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## Late Quaternary environmental change in the Bonneville basin, western USA

D.B. Madsen<sup>a,\*</sup>, D. Rhode<sup>b</sup>, D.K. Grayson<sup>c</sup>, J.M. Broughton<sup>d</sup>, S.D. Livingston<sup>b</sup>,  
J. Hunt<sup>a</sup>, J. Quade<sup>e</sup>, D.N. Schmitt<sup>a</sup>, M.W. Shaver III<sup>a</sup>

<sup>a</sup>Utah Geological Survey, Salt Lake City, UT 84116, USA

<sup>b</sup>Desert Research Institute, Reno, NV 89512, USA

<sup>c</sup>University of Washington, Seattle, WA 98195, USA

<sup>d</sup>University of Utah, Salt Lake City, UT 84102, USA

<sup>e</sup>University of Arizona, Tucson, AZ 85721, USA

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### Abstract

Excavation and analyses of small animal remains from stratified raptor deposits spanning the last 11.5 ka, together with collection and analysis of over 60 dated fossil woodrat midden samples spanning the last 50 ka, provide a detailed record of changing climate in the eastern Great Basin during the late Pleistocene and Holocene. Sagebrush steppe dominated the northern Bonneville basin during the Full Glacial, suggesting that conditions were cold and relatively dry, in contrast to the southern basin, which was also cold but moister. Limber pine woodlands dominated ~13–11.5 ka, indicating increased dryness and summer temperatures ~6–7°C cooler than present. This drying trend accelerated after ~11.5 ka causing Lake Bonneville to drop rapidly, eliminating 11 species of fish from the lake. From ~11.5–8.2 ka xerophytic sagebrush and shadscale scrub replaced more mesophilic shrubs in a step-wise fashion. A variety of small mammals and plants indicate the early Holocene was ~3°C cooler and moister than at present, not warmer as suggested by a number of climatic models. The diversity of plants and animals changed dramatically after 8.2 ka as many species disappeared from the record. Some of the upland species returned after ~4 ka and Great Salt Lake became fresh enough at ~3.4 and ~1.2 ka to support populations of Utah chub. © 2001 Elsevier Science B.V. All rights reserved.

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### 1. Introduction

The Bonneville basin is the biggest drainage basin in the Great Basin of western North America, and, at times, contains one of the largest lakes on the continent (Fig. 1). Over the past several decades the amount of information on late Quaternary paleoen-

vironmental change in and around the basin has increased dramatically. Extant data are strongly biased towards geomorphological analyses of lake-level changes (e.g. Currey, 1990; Oviatt et al., 1992), yet provide a foundation for our understanding of the evolution of biotic communities in the region. We have attempted to construct a more comprehensive picture by developing a long-term interdisciplinary research project focused on placing changes in Bonneville basin flora and fauna in a

\* Corresponding author. Fax: +1-801-537-3500.

E-mail address: dmadsen@state.ut.us (D.B. Madsen).

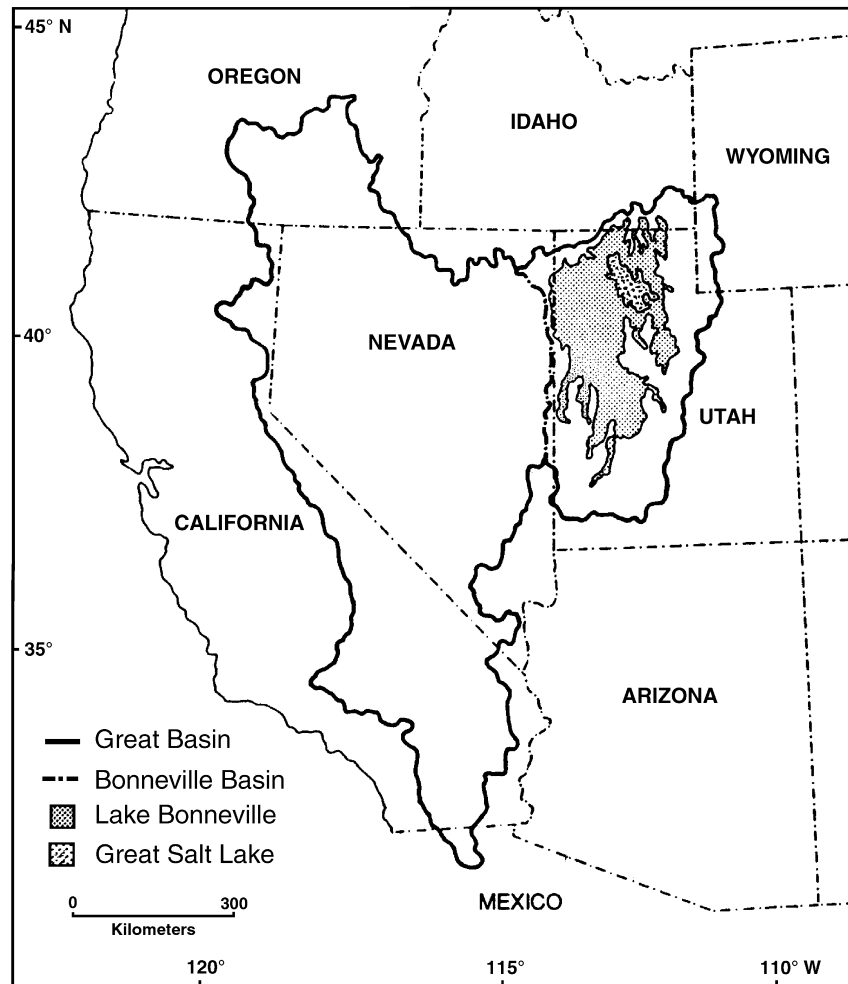


Fig. 1. Locations of the Great Basin, Bonneville basin, and Great Salt Lake in the southwestern USA (after Sack, 1989; Currey, 1990).

geomorphological context. Here we briefly report major aspects of this project.

### 1.1. Lake-level history

There have been closed-basin lakes in the Bonneville basin for at least the last two million years (Machette et al., 1992; Morrison, 1991), but exposed shoreline features are primarily associated with the last major lake cycle. The transgressive phase of the Lake Bonneville cycle probably began sometime between about 32 ka (Currey, 1990) and 30 ka (Oviatt et al., 1992), and consisted of a long 10,000–15,000 year period of oscillating, but gener-

ally rising lake cycles peaking at the Bonneville level about 15.3–15.0 ka.<sup>1</sup> This general trend was interrupted by a climatically controlled stillstand which formed the Stansbury shoreline complex, and a ~45 m lake-level regression dated to sometime between 22 and 20 ka (Oviatt et al., 1990, 1992). The continued rise of Lake Bonneville over the course of the next 6 ka was probably interrupted by a number of minor climatically induced oscillations, but these are poorly represented in the shoreline features (see Oviatt, 1997).

<sup>1</sup> All dates within the radiocarbon time scale are given in radiocarbon years (ka) unless otherwise noted.

