

## Influence of Late-Holocene Climate on Northern Rocky Mountain Mammals

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An exceptionally rich paleontological site containing thousands of mammalian fossils and well-dated with 18 radiocarbon samples provides evidence of late-Holocene ecological response to climatic change in northern Yellowstone National Park, Wyoming. The mammalian fauna, composed of 10,597 identified specimens, shows surprising affinity to the local habitat with little evidence of long-distance transport of faunal elements, thus revealing the faithfulness of a fossil site to the community from which it is derived. The mammals illustrate ecological sensitivity to a series of mesic to xeric climatic excursions in the sagebrush-grassland ecotone during the past 3200 yr. From 3200 cal yr B.P. to a maximum of 1100 cal yr B.P., the species composition of mammals indicates wetter conditions than today. Beginning about 1200 cal yr B.P., the fauna becomes more representative of xeric conditions with maxima in xeric-indicator taxa and minima in mesic-indicator taxa, concordant with the Medieval Warm Period (circa 1000 to 650 yr B.P.). Cooler, wetter conditions which prevailed for most of the Little Ice Age (700 to 100 yr B.P.) in general correspond to a return to a more mesic mammalian fauna. A warm period within the Little Ice Age is documented by a xeric fauna. These data show that mammalian ecological sensitivity to climatic change over this intermediate time scale holds promise for predictions about the impacts of future global warming. © 1996 University of Washington.

### INTRODUCTION

Environmental factors directly or indirectly limit many aspects of organismal distribution and abundance (e.g., Andrewartha and Birch, 1954; Caughley *et al.*, 1988; Connell, 1975; Mayr, 1947). Species may remain unaffected by environmental change or may respond with dispersal, population size change, clinal shifts, evolution, extirpation, or extinction. Though modern distributional studies emphasize the importance of spatial and temporal variability in environmental conditions, there is broad congruence between a community and the distribution of individual component species for the short term ( $\leq 10$  yr). However, spe-

cies are thought to respond individualistically to climate change at the scale of paleontological time ( $> 10^4$  yr) which includes global climatic change such as continental deglaciation (Bartlein and Prentice, 1989; Bennett, 1990; Davis, 1986; Graham and Grimm, 1990). In this study I investigate mammalian community response to climatic change at the intermediate time scale ( $10^2$  to  $10^3$  yr) through the late Holocene. Few records of faunal response exist for this time period (Potts and Behrensmeyer, 1992; Vrba, 1992), which is of interest as it is the scale at which evolution and community change initially may be detected, especially in response to climatic change due to global warming (Schneider, 1993). Also, mammalian taxa from this time period remain extant, thus permitting comparisons of their natural history between the present and the past. The purpose of this study is to examine the response of mammals to these mid-scale climatic intervals and to discern whether patterns of mammalian response may be used to generalize about faunal response during climatic transitions. Few studies have dealt with mammalian response to climatic change at this time scale (e.g., Holbrook, 1977; Semken, 1984; Semken and Falk, 1987). The evolutionary effects of climatic change on mammals are the topic of another study (Hadly, *in press*).

Data for this study were gathered from a paleontological site, Lamar Cave, in northern Yellowstone National Park, Wyoming (Fig. 1A). The record from Lamar Cave spans the past 3000 yr, contains thousands of mammalian fossils necessary to investigate faunal change through time, and has exceptionally good radiocarbon time-control for a fossil mammal site. Because the modern ecosystem in Yellowstone National Park is functioning in a nearly natural state with little human impact (Barnosky, 1994; Hadly, 1990), the existing mammal fauna in the vicinity of Lamar Cave can be meaningfully compared to the fossil record from the cave (taking taphonomy into account). The cave is located in a sagebrush (*Artemisia* spp.) grassland patchily composed of xeric and mesic microhabitats. Douglas fir (*Pseudotsuga menziesii*) is present on north-facing slopes (Fig. 1B).

Several studies have shown that historic climatic changes at a regional scale have resulted in mammalian redistribution

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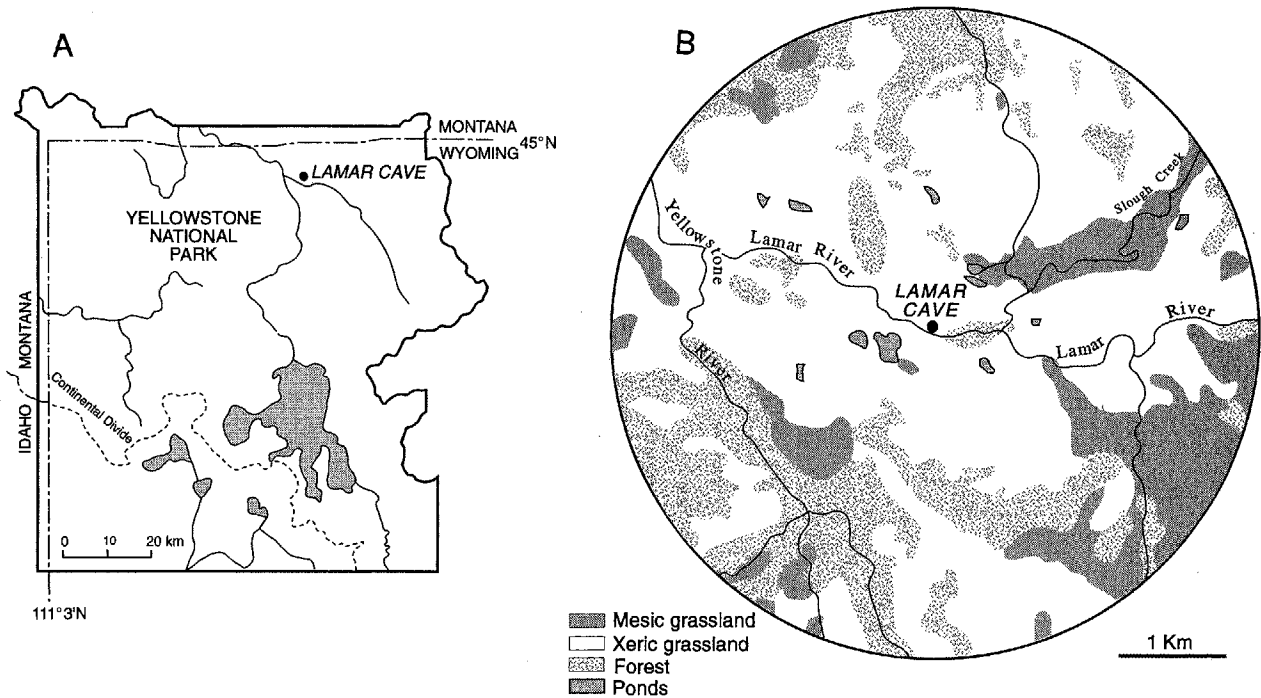


FIG. 1. (A) Map of the study area showing Lamar Cave. (B) Vegetation map within a 5 km radius of Lamar Cave showing mosaic sagebrush grassland with contrasting open xeric habitats and dense mesic habitats. Figure modified from GIS data generated by National Park Service, Yellowstone National Park (Despain, 1990).

and population fluctuations (e.g., French *et al.*, 1976; Hoffmann and Jones Jr., 1970). Locally, mammalian population size (Houston, 1982; Meagher, 1976; Merrill, 1991) and reproductive capacity (Picton, 1978) are shown to be affected by climate at the 10 yr time scale. At the  $10^4$  yr time scale, the Yellowstone region witnessed major glaciation and the present ecosystem was derived from major biotic dispersal and *in situ* community organization since the Pleistocene. The intermediate time scale ( $10^2$  to  $10^3$  yr) includes globally important, though not demonstrably globally synchronous, climatic transitions: for example, the Younger Dryas event and the cool early Holocene, the Hypsithermal (or warm middle Holocene), and the Neoglacial period of the cooler late Holocene, most of which are well documented by palynological evidence (Baker, 1984; Gennett, 1977; Gennett and Baker, 1986; Whitlock, 1990, 1993; Whitlock and Bartlein, 1993). At a finer scale, the past 3000 yr include several time-transgressive but global mesic to xeric climatic excursions including the Little Ice Age from about 700 to 100 yr B.P., with a warmer interval from 500 to 350 yr B.P. (Jones and Bradley, 1992; Porter, 1986) and the Medieval Warm Period from ca. 1000 to 650 yr B.P. with a probable peak at 950 to 700 yr B.P. (Hughes and Diaz, 1994; Lamb, 1977). Examples of late-Holocene evidence of local climate change at the  $10^2$  to  $10^3$  yr time scale (Fig. 2) include alluvial chronology and changes in fire frequency for the northeastern Yellowstone region (Meyer, 1993; Meyer *et al.*, 1992), palynological evidence (e.g., Baker, 1984; Gennett,

1977; Whitlock, 1993), and Neoglacial activity (Richmond, 1986).

