example, woodrats must deal with secondary compounds and other substances that influence plant quality (Justice and Smith, 1992; Smith, 1995). Vegetation shifts also may be instrumental in determining when species replacements occur. We suspect, for example, that a species replacement occurred at Lyman Lake (Fig. 3e). Estimated maximum body mass at this site during the mid-Holocene is below that seen among contemporary populations of *N. cinerea* at their southern distributional limit (~300 g; Smith, 1997; Fig. 2). Lyman Lake is situated at about the modern southern distributional limit of *N. cinerea,* well within the distributions of a number of other woodrat species (Hall, 1981). During the warmer conditions of the Altithermal, *N. cinerea* may have retreated to a higher elevation site, allowing occupation by another more xeric species (e.g., *N. albigula, N. mexicana*). At other ''marginal'' sites, we have observed rapid species shifts during the mid to late Holocene, re-

TABLE 3
Plant Macrofossils Associated with Various Middens Used in Study

Midden ID	Plant species present[a]											
	Pi	Rt	Jo[b]	Pf	Pe	Pp	Pm	Ppu	Jm	Js	Pt	Ce
LL 1	0	0	5	0	0	0	0	0	0	0	0	0
LL 2	0	0	5	0	0	0	0	0	0	0	0	0
LL 3	0	2	5	0	0	0	0	0	0	0	0	0
LL 4	0	0	3	0	0	0	0	0	0	0	0	0
LL 5	0	0	5	0	3	0	0	0	0	0	0	0
LL 6	0	0	0	2	2	0	0	0	0	5	0	0
LL 7	0	2	5	0	2	0	0	0	0	0	0	0
LL 8	0	2	0	1	2	0	0	0	0	4	0	0
LL 9	0	2	4	0	2	0	0	0	0	0	0	0
LL 10	0	0	0	0	0	0	0	0	0	4	0	0
LL 11	0	0	0	0	0	0	0	0	0	3	0	0
LL 12	0	0	0	0	2	0	0	0	0	5	0	0
LL 13												
LL 14	0	2	2	0	5	0	0	0	0	5	0	0
LL 15	0	2	0	4	5	0	0	0	0	4	0	0
ATC M	0	2	0	0	0	0	0	0	2	0	0	3
ATC 3		2		3	0	0	5	1	0	5		
ATC 4A		2		0	4	2	2	0	5	0		
ATC 4B		2		3	0	0	5	1	0	5		
ATC 5B	0	2	0	0	5	2	2	0	5	0	0	0
ATC 6A	0	1	0	0	5	0	0	0	5	0	0	0
ATC 11	0	3	0	0	4	4	4	0	5	3	0	0
AC M	0	0	X	0	X	X	X	0	0	0	X	0
AC 1	0	0	1	4	0	1	5	2	0	0	0	1
AC 7	5	0	0	5	0	0	2	0	0	0	0	0
BA M												
BA 1		0	0	X	0		X	X				
BA 2		0	0	X	0		X	X				
BA 3		X	0	X	0		X	X				
BA 5		X	X	0	X		0	0				
BA 9-t												
BA 9-b												
BA 11												
BA 12		0	0	X	0		X	X				
BA 13		0	0	X	0		0	0				
BA 14												
BA 16												
BA 17												
FMC-M	0	X	X	0	0	0	0	0	0	0	0	X
FMC 1	0	0	0	5	0	0	5	2	0	4	0	2
FMC 4	0	2	5	1	0	0	3	0	0	0	0	3
FMC 5	0	1	5	0	0	0	3	0	0	0	0	3
FMC 6	0	3	5	0	0	0	1	0	0	0	0	2
FMC 12	0	0	0	3	0	0	5	2	0	2	0	0

[a] Plant species: Pi = *Picea englemani;* Rt = *Rhus tribobata,* Jo = *Juniperus osteosperma,* Pf = *Pinus flexilis,* Pe = *Pinus edulis,* Pp = *Pinus ponderosa,* Pm = *Pseudotsuga menziesii,* Ppu = *Pices pungens,* Jm = *Juniperus monosperma,* Js = *Juniperus scopulorum,* Pt = *Populus tremuloides,* Ce = *Cercocarpus* spp. Plant macrofossil data derived from Betancourt (1984, 1990), Koehler (written communication, 1995), and Sharpe (1991). Scale: 0 = absent, X = present (1 = rare . . . 5 = abundant); blanks indicate data were not available.