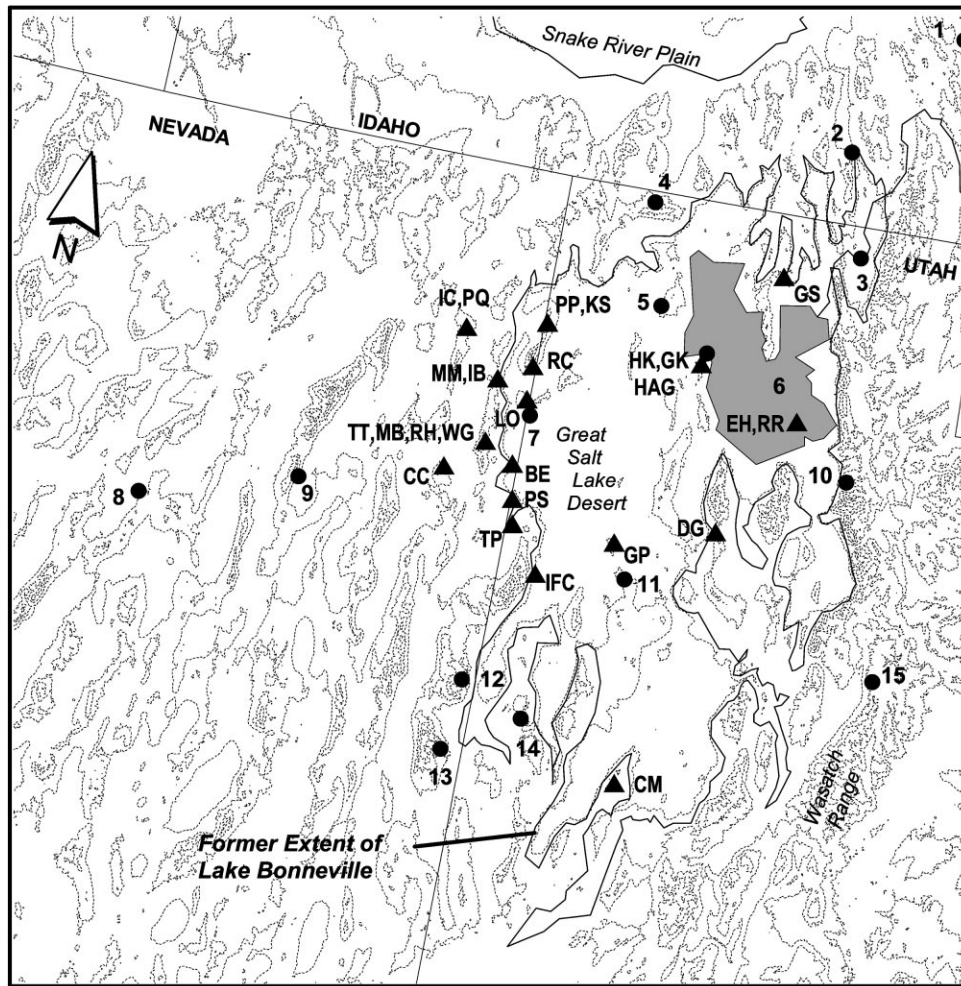


Fig. 2. Letters show midden localities reported here (TT is the Top of the Terrace locality). Numbers show the location of other paleoenvironmental records discussed in the text: 1, Grays Lake; 2, Swan Lake/Zenda Threshold; 3, Bear River; 4, Raft River Mountains; 5, Crescent Spring/Hogup Cave; 6, Great Salt Lake; 7, Danger Cave; 8, Potato Canyon Bog; 9, Ruby Marsh/Lake Franklin; 10, Little Cottonwood Canyon/Snowbird Bog; 11, Old River Bed; 12, Council Hall Cave/Northern Snake Range; 13, Southern Snake Range; 14, Confusion Range; 15, Huntington Canyon.

By about 15.0 ka, the lake reached the Zenda threshold in southern Idaho and began to overflow into the Snake/Columbia River drainage (Oviatt et al., 1992). Catastrophic downcutting at Red Rock Pass about 14.5 ka reduced the level of the lake 108 m in less than a year (Currey and Oviatt, 1985; Jarrett and Malde, 1987). This threshold-controlled Provo level lake elevation was maintained until after about 14.0 ka when the lake began to enter a regressive phase that continued with some interruption for the next 6 ka (Currey, 1990; Oviatt et al., 1992). This

regressive phase is poorly known, but extant data suggest that the lake may have reached modern levels or lower by sometime after 12 ka before rebounding to reach the Gilbert level sometime between 11 and 10 ka (Currey, 1990; Oviatt et al., 1992; but see Zachary and Oviatt, 1999).

### 1.2. Plant communities

Our understanding of late Quaternary changes in the structure of Bonneville basin plant communities

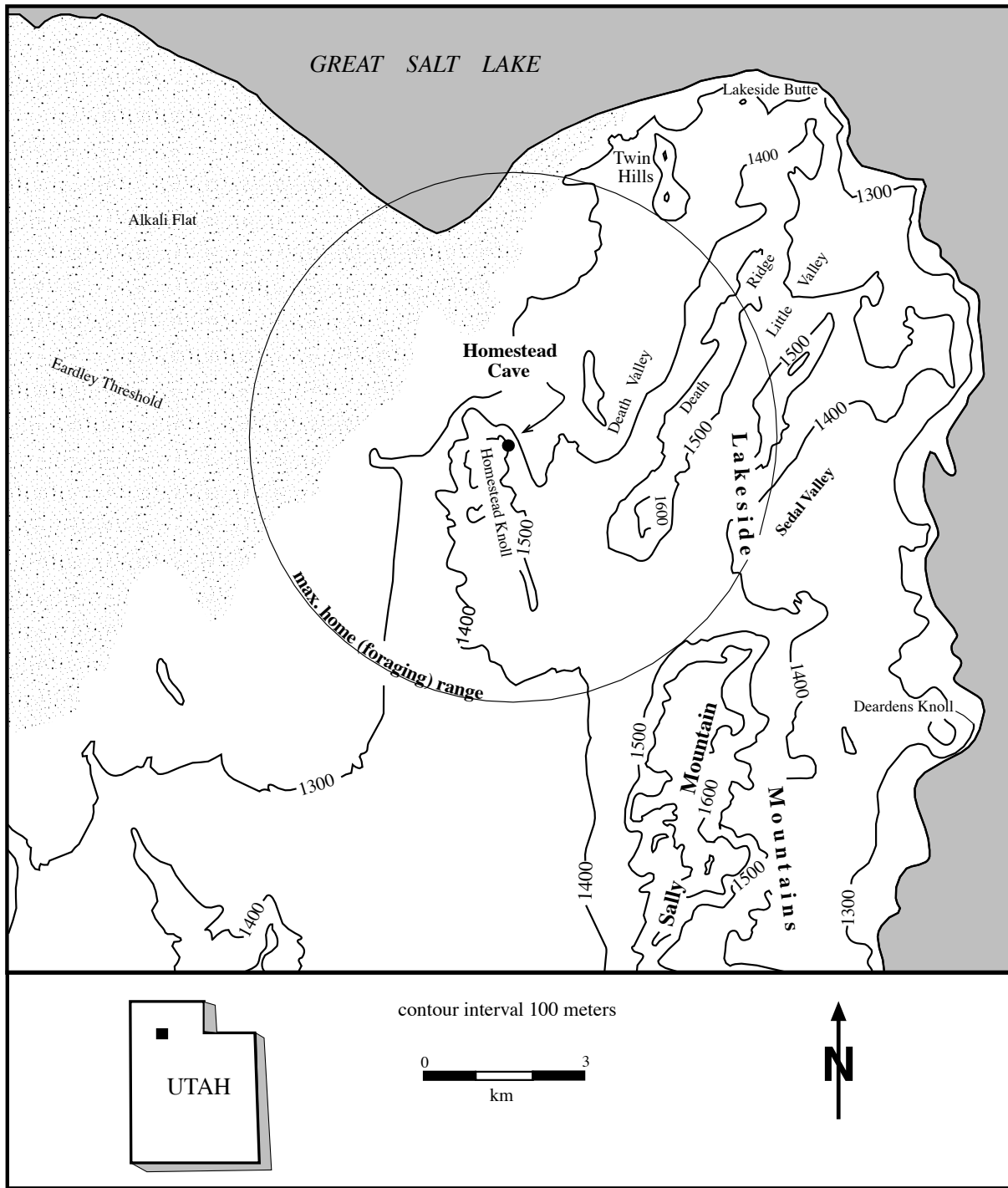


Fig. 3. Map of the north end of the Lakeside Mountains showing the location of Homestead Cave along the margin of Great Salt Lake and the maximum foraging area of raptors operating from the cave.

is based largely on the identification and dating of plant macrofossils from fossil woodrat (*Neotoma* spp.) middens, but is supplemented by pollen records from a number of locations in and around the basin. We collected and dated 62 samples from middens collected at 40 localities in and adjacent to the Great Salt Lake basin, the northernmost major sub-basin of the Bonneville basin (Fig. 2).<sup>2</sup> Many of these middens date to a period of 14–10 ka spanning the Pleistocene/Holocene transition, but a number are 30,000–40,000 years old or older and 37 samples are of Holocene age. The older middens remain under analysis and we provide only an initial assessment here. The number of younger middens, in conjunction with plant remains from stratified caves around the margin of the Great Salt Lake Desert and from previously recovered middens, is now sufficient to estimate the nature of changing plant communities in the Bonneville basin during the Pleistocene/Holocene transition and later.

The middens contain vegetation which grew within 50–100 m of their location (Dial and Czaplowski, 1990; Frase and Sera, 1993), and were found in caves, overhangs, and crevices, principally in limestone bedrock outcrops. Midden preservation depends on long-term protection from moisture; rock outcrops with abundant fractures, or with exfoliating surfaces, tend not to contain very old middens. The abundant caves and shelters found in rock outcrops at the margins of the Bonneville basin often contain older middens, while the equally abundant shelters in the basin's center lack them, perhaps due to fracturing associated with isostatic rebound following the decline of Lake Bonneville. As a result, the midden record is biased toward locations on the western margin of the Great Salt Lake Desert, with relatively little coverage in the mountains of the central Bonneville basin. Nor have older middens been found in the mountains of the eastern Bonneville basin, perhaps because these are better watered and middens are subject to greater destruction through time.