#### SITE DESCRIPTION AND METHODS

##### Excavation

Lamar Cave is located in northeastern Yellowstone National Park, 4 km east of Tower Junction at an elevation of 1835 m (6020 ft). Lamar Cave is a shallow cave having maximum dimensions of 2.0 m high, 3.7 m wide, and 6.2 m deep. The cave was discovered in 1986 and excavated from 1987 through 1993 (Hadly, 1990, 1995). Before excavation, the cave floor was covered with organic and inorganic detritus, including animal bones, plant fragments, sticks, pine cones, alluvium, and roof fall debris. The excavation pit was positioned to avoid the talus rampart at the cave mouth. This placement maximized the interfingering of organic and inorganic units, which facilitated excavation in natural stratigraphic units (Fig. 3). Unit numbers from 1 to 16 were assigned from top to bottom for the natural strata; strata thicker than 10 cm were subdivided into arbitrary units A through E, although these subunits are not used in this study. The southern portion of the pit consisted mostly of alluvial deposits while the northern portion of the pit was mainly organic deposits (Table 1).

A single pit was excavated near the middle of the cave.

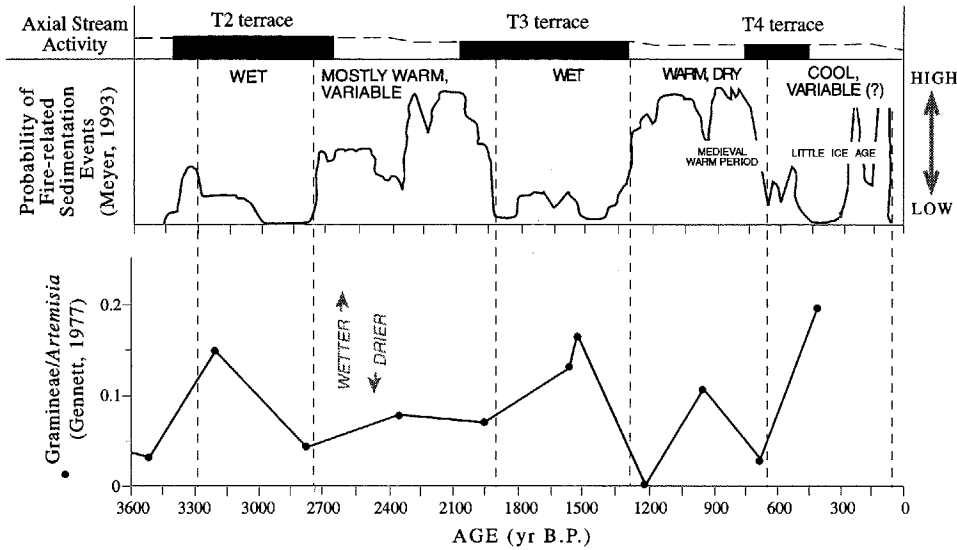


FIG. 2. Late-Holocene climatic oscillations in vicinity of Lamar Cave based on probability of fire-related debris-flow activity and alluvial chronology from northeastern Yellowstone National Park (Meyer, 1993), and Gramineae/Artemisia pollen ratios from Blacktail Pond (Gennett, 1977). The pollen ratios are used as an index of effective moisture (Hadly, 1990; Mehringer and Wigand, 1990) but are based on actual counts, for which sample size of the two taxa is low ( $N \leq 98$ ).

The pit was 175 × 200 cm wide and 272 cm deep. All excavation was done by hand with a trowel. Excavated material was placed in buckets and washed through a series of five stacked screens of decreasing mesh size (4, 8, 16, 20, and 30 squares per square inch). Matrix was dried in the field, bagged, and transported to the lab. Preservation at all levels was generally excellent for identification,

although bones were frequently broken and no articulated skeletons were found. Specimens will be curated into the University of California Museum of Paleontology at Berkeley (UCMP Locality V96017) and with the National Park Service. A voucher collection will be maintained by the National Park Service Museum at Yellowstone National Park.

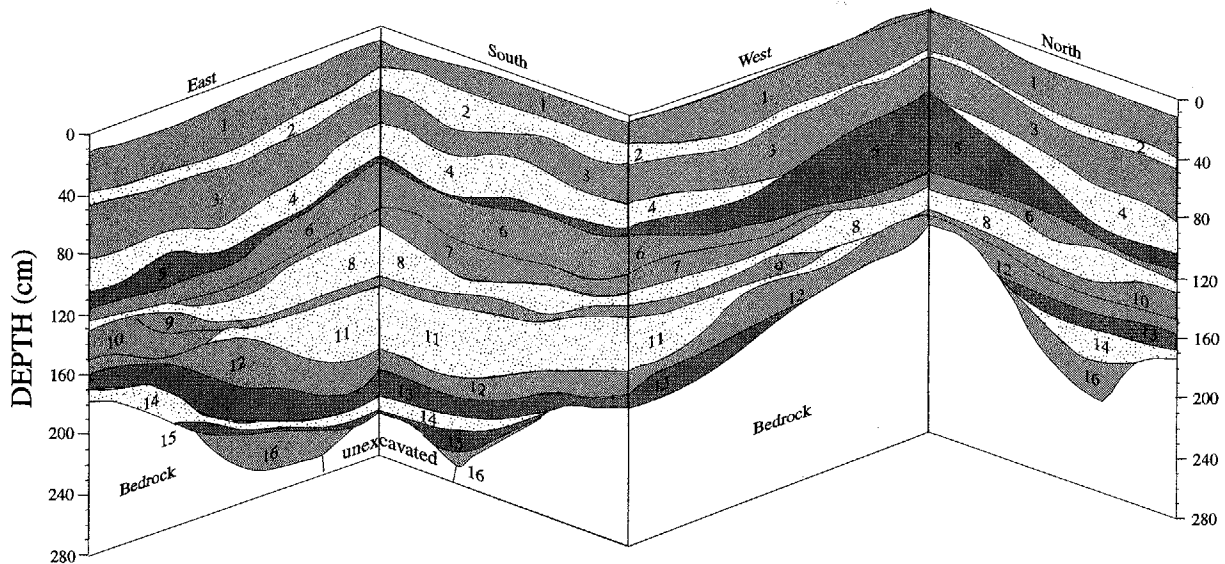


FIG. 3. Stratigraphic section showing Lamar Cave excavation. Drawn to scale. East and West walls are approximately 200 cm long; North and South walls are approximately 175 cm long. Numbers refer to levels; see Table 2 for lithologic descriptions. Darkest shading represents burned organic level; medium shading represents unburned organic level; light stipple represents inorganic levels high in alluvium.

TABLE 1  
Lithology and Thickness of Stratigraphic Levels  
from the Deposits of Lamar Cave

| Stratigraphic level | Average depth below datum (cm) <sup>a</sup> | Thickness (cm) | Lithology                  |
|---------------------|---|----------------|----------------------------|
| 1                   | 26  | 17-35          | organic w/ some alluvium   |
| 2                   | 42  | 10-22          | alluvial                   |
| 3                   | 65  | 13-33          | organic                    |
| 4                   | 84  | 12-25          | alluvial                   |
| 5                   | 95  | 3-20           | burned organics            |
| 6                   | 115   | 10-30          | organic                    |
| 7                   | 130   | 0-30           | organic                    |
| 8                   | 140   | 0-20           | organic and alluvial       |
| 9                   | 143   | 0-5            | organic                    |
| 10                  | 154   | 0-22           | organic                    |
| 11                  | 179   | 0-50           | alluvial w/ organics       |
| 12                  | 204   | 10-40          | organic                    |
| 13                  | 214   | 0-20           | (charcoal) burned organics |
| 14                  | 226   | 10-15          | alluvial w/ organics       |
| 15                  | 231   | 0-10           | burned organics            |
| 16                  | 241   | 0-20           | organic                    |

<sup>a</sup> Depth used to produce age-vs-depth curve in Figure 4.