[b] *Juniperus osteosperma* macrofossils for the Lyman Lake site may actually be *Juniperus scopulorum;* we have not independently verified their identification.

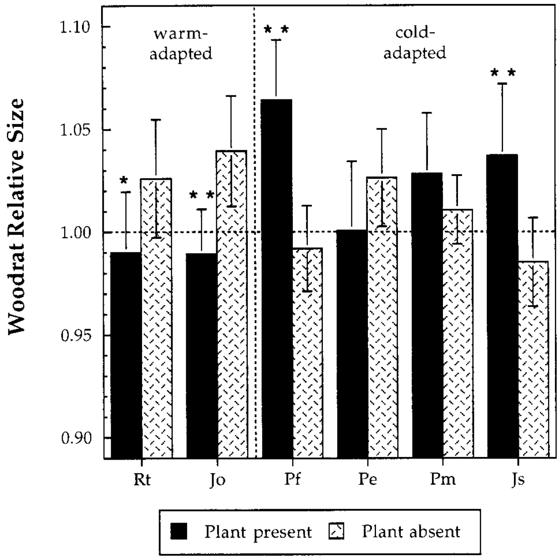

FIG. 5. Woodrat relative size (mean_{20} of paleomidden divided by mean_{20} of modern midden from the same location) plotted vs. presence and absence of selected plant macrofossils. Plants to left of dotted line are considered to be adapted to warm conditions; those to the right, cold climatic regimes. Legend: Rt = *Rhus tribobata,* Jo = *Juniperus osteosperma,* Pf = *Pinus flexilis,* Pe = *Pinus edulis,* Pm = *Pseudotsuga menziesii,* Js = *Juniperus scopulorum.* * $p < 0.05$; ** $p < 0.01$

flecting the rapidly changing climate and precipitation regimes.

The robust relationship between maximum *and* minimum temperatures and body mass found among contemporary animals (Fig. 2), suggests that both are important selective agents on woodrat populations. We currently have no way of disentangling the combined effects of summer and winter temperatures from the relative effects of each. The regressions with contemporary animals yield statistically indistinguishable slopes, leading to identical estimates of January and July temperature anomalies in the paleorecord (Fig. 4). However, winter and summer temperatures likely have changed independently at different times in the past. An alternative explanation for vegetation change lagging behind that of woodrat body size is that winter temperatures within the Colorado Plateau warmed earlier than did summer ones. Forest/woodland plants growing near their lower limits may be fairly insensitive to milder winters, but very responsive to changes in summer temperatures. Woodrats, however, respond to both summer and winter climate (Fig. 2). If warmer winters were evident a few centuries or millennia before summer temperatures increased, we would expect to see a response in woodrat body size and little change in plant composition. Thus, conceivably the observed difference between woodrat and vegetation response reflects inequitability of the climate (Fig. 3, Table 3). In the future we hope to obtain chronosequences with finer temporal resolution to investigate these ideas further.

ACKNOWLEDGMENTS

Bison Alcove specimens are archived in the National Park Service repository at Northern Arizona University; we thank J. Mead and S. Sharpe for facilitating access to these specimens. P. Koehler kindly provided access to and information about the Lyman Lake middens, including unpublished vegetation lists. S. M. Elliott made numerous helpful comments on the manuscript. We thank S. Elias for providing us with copies of unpublished manuscripts. K. Aasen Rylander helped in selecting and preparing midden samples for pellet measurements. Funding was provided by NSF Grants BIR-9308033 and DEB-9508715 to F.A. Smith, and support from the U.S. Geological Survey's Global Change Program to J. L. Betancourt.

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