### 1.3. Faunal assemblages

Our understanding of animal assemblages asso-

ciated with lower elevation plant communities in the central Bonneville basin is derived primarily from the sampling of stratified raptor deposits in a cave on the western margin of Great Salt Lake (Fig. 3), together with extant collections from a number of other stratified caves around the Bonneville basin (e.g. Grayson, 1988). Homestead Cave was selected after an extensive reconnaissance and testing of sites in the western Bonneville basin. The goal was to identify a cave with stratified deposits that could be cleanly separated and that contained extensive deposition by owls, but with little contamination by human foragers. Many species of owls feed on a variety of small mammals, reptiles, birds, fish and insects (e.g. Marti, 1986; Andrews, 1990; Marti and Kochert, 1996). They thus can produce a useful sample of small-animal communities within their foraging radius. Owls typically roost on interior ledges where regurgitated pellets form cones on the cave floor containing tens of thousands of bones (Andrews, 1990; Kusmer, 1990). Perches in Homestead Cave are currently active and consolidated cones comprised of droppings, pellet matter and bone are situated on the modern surface below several different roosts. The foraging radius of owls is typically less than 5 km from their roosts (e.g. Craighead and Craighead, 1969; Smith, 1971). While this foraging radius may overlap that of prey species and thus extend the range from which animals represented in pellet cones may come, virtually all the faunal remains deposited by owls at Homestead Cave come from within a 10 km radius of the site. A very small portion of the faunal assemblage in the cave may come from vectors other than owls, such as coyotes.

Homestead Cave is a wave-constructed cavern in a limestone ridge on the northwestern margin of the Lakeside Mountains. This range borders Great Salt Lake on the east, and, on the west, overlooks the Eardley Threshold through which the lake intermittently floods the western Utah desert at high lake levels. The range is at the point of maximum isostatic rebound (Currey, 1988) and until well into the Holocene it formed a narrow peninsula extending into the lake. Elevations in the Lakeside Mountains reach 1685 m within a raptor foraging area centered at Homestead Cave, but most of this area lies below 1500 m. Within this zone modern vegetation consists primarily of mixed greasewood, shadscale, saltbush

<sup>2</sup> Tabular summaries of the floral and faunal data discussed here are available in Madsen (2000a).

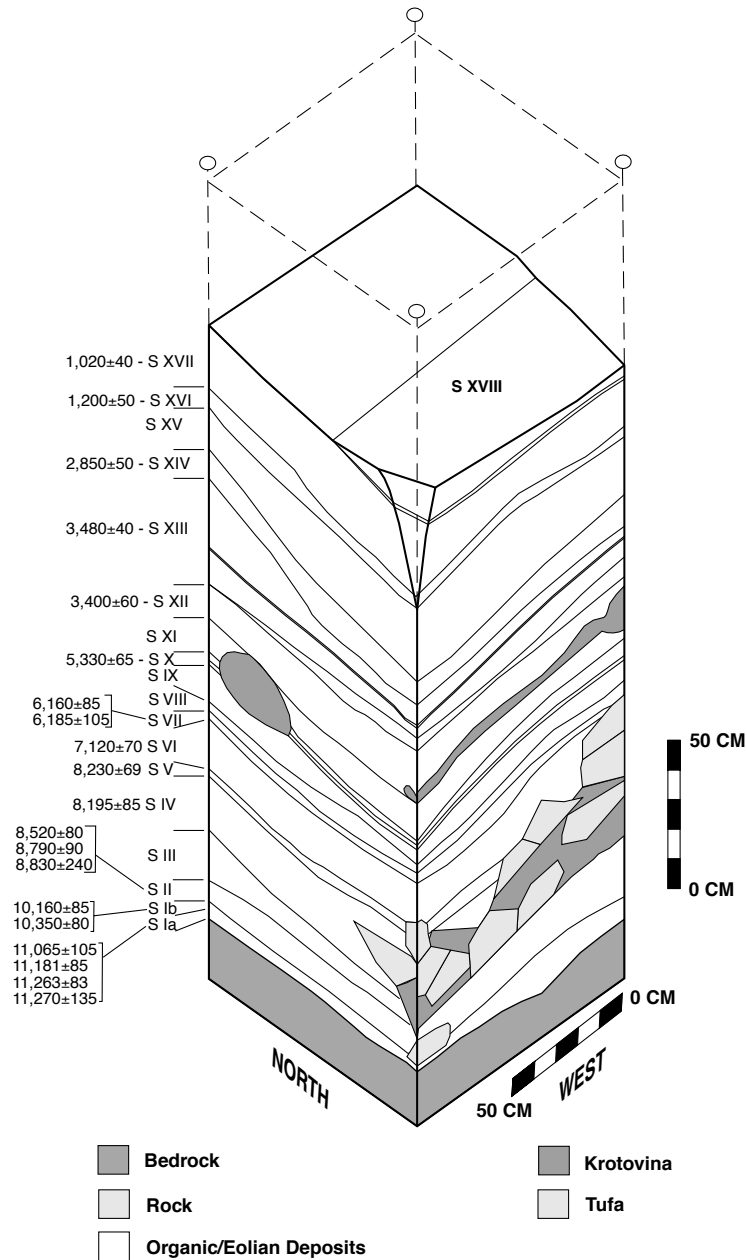


Fig. 4. Block diagram of the Homestead Cave sample column stratigraphy showing the north and west profiles, strata designations, and radiocarbon ages.

and spiny horsebrush communities. The cave is at 1406 m above sea level, midway between the Provo (1503 m) and Gilbert (1311 m) levels of Lake Bonneville.

We isolated and removed a 1 m<sup>2</sup> sample column

from deposits on the cave floor. Eighteen depositional units spanning the last 11.3 ka were identified and separately removed (Fig. 4). More than two hundred thousand faunal elements from the column could be identified to a useful taxonomic level. We attempted

Table 1  
Approximate age of Bonneville basin Holocene climatic cycles (adapted from Mayewski et al., 1997; calibration from Stuiver et al., 1998)

Approximate calendar age	Approximate radiocarbon age
0–100 BP	–
100–580 BP	50–550 BP
580–2400 BP	550–2400 BP
2400–3100 BP	2400–2950 BP
3100–5000 BP	2950–4450 BP
5000–6100 BP	4450–5300 BP
6100–7800 BP	5300–7000 BP
7800–8800 BP	7000–8000 BP
8800–11,300 BP	8000–9950 BP
11,300–12,900 BP	9950–10,900 BP

to limit problems of bioturbation by focusing only on depositional layers that could be mapped across all faces of the column and that could be cleanly and completely separated from one another. Microlaminae were evident within each of these stratigraphic units, but were not separately excavated. Changes in the fish fauna through the lowest stratum were detected by arbitrarily sampling the upper and lower halves and upper and lower thirds of the unit. Radiocarbon samples from this unit were collected from the upper and lower 5 cm. The entire column was transported in bulk to the laboratory where material was passed through a series of graded screens to facilitate sorting and identifications. With the exception of fish, faunal materials that passed through a 3.2 mm mesh have not yet been identified. Only mammal, fish and bird skeletal elements have been identified to date. A variety of other fauna, such as reptiles and insects, were also recovered but have not yet been analyzed. In some instances the large size of the collection made analytical choices necessary. For small mammals, several strata were not analyzed. For birds, only those specimens that did not pass through a 3.2 mm mesh screen were analyzed. We identified 183,798 mammal bones and teeth to at least the genus level from the 6.4 mm sample fraction. This represents the most substantial late Pleistocene and Holocene mammal sequence ever identified from the Great Basin and the record is particularly rich and complete for the early Holocene.

Chronological controls are provided by 25 radiocarbon assays. Four of these were taken for control

purposes and are not reported here. The remaining 21 samples were collected directly from the column profile (Fig. 4). Most of these samples consisted of individual rodent or artiodactyl fecal pellets. Multiple samples were analyzed from the lower depositional units to assess the contemporaneity of materials within the unit. The consistency of the age estimations suggests bioturbation is limited and faunal materials within these units are directly associated with the dated samples. Deposition appears to have been relatively continuous, with periods of slow, or no, deposition at ~11,000, ~8500 and ~5000 calibrated calendar years ago.

#### 1.4. Organizing the environmental record

Fluctuations of Great Basin lakes appear to reflect change in the regional water budget due to broad changes in precipitation and evaporation rates linked to the ocean-atmospheric system via the polar jet stream (e.g. Benson et al., 1997). Both long-term climatic cycles driven by orbital mechanics and shorter term millennial-scale cycles, evident in Greenland and North Atlantic core records (e.g. Bond et al., 1997; Mayewski et al., 1997), are also evident in Lake Bonneville deposits (e.g. Oviatt, 1997). Just how precisely the millennial-scale cycles evident in the lake history are correlated with those in the ice and ocean core records remains unclear, however. To organize the Holocene portion of the environmental record reported here, we employ the age of cycles identified by Mayewski et al. (1997) for the last 11 ka (Table 1), but note that the precise timing of these cycles, as well as their geomorphological and biological expression, remains open to debate and is subject to confirmation. As yet the environmental record for the preceding 40,000 years is not sufficiently fine-grained to allow organization at the level of millennial-scale climatic cycles.