### Identification

Fossil material was removed from bulk matrix by hand or with forceps and sorted into taxonomic class. Plant, fish, bird, reptile, and amphibian material has not been identified. Mammalian remains were identified to species when possible. Only craniodental material was used to identify animals smaller than a rabbit; all other mammals were identified based on whatever diagnostic specimens were present. Comparative material from the University of California Museum of Vertebrate Zoology, University of California Museum of Paleontology, Museum of Northern Arizona, and The Carnegie Museum of Natural History was used to aid identifications.

### Taphonomy

The primary method of bone deposition was from collection by wood rats of carnivore scats, raptor pellets, and pieces of dead animals from within a 100 m radius of the cave entrance (Barnosky, 1994; Hadly, 1990, 1995; Hoffman, 1988). Many of the larger bones show rodent gnaw marks. A minority of material accumulated as carnivores, such as coyotes, wolves, mountain lions, bears, or badgers, chewed their food in the cave, as evidenced by carnivoran gnaw marks on larger bones as well as carnivoran bones in the deposit. Taking into account all vectors of the taphonomic pathway, the collection radius from the mouth of the cave is about 5 km. The available evidence suggests that whatever taphonomic biases operated in the deposition of

fossils in Lamar Cave, they were constant throughout the time spanned by the deposits (Barnosky, 1994; Hadly, 1990, 1995), hence validating comparisons between levels and with modern samples collected from similar taphonomic vectors.

## RESULTS

### Chronology

The time spanned by the Lamar Cave deposit was determined by radiocarbon analyses of 18 organic samples (Table 2). Wood, charcoal, and bone were submitted for dating. The amount of contaminants necessary to bias material less than 3000 yr old is extremely high and therefore significant contamination is unlikely for the Lamar Cave deposits (T. W. Stafford, personal communication, 1995). Radiocarbon samples were selected broadly across levels to span the deposits of the cave. Duplicate samples for some levels were dated in order to enhance within-level age variation and to discern the degree of time-averaging in the deposits.

Large, angular pieces of charcoal were selected in order to minimize the possibility of reworking. The bone samples, all complete rodent dentaries, were selected to include the range of relatively good preservation from any one level; hence, there was a bias toward dating the better-preserved specimens. The better-preserved specimens have higher protein content remaining in the bone, and generally, the better the preservation, the younger the specimen (Table 2; T. W. Stafford, personal communication, 1995). Within any one stratigraphic level, however, well-preserved specimens make up only a small component of the total sample; most bones are relatively poorly preserved. Therefore, by virtue of selecting only the best-preserved specimens for dating, the range of bone radiocarbon dates from one level is likely to be skewed toward younger dates; this is caused by dating a disproportionately large amount of fossils that may have infiltrated from higher levels than would be obtained by dating most of the (poorly preserved) fossils from the level from which they were selected. For the bone samples, the chemical fraction dated is the gelatin from KOH-extracted collagen, which considerably decreases fulvic acid contamination. All but three samples (Beta-23031, Beta-63870, and Beta-63871) were dated with the accelerator mass spectrometry (AMS) technique. The three samples noted above were dated utilizing the benzene method of conventional radiometric analysis.

Although the data suggest some high sedimentation rates or some vertical mixing of fossils through bioturbation, the radiocarbon dates generally increase in age with depth (Fig. 4). The youngest dates of the deposit, from Level 3 (CAMS-20348 and CAMS-20349), are modern with an estimated error of  $\pm 40$  yr. The oldest sample, dated  $2860 \pm 70$  yr B.P. (CAMS-20356), is from Level 16, which rests on bedrock

TABLE 2  
Radiocarbon Ages from the Deposits of Lamar Cave, Yellowstone National Park, Wyoming

| Stratigraphic level | Material dated            | Uncalibrated $^{14}\text{C}$ data <sup>a</sup><br>( $^{14}\text{C}$ yr B.P. $\pm 1\sigma$ ) | Calibrated age range<br>at $2\sigma$<br>(cal yr B.P.) <sup>b,c</sup> | Laboratory number       | Protein remaining (%) |
|---------------------|---------------------------|---|--|-------------------------|-----------------------|
| 3                   | <i>Spermophilus</i> ramus | Modern  | 0–40 <sup>d</sup>  | CAMS-20348              | 14.2                  |
| 3                   | <i>Spermophilus</i> ramus | Modern  | 0–40 <sup>d</sup>  | CAMS-20349              | 14.7                  |
| 3                   | wood                      | 80 $\pm$ 110  | 0 (none) 333 <sup>d</sup>  | Beta-24418;<br>ETH-3675 | na                    |
| 5                   | charcoal                  | 960 $\pm$ 60 <sup>e</sup>   | 733 (917) 967  | Beta-23031              | na                    |
| 6                   | <i>Spermophilus</i> ramus | 300 $\pm$ 40  | [0 (318) <sup>f</sup> 496] <sup>g</sup>                              | CAMS-20350              | 13.1                  |
| 6                   | <i>Spermophilus</i> ramus | 550 $\pm$ 60  | 483 (542) <sup>f</sup> 669   | CAMS-20351              | 13.4                  |
| 9                   | <i>Spermophilus</i> ramus | 280 $\pm$ 50 <sup>e</sup>   | [0 (309) 483] <sup>g</sup>   | CAMS-20352              | 13.3                  |
| 9                   | <i>Spermophilus</i> ramus | 550 $\pm$ 50  | 489 (542) <sup>f</sup> 664   | CAMS-20353              | 13.9                  |
| 9                   | <i>Microtus</i> ramus     | 1120 $\pm$ 60   | 919 (1004) <sup>f</sup> 1214   | CAMS-20345              | 9.3                   |
| 9                   | charcoal                  | 1695 $\pm$ 60 <sup>e</sup>  | 1450 (1573) 1737   | Beta-30016;<br>ETH-5044 | na                    |
| 12                  | <i>Spermophilus</i> ramus | 520 $\pm$ 50  | 477 (528) <sup>f</sup> 648   | CAMS-20354              | 11.0                  |
| 12                  | <i>Microtus</i> ramus     | 850 $\pm$ 60  | 664 (740) <sup>f</sup> 939   | CAMS-20346              | 11.4                  |
| 12                  | <i>Spermophilus</i> ramus | 1110 $\pm$ 60   | 912 (985) <sup>f</sup> 1199  | CAMS-20355              | 11.6                  |
| 13                  | charcoal                  | 1370 $\pm$ 70   | 1099 (1289) <sup>f</sup> 1395  | Beta-63870              | na                    |
| 13                  | charcoal                  | 1670 $\pm$ 80   | 1352 (1550) <sup>f</sup> 1778  | Beta-63871              | na                    |
| 16                  | <i>Spermophilus</i> ramus | 2030 $\pm$ 50   | 1828 (1962) <sup>f</sup> 2136  | CAMS-20357              | 10.8                  |
| 16                  | <i>Microtus</i> ramus     | 2340 $\pm$ 60   | [2141 (2347) <sup>f</sup> 2664] <sup>g</sup>                         | CAMS-20347              | 10.0                  |
| 16                  | <i>Spermophilus</i> ramus | 2860 $\pm$ 70   | 2777 (2955) <sup>f</sup> 3222  | CAMS-20356              | 10.3                  |

<sup>a</sup>  $\delta^{13}\text{C}$  value estimated at  $-25.0\%$ .

<sup>b</sup> Calibrated using Stuiver and Reimer (1993), with 100-yr moving average and  $f^2 = 50$  (Clark, 1975).

<sup>c</sup> Minimum age (intercept) maximum age of 95% confidence interval.

<sup>d</sup> Midpoint of range used to produce age-vs-depth curve in Figure 4.

<sup>e</sup> Age not used to produce age-vs-depth curve in Figure 4; discussion in text.

<sup>f</sup> Intercept used to produce age-vs-depth curve in Figure 4.

<sup>g</sup> Minimum and maximum of 95% confidence sets.

<sup>na</sup> Not applicable.

272 cm below datum. To determine the age of each level, each radiocarbon date was assessed for possible vertical dislocation and whether deposition of the dated item was contemporaneous with the majority of the material comprising the level. All radiocarbon dates were calibrated (Stuiver and Reimer, 1993). Late-Holocene interpretations rely on calibrated age ranges at the 95% confidence level. A detailed discussion of the radiocarbon dates is found in Hadly (1995).

#### Stratigraphic Interpretation

Dating of the Lamar Cave deposits reveals both time-averaging within stratigraphic levels and, to some extent, time-transgression among levels. This makes level-by-level comparisons potentially inappropriate, since time-averaging could smear the faunal signal across levels. However, it is still possible to uncover the effects of climatic change on mammals by lumping stratigraphic levels into time intervals A through E. These intervals are based on the time curve produced by a regression of the intercepts of calibrated radiocarbon ages with depth (Fig. 4) (Table 2). Boundaries were chosen at points that yield the largest number of intervals

with the least probability of mixing across the intervals. Further faunal analyses utilize these time intervals, rather than individual stratigraphic units. Figure 4 shows independently calibrated climatic periods in order to reveal which climatic regime a given interval spans.

The age range for any given time interval results from one or several of the following factors: (1) The  $2\sigma$  (95% probability) measurement error of the Lamar Cave conventional radiocarbon dates varies from  $\pm 80$  to  $\pm 220$  yr, or a range of 160 to 440 yr. (2) Derivation of actual calendric dates from radiocarbon samples requires a calibration curve based on fluctuations of the atmospheric ratio of  $^{14}\text{C}$  and  $^{12}\text{C}$  (Stuiver and Reimer, 1993); variance (Clark, 1975) and calibration error encountered when fitting the analytically determined radiocarbon data from Lamar Cave to a curve produced from fluctuations in atmospheric carbon isotope ratios result in an age range from 171 to 496 yr at the  $2\sigma$  level. (3) True synchrony of levels may be produced by bioturbation and/or extremely high sedimentation rates. (4) The deposition of material into a level may postdate the actual age of the material. Examples of this include the

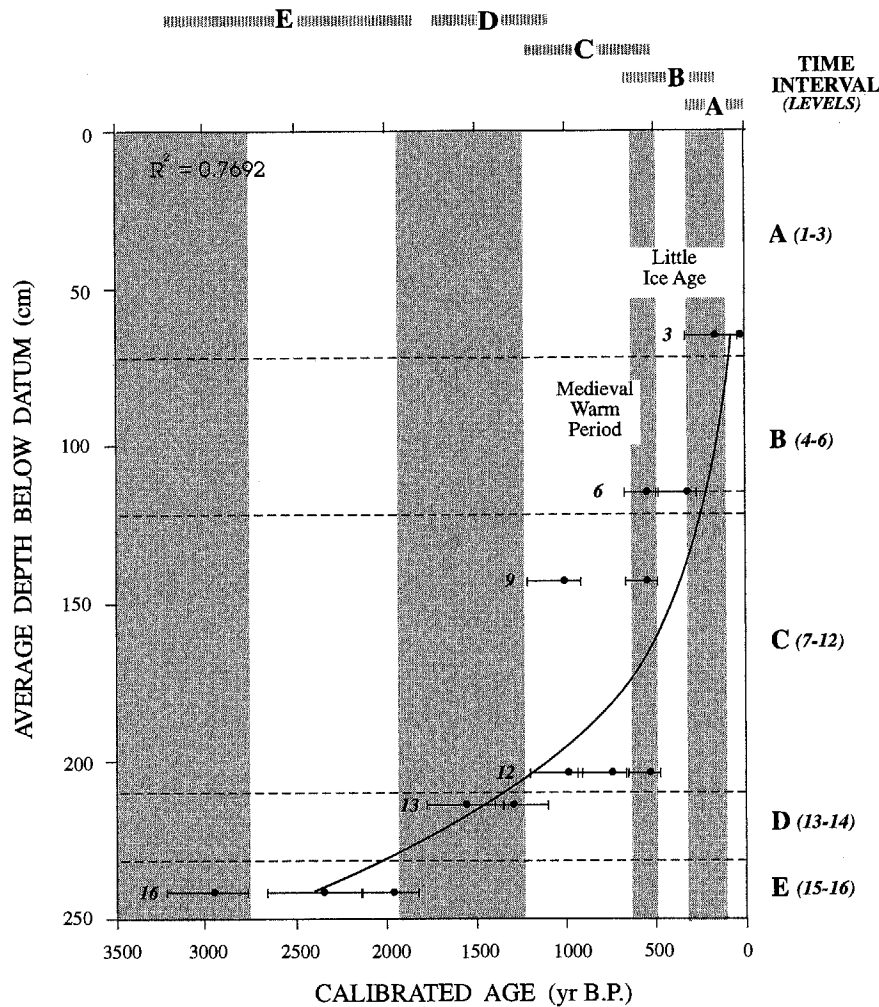


FIG. 4. Age-vs-depth curve for Lamar Cave based on 15  $^{14}\text{C}$  dates. Exponential regression is model produced to fit to the calibration intercepts (listed in Table 2 in parentheses). Regression intercept is set for 20 yr at zero depth, which is concordant for estimated error for modern dates from Level 3. Error bars indicate the 95% confidence intervals which are derived from the calibration procedure (Stuiver and Reimer, 1993); dotted error bar shows unlikely confidence set (0–7 cal yr B.P.) for Level 6. Numbers to left of data refer to the level that yielded the date(s). Time intervals A through E are shown. A period of high sedimentation is suggested by a reduced fit of the curve for interval C (levels 9–12). Note that intervals A (0–333 cal yr B.P.), B (272–669 cal yr B.P.), C (477–1214 cal yr B.P.), and D (1099–1778 cal yr B.P.) are time-transgressive, overlapping the ages they span. Interval E spans 1828 to 3222 cal yr B.P. Shading indicates more mesic conditions; no shading indicates more xeric conditions. Climatic interpretations are based on local fire-related debris-flow activity (Meyer, 1993) and glacial data from the northern hemisphere (Porter, 1986).

old wood effect and long environmental residence time for charcoal.

The implications of overlapping  $^{14}\text{C}$  dates are that events within the overlap may not be assigned unambiguously to a time interval, and the faunal signal for the interval may be unclear. In particular, the Little Ice Age (700–100 yr B.P.) is encompassed by both time interval A (333–0 cal yr B.P.) and time interval B (669–272 cal yr B.P.). Also, the radiocarbon calibration curve for the last 450 yr has particularly large oscillations. Samples that predate nuclear testing (ca. A.D. 1950) do not yield unique calendric dates and results may span as much as 400 yr. As a consequence, establishment of a  $^{14}\text{C}$  chronology for the Little Ice Age is difficult

and a precise chronology for this climatic interval relies primarily on historical records. For the Lamar Cave faunal record, temporal resolution is not great enough to determine unambiguously which time interval contains the fauna representative of the Little Ice Age.

#### Description of Fauna

Mammalian faunal remains recovered from Lamar Cave span approximately 3000 yr and represent 6 orders, 16 families, 31 genera, and 40 species (Table 3); 10,597 bones were identifiable to at least generic level. Minimum numbers of individuals (MNI) and number of identified specimens