## 2. Major environmental characteristics of Bonneville basin climatic cycles

### 2.1. Middle Wisconsin (isotope stage 3) interstadial period, 50,000–28,000 BP

Middens older than 14,000  $^{14}\text{C}$  years come from a single rockshelter location at an altitude of 2012 m in

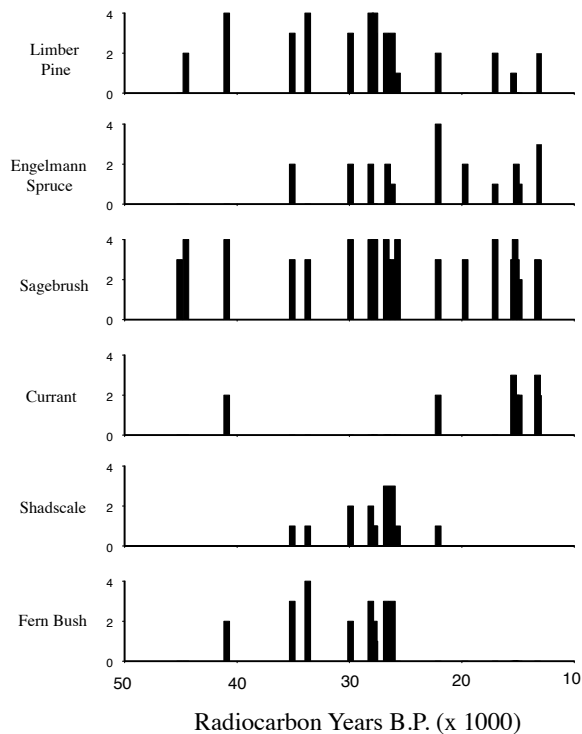


Fig. 5. Major constituents of samples from the Top of the Terrace middens spanning the last 50 ka. 1, rare; 2, present; 3, common; 4, abundant.

the Goshute Range, on the western margin of the Bonneville basin. Preliminary analyses of the Top of the Terrace middens provide a valuable picture of changing vegetation patterns in the poorly known interval from the Middle Wisconsin interstadial through the height of the Late Wisconsin Full Glacial period (Fig. 5). The ages of the oldest samples are beyond the limits of radiocarbon. These contain abundant remains of Utah juniper (*Juniperus osteosperma*), accompanied by sagebrush (*Artemisia* sect. *tridentatae*), horsebrush (*Tetradymia* sp.), snowberry (*Symphoricarpos* sp.) and cactus (*Opuntia* sp.). Utah juniper is also common today, but it disappeared by about 46 ka, and did not re-appear in the area until the middle Holocene. These samples also contain fecal pellets from pika (*Ochotona princeps*), a cold-adapted lagomorph, and marmot (*Marmota* sp.) skeletal remains. Neither has been recorded as living in the Goshute Range today. The combination of

remains from the relatively thermophilic Utah juniper mixed with remains from these sub-alpine mammals may reflect the kind of “non-analogue” or “intermingled” species pairs documented elsewhere in packrat middens (e.g. Spaulding, 1981; Van Devender, 1990) and faunal assemblages (Graham, 1985) dating to the late Pleistocene.

By 46 ka, Utah juniper woodland was replaced by montane meadow vegetation, including shrubs such as sagebrush, currant (*Ribes* cf. *montigenum*) and shrubby cinquefoil (*Potentilla fruticosa*), which suggests that cool, relatively moist conditions prevailed in the region. Montane shrub communities found today in the upper elevations of higher mountains in the interior eastern Great Basin may be analogous to the vegetation represented in the midden samples dating to this age. By about 41 ka, limber pine (*Pinus flexilis*) appeared in the area, and it became a dominant conifer through ~28 ka. This sub-alpine conifer tends to grow in cold, dry, harsh conditions. Fernbush (*Chamaebatiaria millefolium*), a montane woodland shrub of drier habitats, first appeared in large quantities by 36 ka, tracking the abundance of limber pine. Shadscale (*Atriplex confertifolia*) also occurs in small but consistent amounts in midden samples dating to this interval, suggesting drier conditions. Mesophilic shrubs declined during this same time: cinquefoil disappeared from the record after 40 ka, while currant was gone by about 34 ka. The dominance of limber pine and abundance of relatively dry montane shrubs at the expense of mesophiles suggests cold but dry conditions from 30 to 40 ka in montane settings in the northwestern Bonneville basin.

A small number of other paleovegetation and paleolake records in the Bonneville basin and vicinity help to confirm this reconstruction of Middle Wisconsin-age vegetation. Middens dating between 40 and 28 ka from the Snake Range and southern Bonneville basin indicate that montane settings supported coniferous woodlands dominated by bristlecone pine (*Pinus longaeva*), with associates including sagebrush, rabbitbrush, snowberry, Utah juniper and mesophilic shrubs (Thompson, 1984; Wells, 1983). Pollen dating from the same period in Council Hall Cave in the southwestern Bonneville basin (Thompson, 1984) reflects montane vegetation dominated by pine and steppe shrubs including sagebrush, with



conifers such as juniper, spruce and fir represented in very small quantities. The presence of xerophytic shrub pollen may indicate that these taxa dominated valley floors at the time (Thompson, 1984). Pollen from the topmost levels of long sediment cores taken from near Wendover and Knolls contain relatively high values of pine pollen prior to ~30 ka (Martin and Mehringer, 1965), but these are poorly dated and Davis (1998) suggests shadscale and other halophytic shrubs were growing near the core site.

On the Snake River Plain, north of the Bonneville basin, sagebrush steppe was the dominant plant community during this period (Bright and Davis, 1982; Mehringer, 1985; Davis et al., 1986; Beiswenger, 1991). Conifers were apparently limited to foothills and rocky terrain. The pollen sequence from Ruby Marsh, located in Ruby Valley, ~100 km west of the Bonneville basin, indicates the presence of a shallow, saline marsh/playa, surrounded by sagebrush steppe (Thompson, 1984, 1992) from 40 to 28 ka. Pine pollen reaches its highest proportions in the 40,000-year record, but it is not very abundant, indicating that pines (probably limber pine, bristlecone pine and/or whitebark pine (*Pinus albicaulis*)) were “probably present regionally, though not at the edge of the lake, and perhaps not in the southern Ruby Mountains” (Thompson, 1992). The very small amount of juniper pollen present shows that these conifers were apparently absent or very rare by 40 ka.

Together, these records point to cold but dry conditions before ~28 ka in the eastern Great Basin generally. The climatic reconstructions based on vegetation data are consistent with low lake levels in the Bonneville basin before 28 ka (Scott et al., 1983; Oviatt et al., 1992).

## 2.2. Late Wisconsin (isotope stage 2) glacial period, 28,000–14,000 BP

At Top of the Terrace, Engelmann spruce (*Picea engelmannii*) appeared in samples dating as early as 30 ka, and increased in abundance during the next few thousand years. Limber pine declined to low levels. Upper montane meadow plants such as currant and cinquefoil reappeared and expanded in abundance at the expense of fernbush; sagebrush maintained fairly consistent representation throughout. The increased abundance of spruce and mesophilic montane shrubs

suggest increasingly moist and cool conditions by ~22 ka. Much colder conditions are indicated in a midden sample dating to ~17 ka, shortly after the Late Wisconsin glacial period had reached its maximum. Local vegetation was alpine to sub-alpine in character, dominated by sagebrush, some grass and sparse cinquefoil, with rare occurrences of limber pine and spruce. Several wetland plants, including bulrush (*Scirpus* sp.) and pondweed (*Potamogeton* sp.), as well as fish bones, imply a nearby permanent body of water. The record dating between 17 and 14 ka is limited, but it suggests that spruce increased somewhat in abundance, while limber pine was no longer present. Montane mesophilic shrubs such as currant and cinquefoil increased in abundance, suggesting that climatic conditions were moister and somewhat warmer than during the Full Glacial.

This midden record is augmented by a variety of other records from the eastern Great Basin dating to the last glacial interval. Foremost among these is the record from Lake Bonneville, which had begun to rise rapidly after 28 ka (Oviatt et al., 1992). By 26 ka the lake was roughly 100 m deep, and it continued to rise for the next 10,000 years, with several significant fluctuations, including the major Stansbury oscillation dating from 22 to 20 ka (Oviatt et al., 1990, 1992). At its highstand, about 16 ka, Lake Bonneville was 370 m deep and covered an area of about 51,750 km<sup>2</sup>.

Pollen records from the Bonneville basin dating older than ~24 ka show relatively low to moderate values of pine and spruce and relatively large values of sagebrush and shrubs of the Chenopodiaceae family, presumably shadscale, saltbush (*Atriplex canescens*) and greasewood (*Sarcobatus vermiculatus*). These pollen profiles reflect widespread sagebrush–shadscale associations in valley bottoms, with pine and some spruce in montane settings (Mehringer, 1977, 1985; Spencer et al., 1984; Thompson et al., 1990). Large increases in pine pollen, the appearance of spruce, and the decline of chenopods may date the transition to deep-water conditions at ~24 ka (Mehringer, 1985), but this interpretation contrasts somewhat with the geomorphic record of Lake Bonneville’s rise and may be due to the loss of substantial chenopod shrub habitat as rising levels of Lake Bonneville flooded valley bottoms and margins.

In the southern Bonneville basin, the extremely sparse midden record dating from 28 to 20 ka shows

continued dominance of bristlecone pine, without other conifers such as spruce or Utah juniper, but with a diverse shrub cover including abundant mountain mahogany as well as sagebrush, rabbitbrush (*Chrysothamnus* spp.), green Mormon tea (*Ephedra viridis*), currant, snowberry and greasewood (*Forsydia nevadensis*) (Thompson, 1984). After 20 ka, bristlecone pine continued to dominate, but it shared the woodlands with other conifers including spruce, prostrate juniper (*Juniperus communis*), Rocky Mountain juniper (*Juniperus scopulorum*) and (rarely) limber pine; a similar roster of shrubs occurred as before, along with the uncommon addition of shadscale (Wells, 1983; Thompson, 1984). Pollen from Council Hall Cave contains large proportions of pine pollen with small quantities of spruce and variable abundance of juniper-type, and relatively stable amounts of sagebrush pollen during this general interval, though the dating is relatively coarse (Thompson, 1984).

Sagebrush steppe appears to be consistently represented as the dominant vegetation formation through the Full Glacial on the Snake River Plain, north of the Bonneville basin. The Grays Lake record (Beiswenger, 1991) shows that conifer pollen (mainly pine and spruce) increased in abundance after 26 ka, suggesting that woodlands grew at relatively low elevations in the mountains and foothills, as well as isolated rocky terrain in valley bottoms. Beiswenger (1991) suggests that the increase of conifers, continued abundance of sagebrush and negligible increase in grass pollen at Grays Lake supports an interpretation of greater winter and spring precipitation, with no increase in summer precipitation, in an environment with average temperatures 7–10°C colder than today. In Ruby Valley, 100 km west of the Bonneville basin, the lacustrine record from Ruby Marsh shows an increase in lake level after 23 ka (Thompson, 1992). The large, fresh-water Lake Franklin deepened to about 30 m ~18–15 ka, drowning what had been marshland. However, pollen from these sediments show relatively little change in sagebrush steppe composition or abundance in the region.

In sum, the Late Wisconsin vegetation record of the Bonneville basin documents the existence of a cold-adapted sagebrush steppe with scattered stands of spruce and pine, in the northern Bonneville basin and surrounding areas, and a more diversified wood-

land–steppe mosaic in the southern Bonneville basin, dominated by bristlecone pine. This vegetation reconstruction suggests that Full Glacial conditions in the northern Bonneville basin were very cold and also quite dry, while conditions in the southern Bonneville basin were also cold but moister. This north to south vegetation gradient represented in the late-glacial paleobotanical record was noted by Thompson and Mead (1982) (cf. Thompson, 1990; Rhode and Madsen, 1995) and may reflect a stronger latitudinal gradient of temperature and precipitation associated with a postulated southward shift in the position of the jet stream during the Full Glacial (Antevs, 1948; Benson and Thompson, 1987; COHMAP, 1988; Kutzbach et al., 1993; Thompson et al., 1993).

The increased abundance of spruce over limber pine is consistent with the rise of Lake Bonneville. Both conifers prefer cold climates, but limber pine prefers cold and very dry environments, while spruce is better adapted to moister conditions. Limber pine was most abundant before 28 ka, when Lake Bonneville had not yet undergone its rise; as Lake Bonneville expanded, limber pine dropped out and was replaced by spruce. The correspondence between woodland composition and glacial lake history during the time before 14 ka is strikingly close.

### 2.3. Terminal Wisconsin deglaciation, 14,000–10,900 BP

Our midden samples dating between 14 and 11 ka are relatively numerous and the Homestead Cave faunal record becomes useful for at least the latter part of the period. These data reflect a substantial change in the biotic communities and the overall water budget during the terminal Wisconsin deglaciation, trending toward the warmer and drier interglacial climate of the Holocene. After ~14 ka, Lake Bonneville began to retreat from its overflow level at the Provo threshold (Oviatt et al., 1992). Glaciers in nearby mountain ranges had been significantly reduced by this time, but still remained of substantial size, and vegetation records suggest summer temperatures remained quite cool. The Little Cottonwood Canyon glacier, for example, did not retreat past Snowbird Bog until ~12.3 ka (Madsen and Currey, 1979), and may have deposited the mid-canyon Hogum Fork till at an elevation well below the bog

during a period corresponding to an early regressive-phase oscillation of the lake. Mountain shrub vegetation similar to that now found in sub-alpine settings in the Great Basin dominated the foothills along the western margin of the lake, with conifers such as white fir and spruce dominating lower elevations along the eastern lake margin. Large Pleistocene megafauna such as mammoth, camels, ground sloths, musk-ox and the short-faced bear remained around the lake margins, but population sizes may have started to decline (Grayson, 1993).

Sometime between ~14 and ~12 ka, shoreline deposits suggest lake levels dropped rapidly (e.g. Oviatt et al., 1992), but lake waters remained sufficiently cold and fresh that they could support all of the Lake Bonneville fish fauna, including such cold water species as Bear Lake sculpin (*Cottus extensus*), Bonneville cisco (*Prosopium gemmifer*) and Bonneville whitefish (*Prosopium spilonotus*). At the beginning of the regressive phase the western margin of the lake supported a montane shrub vegetation dominated by sagebrush, snowberry and currant. Prostrate juniper and shrubby cinquefoil were also common in some locations. Herbaceous plants, including thistle (*Cirsium* spp.) and wild rye (*Elymus* cf. *cinereus*), were also common. This montane shrub vegetation was similar in many respects to that now found in sub-alpine settings in the Great Basin. With the exception of prostrate juniper, conifers were absent or a minor component of this vegetation, particularly in lowlands. In montane settings mesophilic shrub vegetation was much like that at lower elevations nearer the margins of Lake Bonneville, though Engelmann spruce was present in small numbers, and the midden record indicates that montane shrub vegetation covered altitudes up to at least 2000 m in the interior ranges of the northeastern Great Basin from 14 to 13 ka. The Top of the Terrace middens also contain numerous pika pellets in a range that pikas do not now inhabit (Hall, 1946; Grayson, 1993).

Beginning about 13 ka, limber pine began to spread widely into the lower elevations of the northern Bonneville basin, growing in both the hills and plains adjacent to the lake basin and in at least the lower reaches (above ~1800 m) of neighboring mountains. The transition from mesophilic montane shrub community to limber pine woodland ~13 ka may indicate a significant drying trend within a still-cool

temperature regime. Needles, seeds and cone parts of limber pine are very common in middens dating to 12.9–11.5 ka, but disappear from lower elevations shortly thereafter. Below ~1800 m elevation, limber pine is the only arboreal conifer represented, often occurring in small quantities in middens dominated by sagebrush, snowberry, prostrate juniper, soapberry (*Shepherdia canadensis*) and other shrubs. Several shrubby taxa that dominated the earlier montane steppe vegetation were common understory plants at this time, particularly prostrate juniper, sagebrush and snowberry. Other shrubs that had been common before 13 ka, particularly the mesophilic currant and cinquefoil, became rare or disappeared. In montane settings, above about ~1800 m, limber pine dominated in woodlands that also included other conifers: Engelmann spruce and Rocky Mountain juniper in the Toana Range west of the Bonneville basin, and sub-alpine fir (*Abies lasiocarpa*) in the Stansbury/Onaqui Mountains on the east side.

Fish remains are found in four middens dating to as late as ~11.9 ka, probably incorporated in the middens by woodrats collecting remains left by fish-eating predators or scavengers. Taxa represented include whitefish (*Prosopium* sp.), sucker (*Catostomus* sp.) and a large salmonid, that indicate the existence of a lake large enough to support fish whose preferred habitat is cold, oligotrophic, deep-water lake environments. One midden also contains fecal pellets of pika, a lagomorph that now occurs only in sub-alpine and alpine environments in the region. Hafner's (1993) formula for estimating the local minimum elevation of appropriate pika habitat yields a lower elevation limit of 2316 m. This implies a displacement of at least 805 m, corresponding to a minimum lowered temperature (by the adiabatic lapse rate) of ~4.8°C. Whether pikas could in fact survive at this "local minimum elevation" today is unknown, as pikas no longer live in the area; but pikas have been trapped as low as 2134 m in the Ruby Mountains, the nearest locality where they exist today (Hall, 1946). Xerophytic shrubs were scarce in the regional vegetation before about 11.5 ka, but they began to dominate in the lowlands after that time. Shadscale occurs rarely in middens dated older than 11 ka.