TABLE 3  
Mammalian Faunal List from Lamar Cave, Yellowstone National Park, Wyoming<sup>a</sup>

| Taxon                                    | Level  |     |         |      |        |        |        |         |
|--|--------|-----|---------|------|--------|--------|--------|---------|
|  | 1      | 2   | 3       | 4    | 5      | 6      | 7      | 8       |
| Insectivora                              |        |     |         |      |        |        |        |         |
| Soricidae                                |        |     |         |      |        |        |        |         |
| <i>Sorex cf. hoyi</i>                    | —      | —   | —       | —    | —      | 1-4    | 1-3    | —       |
| <i>Sorex merriami</i>                    | —      | —   | 1-4     | —    | —      | —      | 1-1    | 2-10    |
| <i>Sorex palustris</i>                   | —      | —   | 1-5     | —    | —      | —      | 2-12   | 1-5     |
| <i>Sorex (Otiosorex) sp.</i>             | —      | —   | —       | —    | —      | —      | 1-1    | 1-10    |
| <i>Sorex sp.</i>                         | —      | —   | 1-4     | —    | —      | 2-6    | 1-10   | 1-5     |
| Chiroptera                               |        |     |         |      |        |        |        |         |
| Vespertilionidae                         |        |     |         |      |        |        |        |         |
| <i>Myotis sp.</i>                        | —      | —   | 1-8     | —    | —      | —      | —      | —       |
| Carnivora                                |        |     |         |      |        |        |        |         |
| Canidae                                  |        |     |         |      |        |        |        |         |
| <i>Canis latrans</i>                     | 1-11   | —   | 1-14    | —    | 1-1    | 1-1    | —      | —       |
| <i>Canis lupus</i>                       | —      | —   | —       | —    | —      | 1-3    | —      | —       |
| <i>Canis sp.</i>                         | —      | —   | —       | —    | —      | —      | —      | —       |
| <i>Vulpes vulpes</i>                     | —      | —   | —       | —    | 1-3    | —      | 1-1    | —       |
| Felidae                                  |        |     |         |      |        |        |        |         |
| <i>Lynx sp.</i>                          | —      | —   | —       | —    | —      | —      | —      | —       |
| Mustelidae                               |        |     |         |      |        |        |        |         |
| <i>Mephitis mephitis</i>                 | —      | —   | 1-7     | —    | —      | —      | 1-4    | 1-2     |
| <i>Martes americana</i>                  | —      | —   | —       | —    | —      | —      | —      | —       |
| <i>Mustela erminea</i>                   | —      | —   | —       | —    | —      | —      | —      | —       |
| <i>Mustela cf. frenata</i>               | —      | —   | 1-8     | —    | 1-1    | —      | —      | —       |
| <i>Taxidea taxus</i>                     | —      | —   | —       | —    | 1-2    | —      | —      | —       |
| Ursidae                                  |        |     |         |      |        |        |        |         |
| <i>Ursus arctos</i>                      | —      | —   | —       | —    | —      | —      | —      | —       |
| <i>Ursus sp.</i>                         | —      | —   | —       | —    | —      | —      | 1-1    | —       |
| Artiodactyla                             |        |     |         |      |        |        |        |         |
| Cervidae                                 |        |     |         |      |        |        |        |         |
| <i>Cervus elaphus</i>                    | 2-42   | 1-1 | 1-16    | —    | 1-3    | 1-2    | 1-1    | 1-5     |
| <i>Odocoileus hemionus</i>               | 2-2    | 1-1 | 1-9     | —    | 1-1    | —      | —      | 1-2     |
| Antilocapridae                           |        |     |         |      |        |        |        |         |
| <i>Antilocapra americana</i>             | —      | —   | —       | 1-1  | 1-5    | 1-1    | —      | 1-2     |
| Bovidae                                  |        |     |         |      |        |        |        |         |
| <i>Bison bison</i>                       | —      | —   | —       | —    | 1-2    | —      | 1-2    | 1-1     |
| <i>Ovis canadensis</i>                   | 1-4    | 1-7 | 1-2     | —    | 1-4    | 1-4    | 1-4    | 1-7     |
| Rodentia                                 |        |     |         |      |        |        |        |         |
| Sciuridae                                |        |     |         |      |        |        |        |         |
| <i>Marmota flaviventris</i>              | 3-26   | —   | 3-24    | 1-11 | 1-6    | 1-3    | 4-40   | 2-14    |
| <i>Spermophilus armatus</i>              | 3-32   | —   | 18-225  | —    | 15-112 | 12-151 | 12-168 | 13-177  |
| <i>Spermophilus sp.</i>                  | —      | —   | —       | —    | —      | —      | —      | —       |
| <i>Tamias sp.</i>                        | —      | —   | 2-6     | —    | —      | 2-4    | 1-3    | 1-2     |
| <i>Tamiasciurus hudsonicus</i>           | —      | —   | 1-1     | —    | —      | 1-1    | 1-2    | 2-8     |
| Castoridae                               |        |     |         |      |        |        |        |         |
| <i>Castor canadensis</i>                 | 1-1    | —   | 1-4     | —    | —      | —      | 1-1    | —       |
| Geomyidae                                |        |     |         |      |        |        |        |         |
| <i>Thomomys talpoides</i>                | 4-15   | —   | 14-142  | 2-11 | 4-21   | 5-40   | 7-70   | 8-118   |
| Zapodidae                                |        |     |         |      |        |        |        |         |
| <i>Zapus cf. princeps</i> <sup>b</sup>   | —      | —   | —       | —    | —      | —      | —      | 1-4     |
| Muridae                                  |        |     |         |      |        |        |        |         |
| <i>Clethrionomys cf. gapperi</i>         | —      | —   | 1-4     | —    | —      | —      | 3-9    | 1-1     |
| <i>Microtus ochrogaster</i> <sup>c</sup> | —      | —   | 1-2     | —    | —      | —      | 1-1    | 1-1     |
| <i>Microtus pennsylvanicus</i>           | 3-11   | —   | 3-17    | —    | 1-2    | 2-3    | 2-2    | 5-10    |
| <i>Microtus sp.</i>                      | 3-18   | —   | 21-179  | 1-7  | 5-20   | 18-116 | 16-154 | 28-236  |
| <i>Ondatra zibethicus</i>                | —      | —   | 3-18    | —    | —      | 1-8    | 4-16   | 1-1     |
| <i>Phenacomys intermedius</i>            | —      | —   | 3-16    | —    | 2-10   | 2-10   | 4-25   | 3-12    |
| <i>Neotoma cinerea</i>                   | 1-4    | —   | 9-87    | 1-5  | 3-20   | 8-40   | 6-48   | 8-77    |
| <i>Peromyscus cf. maniculatus</i>        | —      | —   | 9-54    | —    | 3-16   | 9-49   | 15-88  | 17-86   |
| Lagomorpha                               |        |     |         |      |        |        |        |         |
| Ochotonidae                              |        |     |         |      |        |        |        |         |
| <i>Ochotona princeps</i>                 | —      | —   | 1-5     | —    | —      | —      | —      | —       |
| Leporidae                                |        |     |         |      |        |        |        |         |
| <i>Lepus cf. americanus</i>              | —      | —   | 2-2     | —    | —      | —      | —      | 1-1     |
| <i>Lepus cf. townsendii</i>              | 1-5    | —   | 4-27    | —    | —      | —      | —      | 1-1     |
| <i>Lepus sp.</i>                         | —      | —   | —       | —    | —      | —      | 1-2    | 1-1     |
| <i>Sylvilagus cf. audubonii</i>          | —      | —   | —       | —    | —      | —      | —      | —       |
| <i>Sylvilagus cf. nuttallii</i>          | —      | —   | 2-6     | —    | —      | —      | —      | —       |
| <i>Sylvilagus sp.</i>                    | —      | —   | 1-4     | —    | —      | 1-1    | —      | 1-3     |
| Leporidae                                | —      | —   | 2-3     | —    | 1-2    | —      | 1-3    | —       |
| Total                                    | 25-171 | 3-9 | 111-903 | 6-35 | 44-231 | 70-447 | 91-672 | 106-802 |