Rhode and Madsen (1995) used the modern distribution of limber pine to estimate climatic boundary conditions that permitted limber pine to grow at low

elevations during this period. Today, limber pine grows on similar south-facing slope settings above 2600 m in the Pilot Range, 1100–1200 m above its known level 13–11 ka. If the dry air thermal lapse rate applies ( $0.6^{\circ}\text{C}/100\text{ m}$ ), this difference in elevation implies that terminal Wisconsin temperatures (at least summer temperatures) were depressed by at least  $6.6^{\circ}\text{C}$  in the northwestern Bonneville basin. However, part of the ecological amplitude of late-glacial limber pine populations may have been lost as those populations became extirpated or severely restricted in distribution during the Holocene (Thompson, 1990). Furthermore, Van de Water et al. (1994) have shown that limber pine populations throughout the intermountain west showed increased water use efficiency during the deglacial interval, possibly in response to increasing  $\text{CO}_2$  in the atmosphere. As a result, limber pine is likely to have altered its sensitivity to climatic parameters during this time period, and this fact alone may account for the rapid spread of limber pine into the lowlands of the northern Bonneville basin during this interval. Despite these potential difficulties, an estimate of terminal-Wisconsin summer-temperature depression of  $\sim 6\text{--}7^{\circ}\text{C}$  is similar in magnitude to that suggested by Thompson (1990) for the east-central Great Basin, and by Betancourt (1990) for the Colorado Plateau. This reconstruction differs in magnitude, though not in direction, from surface temperature estimates produced by the COHMAP model, which predicts summer temperatures only slightly lower than present at 12 ka (Kutzbach et al., 1993; Thompson et al., 1993).

By  $\sim 12.5\text{ ka}$  the lake had receded to elevations below the Old River Bed Threshold which separates the Sevier and Great Salt Lake sub-basins of the Bonneville basin (Oviatt, 1988). Towards the end of the period shadscale and sagebrush began to replace limber pine and common juniper in Bonneville basin lowland settings, particularly on exposed slopes. A midden from Bonneville Estates, dating to  $\sim 11\text{ ka}$ , is dominated by xeric desert shrubs, such as sagebrush, shadscale, horsebrush, snakeweed (*Gutierrezia* sp.) and rabbitbrush. Limber pine and prostrate juniper are rare to uncommon elements in the midden. Sometime after 12.4 ka (dating is unclear), pollen from Great Salt Lake cores (e.g. Spencer et al., 1984; Thompson et al., 1990) indicate that xeric desert shrub species, such as greasewood, and other cheno-

pods began to replace coniferous woodlands. At higher elevations in the southern Bonneville basin bristlecone pine disappears from some of the smaller mountain ranges such as the Confusion Range (Wells, 1983). This change in flora was far from uniform and many sub-alpine species continued to be present in areas of cold air drainage and along stream channels. Pollen from Grays Lake (Beiswenger, 1991) documents a shift by  $\sim 12\text{ ka}$  from a pine-sagebrush parkland, reflecting cold dry glacial conditions, to a woodland/steppe mosaic including spruce, pine and sagebrush, that suggests warmer (but still cool) and moister conditions. Pollen data from Swan Lake, in Idaho, show high values of pine, spruce and fir between 11 and 12 ka (Bright, 1966). The terminal Wisconsin record from Ruby Marsh is limited by a stratigraphic unconformity dating between 15.4 and 10.7 ka, that may represent a turbidite flow in deep water, or alternatively may indicate a period of desiccation of the lake (Thompson, 1992) as does a drying episode in an alpine lake in the mountains east of the Bonneville basin (Gillette and Madsen, 1993; Madsen, 2000b).

This period of desiccation appears to be represented by fish remains in the earliest Homestead Cave deposits. The 14,866 identified fish specimens represent four families (Salmonidae, Cyprinidae, Catostomidae and Cottidae) and eleven species. These include bull trout (*Salvelinus confluentus*), cutthroat trout (*Oncorhynchus clarki*), Bonneville whitefish, Bear Lake whitefish (*Prosopium abyssicola*), Bonneville cisco, Utah chub (*Gila atraria*), redbreast shiner (*Richardsonius balteatus*), Utah sucker (*Catostomus ardens*), bluehead sucker (*Catostomus discobolus*), mottled sculpin (*Cottus bairdi*) and Bear Lake sculpin. Four of the identified species (bull trout, Bear Lake whitefish, redbreast shiner and bluehead sucker) represent the first records for Lake Bonneville. The bull trout premaxilla is the first specimen record of any kind for that taxon in the Great Basin. The bluehead sucker specimens represent the first fossil record of the subgenus *Pantosteus* in the Great Basin. Most of the represented species prefer cold, fresh waters; eight of them now occur in Bear Lake, a cold, deep, oligotrophic body of water on the Utah–Idaho border, and four of them (Bonneville whitefish, Bear Lake whitefish, Bonneville cisco and Bear Lake sculpin) are now endemic to that lake (Sigler and Sigler, 1996).

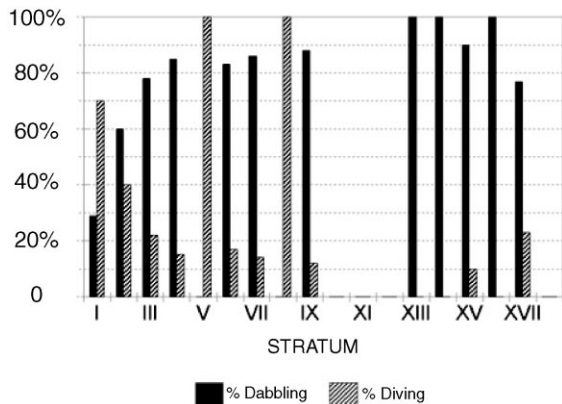


Fig. 6. Relative abundances of dabbling and diving ducks in the Homestead Cave column.

The fish remains at Homestead Cave are concentrated in the base of Stratum I. Four radiocarbon dates on woodrat fecal pellets from the lowest 5 cm of Stratum Ia have a weighted average of  $11,201 \pm 76$  yr BP.  $^{87}\text{Sr}/^{86}\text{Sr}$  ratios of six fish vertebrae from the basal section suggest the fish come from a low-elevation lake near the Gilbert shoreline (Broughton et al., 2000). If the  $^{14}\text{C}$  age estimates on lower Stratum I represent the ages of the fish remains—as they probably do—we conclude that a fresh, cold, oligotrophic lake was present within the foraging radius of the Homestead raptors at or shortly before 11.2–11.3 ka.

#### 2.4. 10,900–9950 BP

In ice core records, the Younger Dryas is characterized by a rather abrupt return to near full-glacial conditions and by a high degree of annual to decadal climatic volatility (Mayewski et al., 1993). In the Bonneville basin, the Younger Dryas may be correlated with a return of Lake Bonneville to the relatively high Gilbert level. However, available proxy data do not reflect an abrupt change and the lake rose relatively slowly during the initial part of the period (Oviatt et al., 1992). To the west, sediments in the Ruby Marshes dating between 10.7 and 10.4 ka indicate a moderately large, fresh-water lake in the basin, coeval with the Gilbert Lake phase in the Bonneville basin (Thompson, 1992). To the east, a high-elevation lake in Huntington Canyon on the Wasatch Plateau also refilled during this period (Madsen, 2000b).

A change in fish size across the two divisions of Stratum I suggests that after  $\sim 11.2$  ka, but prior to  $\sim 10.4$  ka, the lake was at times deep enough and cold enough to support a recolonization of the lake by much of the Lake Bonneville fish fauna. After the initial recolonization, the Stratum I fish assemblage was apparently derived from a process involving a series of die-offs that occurred either seasonally or over periods of many years during which lower lake levels at times exceeded the temperature or salinity tolerances of the fishes (Broughton et al., 2000). These die-offs were over sometime prior to 10.4 ka to judge from the virtual lack of fish remains in the upper third of Stratum I, a context that provided  $^{14}\text{C}$  dates of  $10,350 \pm 80$  and  $10,160 \pm 85$  yr BP.

Although the entire Bonneville fish fauna appears to have been involved in these recolonizations of the lake, species better adapted to warmer and more saline conditions were relatively more successful. At Homestead Cave, there is a significant decline in the relative abundances of salinity intolerant taxa (*Prosopium sylonotus*, *Prosopium gemmifer*, *Prosopium abyssicola*, *Catostomus ardens*, *Cottus extensus* and *Cottus bairdi*) across the two divisions of Stratum I. There is also a significant decline in the relative abundances of taxa that are intolerant of high water temperatures (*Oncorhynchus clarki*, and the represented *Prosopium* and *Cottus* species) across these stratigraphic divisions. Because many species are intolerant of both salinity and temperature extremes, however, the relative roles these factors played in mediating Lake Bonneville's fish populations during the Younger Dryas period remains unclear.

The avian faunal record from Homestead Cave is consistent with a lake in the cave vicinity. Ducks account for only 15% of the total assemblage, but they are the most abundant family of birds in Stratum I, making up almost 50% of the identified assemblage. Ducks are commonly divided into two categories on the basis of feeding adaptation: the dabbling, or shallow water, species (all members of the genus *Anas*) and diving ducks (members of the genera *Aythya*, *Bucephala*, *Mergus* and *Oxyura*), and the relative abundances in these two categories through time in the Homestead Cave deposits provides a significant indicator of relative levels of Lake Bonneville and its successor, Great Salt Lake. Of the 321 duck specimens identified to at least genus, and consequently

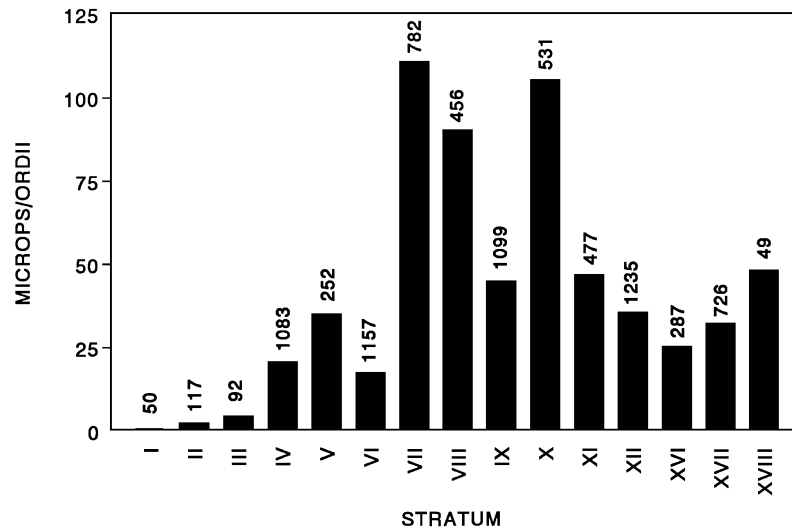


Fig. 7. The changing proportions of *D. microps* to *D. ordii* at Homestead Cave. The numbers above the bars provide the total number of *Dipodomys* specimens identified as either *D. microps* or *D. ordii*.

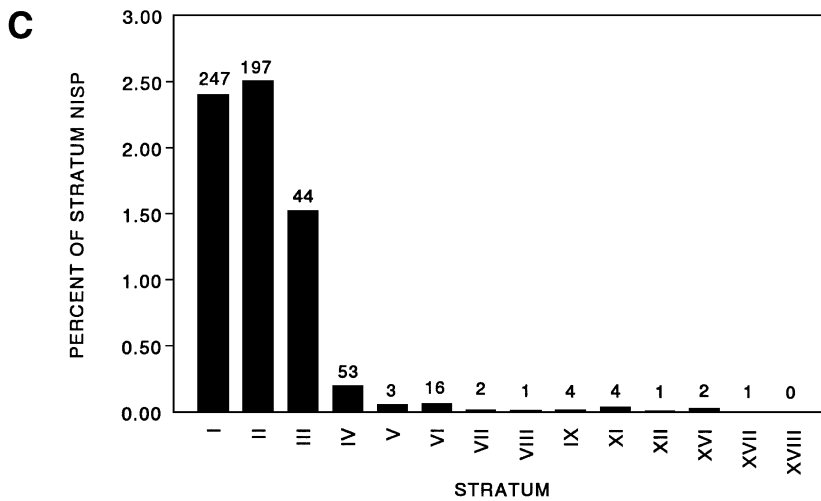
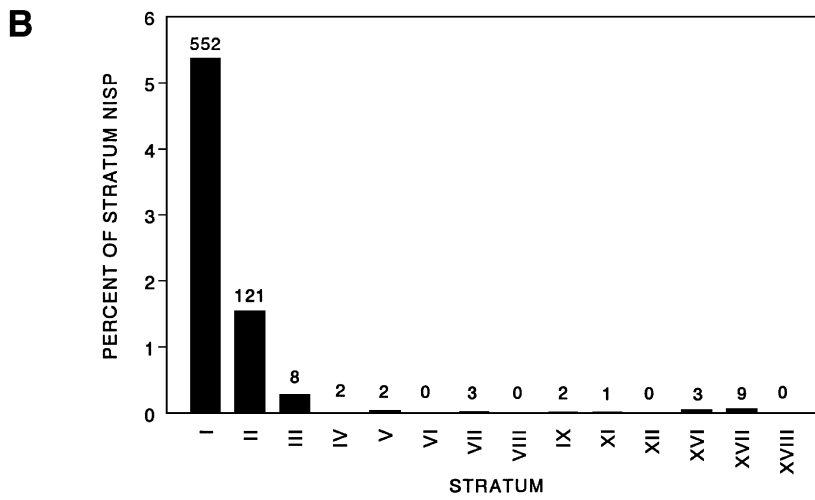
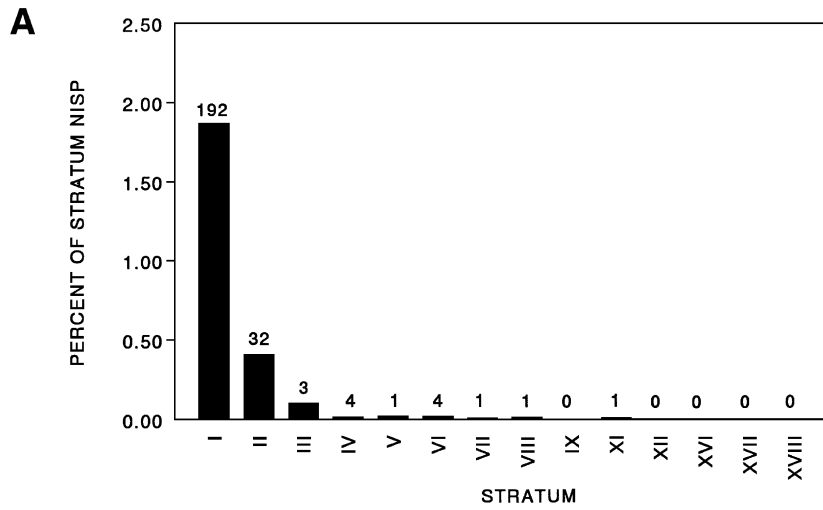
assignable to feeding adaptation category, slightly more than half (54%) are from shallow water species. However, distribution across strata varies considerably. The majority of the waterfowl are from Strata I through IV, and most of the diving ducks in the entire assemblage are from Stratum I (Fig. 6). After Stratum III diving ducks are extremely rare.

The paleovegetation record from this time period is at present quite sparse. What little data exist suggest a substantial reduction in pine woodlands and an increase in sagebrush-grass and shadscale associations shortly before 11 ka. Unfortunately, there is not presently enough evidence to document the kinds of vegetation changes that occurred during the Younger Dryas, or whether vegetation changes reflect the enhanced moisture conditions postulated for the lake-level rise (Oviatt, 1988; Currey, 1990; Benson et al., 1992). At lower elevations, vegetation in the Bonneville basin during this period is composed primarily of open brush communities with limited amounts of woodland elements (Rhode and Madsen, 1995; Wigand and Rhode, 2001). While these are primarily the same xeric desert shrubs found in the

area today, such as sagebrush, shadscale, horsebrush, snakeweed and rabbitbrush, their distribution was different. The Homestead Cave mammal record, for example, suggests relatively more mesic sagebrush was growing in areas now covered with greasewood and horsebrush. In the northern Bonneville basin limber pine and prostrate juniper were largely gone, Rocky Mountain juniper was common, and neither Utah juniper nor singleleaf pinyon (*Pinus monophylla*) had yet invaded. In the southern Bonneville basin, bristlecone pine remained a common woodland conifer until shortly before 10 ka, but Utah juniper and douglas fir began to appear by the end of the Younger Dryas (Wells, 1983; Thompson, 1984). Woodpeckers in the Homestead Cave sequence suggest that many of the small, dry washes common on lower elevation Bonneville basin slopes contained enough water to support riparian communities including small deciduous trees such as chokecherry (*Prunus virginiana*). Along the stream channels at slightly higher elevations, limber pine and sub-alpine fir continued to grow.