TABLE 3—Continued

| Taxon                             | Level   |        |        |          |          |        |        |        |
|-----------------------------------|---------|--------|--------|----------|----------|--------|--------|--------|
|                                   | 9       | 10     | 11     | 12       | 13       | 14     | 15     | 16     |
| Insectivora                       |         |        |        |          |          |        |        |        |
| Soricidae                         |         |        |        |          |          |        |        |        |
| <i>Sorex cf. hoyi</i>             | 2-7     | —      | —      | —        | —        | —      | —      | —      |
| <i>Sorex merriami</i>             | 1-2     | —      | —      | 1-3      | 3-21     | —      | —      | —      |
| <i>Sorex palustris</i>            | 2-9     | —      | —      | 1-4      | 1-5      | —      | —      | —      |
| <i>Sorex (Otiosorex) sp.</i>      | 1-2     | —      | —      | 3-20     | 1-1      | —      | —      | 1-5    |
| <i>Sorex sp.</i>                  | 5-25    | —      | —      | 1-3      | 1-9      | —      | 1-1    | —      |
| Chiroptera                        |         |        |        |          |          |        |        |        |
| Vespertilionidae                  |         |        |        |          |          |        |        |        |
| <i>Myotis sp.</i>                 | 1-2     | —      | —      | 2-10     | 1-4      | —      | 1-2    | —      |
| Carnivora                         |         |        |        |          |          |        |        |        |
| Canidae                           |         |        |        |          |          |        |        |        |
| <i>Canis latrans</i>              | —       | 1-3    | 1-2    | 1-5      | —        | —      | —      | —      |
| <i>Canis lupus</i>                | —       | 1-2    | 1-4    | 1-2      | 1-1      | —      | —      | —      |
| <i>Canis sp.</i>                  | —       | —      | —      | 1-1      | —        | —      | —      | —      |
| <i>Vulpes vulpes</i>              | 1-1     | —      | —      | 1-6      | 1-1      | —      | 1-2    | —      |
| Felidae                           |         |        |        |          |          |        |        |        |
| <i>Lynx sp.</i>                   | —       | —      | —      | 1-1      | —        | —      | —      | —      |
| Mustelidae                        |         |        |        |          |          |        |        |        |
| <i>Mephitis mephitis</i>          | 1-2     | —      | —      | 1-2      | 1-2      | —      | —      | —      |
| <i>Martes americana</i>           | —       | —      | —      | 1-7      | —        | —      | —      | 1-3    |
| <i>Mustela erminea</i>            | —       | 1-2    | —      | —        | —        | —      | —      | 1-3    |
| <i>Mustela cf. frenata</i>        | 1-9     | 2-12   | 1-4    | 2-20     | 1-2      | —      | 1-1    | 2-13   |
| <i>Taxidea taxus</i>              | —       | —      | —      | 1-1      | —        | —      | —      | —      |
| Ursidae                           |         |        |        |          |          |        |        |        |
| <i>Ursus arctos</i>               | 1-1     | 1-3    | —      | 1-4      | 1-1      | —      | —      | —      |
| <i>Ursus sp.</i>                  | —       | —      | —      | —        | 1-1      | —      | —      | —      |
| Artiodactyla                      |         |        |        |          |          |        |        |        |
| Cervidae                          |         |        |        |          |          |        |        |        |
| <i>Cervus elaphus</i>             | 1-1     | —      | —      | 1-5      | —        | —      | —      | —      |
| <i>Odocoileus hemionus</i>        | —       | 1-1    | —      | 1-1      | 1-1      | 1-1    | —      | 1-1    |
| Antilocapridae                    |         |        |        |          |          |        |        |        |
| <i>Antilocapra americana</i>      | 1-5     | 1-8    | 1-3    | —        | —        | —      | —      | —      |
| Bovidae                           |         |        |        |          |          |        |        |        |
| <i>Bison bison</i>                | 1-1     | 1-1    | 1-2    | 1-10     | —        | 1-2    | 1-2    | —      |
| <i>Ovis canadensis</i>            | 1-2     | 1-2    | 1-3    | 1-6      | 1-3      | 1-4    | —      | —      |
| Rodentia                          |         |        |        |          |          |        |        |        |
| Sciuridae                         |         |        |        |          |          |        |        |        |
| <i>Marmota flaviventris</i>       | 2-8     | 2-23   | 2-30   | 8-100    | 5-37     | 1-5    | 1-8    | 2-7    |
| <i>Spermophilus armatus</i>       | 11-164  | 12-101 | 21-216 | 66-609   | 15-123   | 3-19   | 4-31   | 7-71   |
| <i>Spermophilus sp.</i>           | 3-4     | —      | —      | —        | 2-7      | —      | —      | —      |
| <i>Tamias sp.</i>                 | 1-2     | 1-4    | —      | 1-2      | 1-2      | 1-1    | —      | —      |
| <i>Tamiasciurus hudsonicus</i>    | 1-5     | 1-4    | 1-1    | 1-3      | —        | —      | —      | —      |
| Castoridae                        |         |        |        |          |          |        |        |        |
| <i>Castor canadensis</i>          | —       | —      | —      | 1-1      | —        | —      | —      | —      |
| Geomyidae                         |         |        |        |          |          |        |        |        |
| <i>Thomomys talpoides</i>         | 11-114  | 7-68   | 6-11   | 44-362   | 29-389   | 4-29   | 8-74   | 16-88  |
| Zapodidae                         |         |        |        |          |          |        |        |        |
| <i>Zapus cf. princeps</i>         | 3-7     | 1-3    | —      | 1-3      | —        | —      | 1-2    | 1-2    |
| Muridae                           |         |        |        |          |          |        |        |        |
| <i>Clethrionomys cf. gapperi</i>  | 2-4     | —      | 1-3    | 2-20     | 3-7      | —      | —      | —      |
| <i>Microtus ochrogaster</i>       | 1-3     | —      | 1-2    | 4-8      | 2-3      | 1-3    | —      | 3-12   |
| <i>Microtus pennsylvanicus</i>    | 5-8     | 1-1    | 2-9    | 5-21     | 5-9      | —      | 2-2    | 3-11   |
| <i>Microtus sp.</i>               | 27-256  | 13-77  | 10-61  | 97-680   | 71-589   | 15-69  | 12-67  | 25-165 |
| <i>Ondatra zibethicus</i>         | 1-1     | 2-13   | 2-9    | 3-17     | 1-4      | 1-2    | 1-2    | 1-3    |
| <i>Phenacomys intermedius</i>     | 3-19    | 2-6    | —      | 7-41     | 6-22     | 1-3    | 2-3    | 2-10   |
| <i>Neotoma cinerea</i>            | 10-80   | 7-50   | 16-89  | 42-368   | 27-206   | 5-30   | 7-32   | 8-58   |
| <i>Peromyscus cf. maniculatus</i> | 38-164  | 18-84  | 26-98  | 76-409   | 27-155   | 5-23   | 8-27   | 12-57  |
| Lagomorpha                        |         |        |        |          |          |        |        |        |
| Ochotonidae                       |         |        |        |          |          |        |        |        |
| <i>Ochotona princeps</i>          | —       | —      | —      | 1-7      | —        | —      | —      | —      |
| Leporidae                         |         |        |        |          |          |        |        |        |
| <i>Lepus cf. americanus</i>       | —       | —      | —      | 2-12     | 2-3      | 1-3    | —      | —      |
| <i>Lepus cf. townsendii</i>       | 1-5     | 1-6    | 1-3    | 2-11     | 1-2      | —      | —      | 2-4    |
| <i>Lepus sp.</i>                  | 1-3     | —      | —      | 1-4      | 1-1      | 1-1    | 1-1    | 1-2    |
| <i>Sylvilagus cf. audubonii</i>   | —       | —      | 1-5    | —        | —        | —      | —      | —      |
| <i>Sylvilagus cf. nuttallii</i>   | —       | —      | —      | —        | —        | —      | —      | —      |
| <i>Sylvilagus sp.</i>             | 1-2     | —      | —      | 1-1      | 1-1      | 1-1    | —      | —      |
| Leporidae                         | 1-1     | —      | 1-1    | 1-3      | 1-2      | —      | —      | 1-2    |
| Total                             | 143-919 | 78-474 | 97-556 | 389-2793 | 215-1614 | 43-196 | 53-259 | 90-516 |

<sup>a</sup> Minimum number of individuals (MNI) - number of identified specimens (NISP).

<sup>b</sup> Taxon no longer present near Lamar Cave, but present in Yellowstone National Park.

<sup>c</sup> Taxon no longer present near Lamar Cave or present in Yellowstone National Park.



TABLE 4  
Mammals Not Found in Lamar Cave but Present in Yellowstone National Park

| A. Insectivora and Chiroptera                  | B. Closed forest mammals            | C. Open habitat mammals                |
|--|-------------------------------------|--|
| <i>Sorex (Otiosorex) cinereus</i> <sup>a</sup> | <i>Spermophilus lateralis</i>       | <i>Lemmys curtatus</i> <sup>b</sup>    |
| <i>Sorex (Otiosorex) preblei</i> <sup>a</sup>  | <i>Tamias minimus</i> <sup>a</sup>  | <i>Mustela vison</i>                   |
| <i>Sorex (Otiosorex) nanus</i> <sup>a</sup>    | <i>Tamias amoenus</i> <sup>a</sup>  | <i>Spilogale putorius</i> <sup>b</sup> |
| <i>Myotis lucifugus</i> <sup>a</sup>           | <i>Tamias umbrinus</i> <sup>a</sup> | <i>Lutra canadensis</i> <sup>c</sup>   |
| <i>Myotis thysanodes</i> <sup>a</sup>          | <i>Glaucomys sabrinus</i>           | <i>Felis concolor</i>                  |
| <i>Myotis evotis</i> <sup>a</sup>              | <i>Erethizon dorsatum</i>           | <i>Ursus americanus</i>                |
| <i>Myotis yumanensis</i> <sup>a</sup>          | <i>Lynx canadensis</i>              |  |
| <i>Myotis volans</i> <sup>a</sup>              | <i>Odocoileus virginianus</i>       |  |
| <i>Pipistrellus subflavus</i>                  | <i>Alces alces</i>                  |  |
| <i>Lasionycteris noctavagans</i>               |                                     |  |
| <i>Eptesicus fuscus</i>                        |                                     |  |
| <i>Lasiurus cinereus</i>                       |                                     |  |
| <i>Euderma maculata</i>                        |                                     |  |
| <i>Plecotus townsendii</i>                     |                                     |  |

<sup>a</sup> Genus present, but no species designated.

<sup>b</sup> Presence in Yellowstone National Park questionable.

<sup>c</sup> Absence unexpected.

(NISP) (Grayson, 1973, 1978) were calculated for each stratigraphic level, and then stratigraphic counts were lumped within each time interval in order to assess the faunal changes.

The two mammals that dominate the faunal assemblage over the entire 3000 yr are also those most abundant in the current local fauna: the Uinta ground squirrel (*Spermophilus armatus*) and montane vole (*Microtus* cf. *M. montanus*). Other common mammals include the deer mouse (*Peromyscus maniculatus*), pocket gopher (*Thomomys talpoides*), and the bushy-tailed wood rat (*Neotoma cinerea*). Shrews and lagomorphs are present throughout the cave deposits in relatively low frequency. Bats are extremely rare. Although diverse, fossil large mammals such as artiodactyls and carnivores are present in low frequency, much as they are in the present mammalian community.

Taxa found in Yellowstone National Park, but absent from Lamar Cave (Table 4), include most of the diversity of bats in the region, some shrews, some carnivores, and taxa found mainly in lodgepole pine (*Pinus contorta*) and spruce-fir (*Picea engelmannii*-*Pseudotsuga menziesii*) forest habitats. The low frequency of bats in the fauna is expected, given that these taxa do not form large components of carnivore or raptor diets. Shrews are also not abundant in predator diets, although half of the shrew diversity of the park is found in the Lamar Cave fauna. Shrews are difficult to identify based on dental material alone and their low diversity probably is due to complications of identification rather than absence. Carnivores are relatively rare in any mammal community, which may explain the absence of the carnivores listed in Table 4. The absence of both large and small mammals preferring forested habitats is further evidence that the

fauna from Lamar Cave was not collected from a large area; rather, the faunal accumulation for the most part represents the local sagebrush-grassland community of mammals. Exceptions include the pygmy shrew (*Sorex hoyi*), pika (*Ochotona princeps*), snowshoe hare (*Lepus americanus*), prairie vole (*Microtus ochrogaster*), western jumping mouse (*Zapus princeps*), pine marten (*Martes americana*), and ermine (*Mustela erminea*). Although these taxa are rare in the fauna of Lamar Cave, they are habitat specialists and their presence either indicates long-distance transport (>5 km) or an alternate vegetation type ultimately linked to a climate different than conditions around Lamar Cave today (Hadly, 1995).

Two animals, the sagebrush vole (*Lemmys curtatus*) and the spotted skunk (*Spilogale putorius*), are shown as present in Yellowstone National Park on range maps (Clark and Stromberg, 1987; Hall, 1981) but have not been recovered by trapping (Hadly, 1995), nor are they present in the Lamar Cave fauna. Absence of the sagebrush vole is surprising since the habitat preferred by this species is found near Lamar Cave. Presence of these animals in Yellowstone National Park therefore is questionable both currently and prehistorically.

Only one species extralimital to the park is present in the deposits of Lamar Cave: the prairie vole (*M. ochrogaster*). Currently, the closest known occurrence of this taxon is 100 km north of Lamar Cave. The prehistoric presence of this species suggests the existence of taller grass habitats in the vicinity of Lamar Cave at various times during the past than today (Grant *et al.*, 1977).

#### Presence-Absence Data

The habitat specialists in Lamar Cave (Table 5) not typically indicative of the local sagebrush grassland or the imme-

diat forests are all indicative of more mesic environments found presently at higher elevations (*O. princeps*), in taller grass microhabitats (*M. ochrogaster*, *Z. princeps*), or in wetter, closed forest (*L. americanus*, *M. americana*, *M. erminea*). These mesic taxa are all present at time interval C, an interval which paradoxically is a time when a fauna characteristic of warm and probably dry conditions would be expected. The apparently anomalous presence of mesic species in interval C may be due to (1) the high number of identified specimens (NISP = 6216); (2) time-averaging of short mesic intervals within the overall warm trend of the Medieval Warm Period; (3) the persistence of a pocket of mesic habitat nearby; or (4) overlap of interval C with the Little Ice Age.

Several of the mesic taxa also are present in time intervals A, D, and E. No mesic taxa are found in time interval B, which is one of two intervals with apparent temporal overlap with the Little Ice Age, a cooler, wetter time period. But time interval B also overlaps with the Medieval Warm Period and spans a warmer period of reduced glacier activity within the Little Ice Age (Porter, 1986). Absence of all mesic-indicator taxa at interval B suggests that it is the most xeric of all time intervals spanned by the Lamar Cave deposits. Apparently the short Little Ice Age signal of interval B is totally swamped by time-averaging with the more persistent, and perhaps extreme, Medieval Warm Period, and the warmer period within the Little Ice Age, perhaps demonstrated by variable but increased fire frequency (Fig. 2) (Meyer, 1993).

As discussed above, dating resolution for time intervals B and A is particularly difficult, but the evidence from the faunal data does show that time interval A is more representative of a mesic period than time interval B. Although this conclusion may be biased because time interval B contains the fewest specimens (NISP = 713), and taxonomic diversity is a function of sample size (Fig. 5), specimen counts for interval B are equivalent to time interval E (NISP = 775), which contains four of the six mesic-indicator taxa.

TABLE 5

Number of Identified Specimens of Rare Extralocal Mammals Which Prefer More Mesic Habitats Than in the Vicinity of Lamar Cave Today

|                             | Time interval |   |    |   |    |
|-----------------------------|---------------|---|----|---|----|
|                             | A             | B | C  | D | E  |
| <i>Ochotona princeps</i>    | 5             |   | 7  |   |    |
| <i>Lepus cf. americanus</i> | 2             |   | 13 | 6 |    |
| <i>Microtus ochrogaster</i> | 2             |   | 15 | 6 | 12 |
| <i>Zapus princeps</i>       |               |   | 17 |   | 4  |
| <i>Martes americana</i>     |               |   | 7  |   | 3  |
| <i>Mustela erminea</i>      |               |   | 2  |   | 3  |

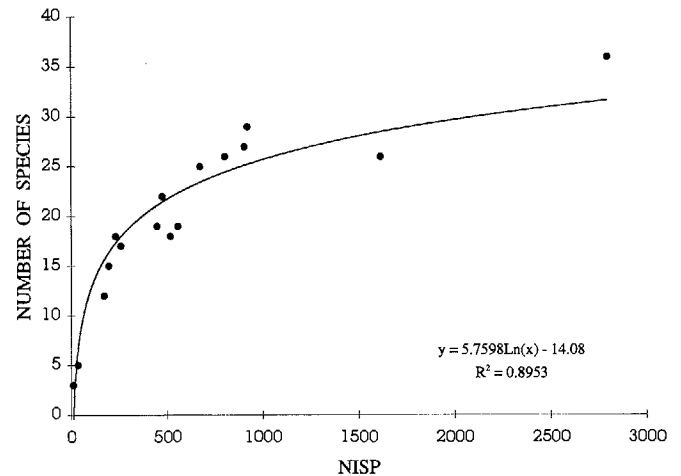


FIG. 5. Plot and logarithmic regression of number of species against number of identified specimens for Lamar Cave mammals.

Not surprisingly, the two carnivores are the rarest of the six mammals, with a combined NISP = 15. Pikas are likewise rare and are confined to intervals A and C. The snowshoe hare, prairie vole, and jumping mouse all have individual NISP > 20. The prairie vole is present in four out of five levels and absent only from time interval B. This species has not been found in the vicinity of the cave today, perhaps indicating a recent return to more xeric conditions.

#### Relative Abundance of Small Mammals

Although the occurrence of mesic-indicator taxa may suggest environmental conditions different than those of today, the taxa shown in Table 5 are rare and their presence or absence in a given depositional unit may be due more to the vagaries of taphonomic collection and time-averaging than to true environmental conditions. Therefore, scrutiny of the patterns of abundance of the most common taxa in a fauna may be a better gauge to environmental variation, particularly when the taxa are known to be environmentally sensitive.

There are five abundant taxa in Lamar Cave (*N. cinerea*, NISP = 1187; *P. maniculatus*, NISP = 1261; *T. talpoides*, NISP = 1548; *Microtus* sp., NISP = 2744; and *S. armatus*, NISP = 1849) (Fig. 6). Trapping studies conducted in the vicinity of the cave show that three of these taxa, *T. talpoides*, *Microtus* sp. (primarily *M. montanus* and *M. pennsylvanicus*), and *S. armatus*, are common constituents of a sagebrush grassland. The other two species, *N. cinerea* and *P. maniculatus*, are considered to be environmentally ubiquitous and not particularly sensitive to habitat differences (Barnosky, 1994), which is corroborated by unfluctuating relative abundances of these two species through the five time intervals of the Lamar Cave deposits. The extremely constant abundance of *Neotoma* further corroborates the taphonomic

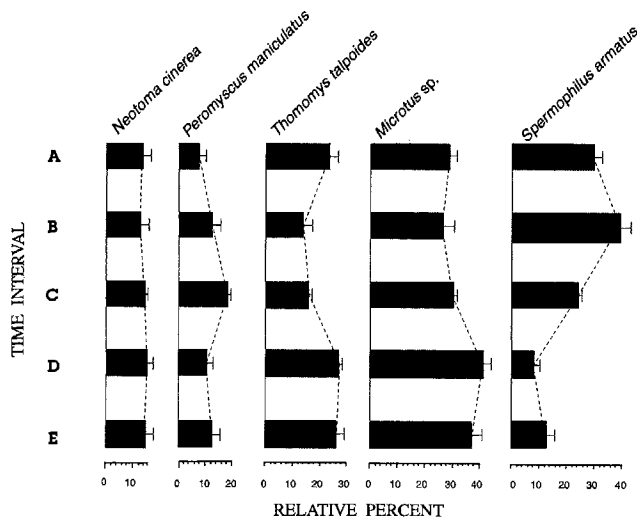


FIG. 6. Relative abundance of the five most common mammals from Lamar Cave for time intervals A through E. Abundances are based on 8589 total number of identified specimens. The 95% confidence intervals for the five common taxa per interval are shown, where

$$SE\hat{p}_t = \left( \sqrt{\frac{\hat{p}_t(1 - \hat{p}_t)}{N_t}} \right) \times 100$$

when

$$\hat{p}_t = \frac{X_t}{N_t};$$

with  $X_t$  = NISP of taxon at interval  $t$  and  $N_t$  = TNISP at interval  $t$ .

interpretations and suggests that variation in the faunal record is not produced by population fluctuation of this species.

Relative abundances of the other three common taxa fluctuate between time intervals. *Microtus* sp. and *T. talpoides* show similar patterns, with highs in abundance at time intervals A and E, a peak at interval D, and lows at intervals B and C. *Microtus* sp. (mostly *M. cf. montanus*) is a relatively mesic indicator taxon which today is found primarily in wetter, denser grass microhabitats within the sagebrush grassland (Fig. 1B) (Barnosky, 1994; Hadly, 1995). *T. talpoides* prefers ecotones with abundant forbs, which are generally, though not entirely, present as mesic microhabitats in the vicinity of Lamar Cave.

In contrast to *Microtus* sp. and *T. talpoides*, the relative abundance of *S. armatus* peaks at interval B, with highs at time intervals A and C and low relative abundances at intervals D and E. Today *S. armatus* is found in the more xeric microhabitats of the sagebrush grassland where cover is sparse and visibility unrestricted (Barnosky, 1994). Vegetation density (cover) in a grassland is influenced to a large extent by effective moisture, mainly mean annual precipitation (French *et al.*, 1976; Grant and Birney, 1979), with

grassy microhabitats in wetter areas and sagebrush in drier areas.

Opposing grassland cover preferences of *Microtus* and *Spermophilus* provide an important tool for interpreting the effects of climatic change on the small mammal community (Barnosky, 1994; Hadly, 1990). Relative abundance of taxa from interval B indicates that the environment was more xeric than at any time during the past 3000 yr. With caveats discussed above, local fire-frequency and alluvial data agree (Fig. 2). A peak in mesic conditions is revealed at time interval D. Less evident from the mammalian signal are the environmental effects of the Little Ice Age and the warm period from 2850 to 2050 yr B.P. This warm period is documented locally, with moderate to high fire frequencies (Meyer, 1993), and overlaps with interval E. Relative to the extremes at intervals B and D, however, the small mammal response indicated in intervals A, C, and E is concordant with the changing local environment. Although there is no strong, unambiguous signal for the Little Ice Age, small mammal relative abundances do display a more mesic signal at interval A than at interval B. These relative abundance data make even a stronger case than the presence/absence data and demonstrate that small mammals are sensors of climatic change in the Yellowstone area.

## CONCLUSIONS

Study of the Lamar Cave fauna reveals mammalian responses to climatic changes at the  $10^2$  to  $10^3$  yr time scale. (1) From 3200 yr B.P. to a maximum at 1100 yr B.P., mammals indicate more mesic conditions than at present, which is partially concordant with evidence of fire frequency and alluvial chronology. High fire frequency for this time demonstrates that the climate was warm, though not necessarily dry, and may have been variable. (2) Beginning about 1200 years ago, the mammals show that the climate became warmer and drier, culminating with the most xeric period during the past 3000 yr, interval B. Pollen data and fire-related alluviation also indicate xeric conditions, generally corresponding to the Medieval Warm Period recognized elsewhere. (3) Mammalian faunal evidence for the Little Ice Age is less clear, in part because the radiocarbon chronology does not have the necessary resolution. However, sometime after peak warm conditions, the mammalian fauna shows a return to more mesic conditions by interval A as the region passed from the Medieval Warm Period through the Little Ice Age to the present.

Generally, mammalian response to climate is threefold. First, climatic change, e.g., to the Medieval Warm Period, is capable of temporarily eliminating rare small mammals that prefer relatively more mesic habitats than found in the vicinity of Lamar Cave today. Presence/absence data indicate that reversal of this effect is possible with reestablish-

ment of more mesic conditions. Second, some common mammals are unaffected by climatic fluctuations. The small mammals fitting this category of response do not show habitat specificity today. Third, late-Holocene climatic conditions have resulted in population fluctuations of common small mammals with well-defined habitat preferences. This probably is accomplished primarily through modification of the relative surface distribution of microhabitats which characterize the sagebrush grassland present near Lamar Cave today. In fact, in experimental manipulations of a montane meadow intended to mimic potential global-warming conditions, sagebrush increased in abundance relative to grass (Harte and Shaw, 1995).

Given these data, the mammalian fauna of Yellowstone National Park is predicted to respond in the following ways as global-warming proceeds: In the sagebrush grassland of northern Yellowstone, the relative abundance of *Spermophilus* will increase while abundances of *Microtus* sp. and *T. talpoides* will decline. Mesic taxa such as *O. princeps*, *L. americanus*, *Z. princeps*, *M. americana*, and *M. erminea* are predicted to decline and eventually disappear from what are currently more mesic areas near the sagebrush grassland. Close monitoring of these species therefore may provide a sensitive gauge on biotic effects of ongoing climatic change in the world's oldest national park.

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