Most of Stratum I at Homestead Cave was deposited

Fig. 8. Changing abundances of: (a) pygmy rabbits; (b) sage voles; and (c) voles at Homestead Cave. NISP equals number of identified specimens. The numbers above the bars provide the total number of specimens of *Brachylagus idahoensis* (a), *Lemmys curtatus* (b), and *Microtus* sp. (c).



during this period and the rich small mammal record at the cave supplements the relatively sparse vegetation record. An array of small mammal species, such as the pygmy rabbit, marmot, bushy-tailed woodrat and northern pocket gopher, currently common to mid-elevation and higher locations today, were also common at lower elevations during the period. Overall conditions can be characterized as those of an open, cold, desert steppe, with sagebrush communities dominating lower slopes and extending down into valley locations.

This interpretation is based on the relative proportions of the chisel-toothed kangaroo rat (*Dipodomys microps*) and Ord's kangaroo rat (*D. ordii*). While both species can exist in other habitats, *D. microps* will tend strongly to be found in shadscale habitats, and *D. ordii* in habitats marked by other plant associations, including those dominated by sagebrush. Fig. 7 provides the ratio of *D. microps* to *D. ordii* through time at Homestead Cave, and shows that the late Pleistocene and early Holocene faunas of this area were marked by abundances of *D. ordii* that have not been seen at this low-elevation location since then. The ratio of *D. microps* to *D. ordii* is particularly high during the Younger Dryas, suggesting the halophytic brush community had not yet become a significant portion of local plant communities.

It is possible that environmental changes other than a replacement of sagebrush by shadscale vegetation might have driven the changing abundances of *D. ordii* documented by the Homestead Cave fauna, since *D. ordii* does not require *Atriplex* in its diet. However, the history of pygmy rabbits (*Brachylagus idahoensis*) at Homestead Cave seems to make sense in no other way. Pygmy rabbits are heavily dependent on dense stands of big sagebrush (*Artemisia tridentata*), both for food (pygmy rabbit winter diets may be composed of almost nothing else) and as locations for their burrows (Green and Flinders, 1980; Weiss and Verts, 1984; Dobler and Dixon, 1990; Katzner and Parker, 1997). Today, pygmy rabbits are found in the sagebrush valleys of the northern two-thirds of the Great Basin and on the immediately adjacent Columbia Plateau, albeit in declining numbers. Within the Great Basin and adjacent Columbia Plateau, they are known to have undergone two separate declines in abundance, one at about 10 ka, and a second at the onset of, or during, the middle Holocene

(Grayson, 1993). Both of these declines appear to be associated with declines in abundance of big sagebrush (see the review in Grayson, 1993). At Homestead Cave these animals were common during the Younger Dryas and were clearly present during the early Holocene, but declined rapidly (Fig. 8a).

The pattern is similar for voles (*Microtus* sp.) and sage voles (*Lemmiscus curtatus*). Most species of *Microtus* occupy grassy habitats and live in cool environments. These animals show poor ability to thermoregulate at high temperatures. In the modern Great Basin, even *Microtus longicaudus*, which is least tied to moist habitats, is more common in cooler, moister settings than in warmer, drier ones (Getz, 1985; Rose and Birney, 1985; Wunder, 1985). *Microtus* was common in the late Pleistocene and early Holocene deposits of Homestead Cave (Fig. 8c). Much the same is true for sage voles (Fig. 8b) which are, as the name suggests, often associated with habitats dominated by stands of tall sagebrush, usually big sage, and grasses, though they can also be found in the communities in which the dominant shrub is rabbitbrush as well as in habitats dominated by grasses alone. Within these habitat parameters, there is also some suggestion that sage vole numbers are highest in settings marked by relatively warm winters coupled with cool and moist summers (Hall, 1946; Maser, 1974; Carroll and Genoways, 1980). Sage voles seem to be able to meet their moisture requirements through the ingestion of green vegetation, and surface moisture is clearly less critical for them than it is for most other voles. In short, sage voles are most abundant in habitats dominated by big sagebrush and grasses in contexts marked by relatively cool summers. These modern habitat preferences likely account for the strong similarity between the Homestead Cave histories of this animal and that of pygmy rabbits. This indication of relatively cool summers suggests that there may have been less variance between summer and winter temperatures during the Younger Dryas in the Bonneville basin, matching other records suggesting the Younger Dryas was more seasonally equable than later periods (Zielinski and Mershon, 1997).

## 2.5. 9950–8000 BP

About 10.1 ka Lake Bonneville (after this period



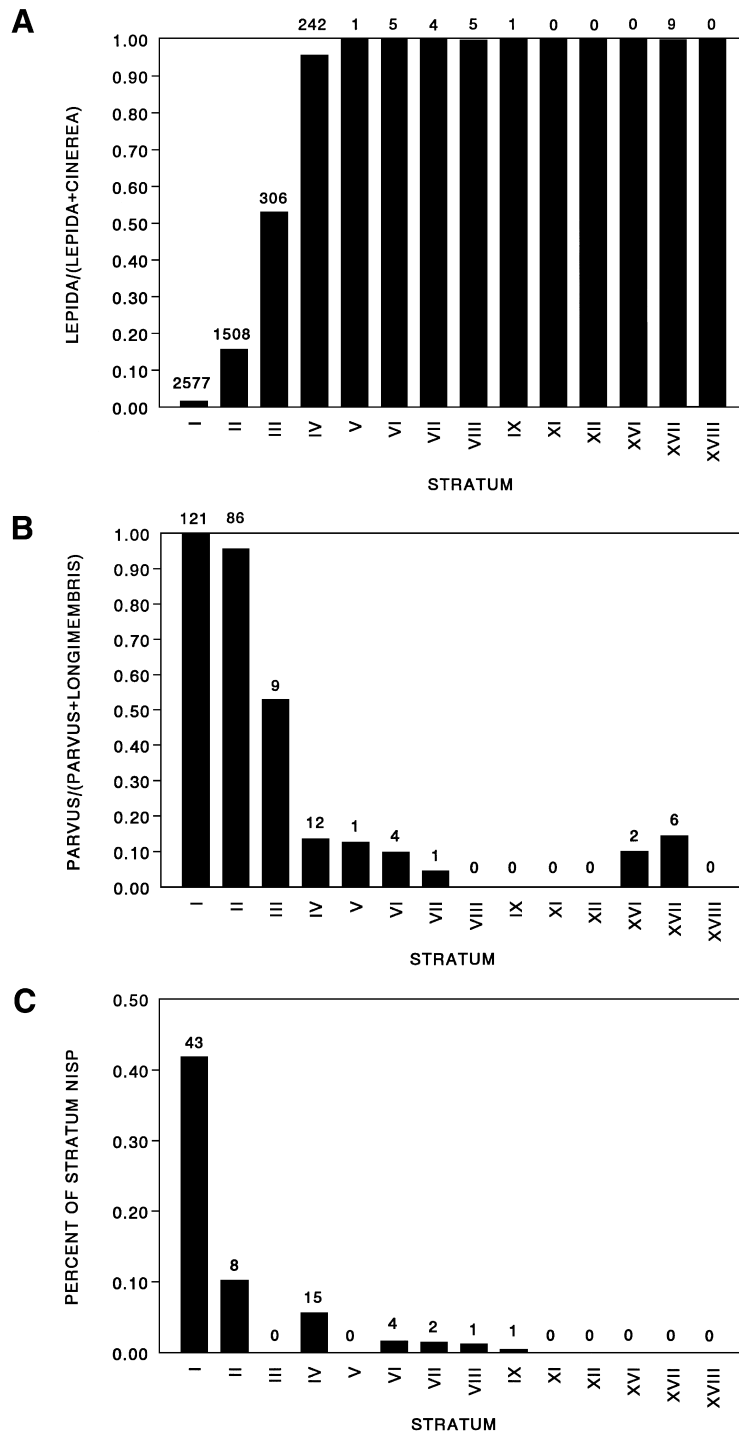


Fig. 9. Changing abundances of: (a) bushy-tailed woodrats; (b) Great Basin pocket mice; and (c) marmots at Homestead Cave. NISP equals number of identified specimens. The numbers above the bars provide the total number of specimens of *Neotoma cinerea* (a), *Perognathus parvus* (b), and *Marmota flaviventris* (c).

called Great Salt Lake) dropped abruptly, but is as yet poorly investigated and dated, and the lake may have peaked again sometime prior to 9 ka (Murchison, 1989; Miller and Langrock, 1997). The Little Cottonwood Canyon glacier retreated past Albion bog near the head of the canyon by ~9.6 ka, but was likely still present in its upper reaches. A deglacial pause during which the Devils Castle till was deposited occurred sometime between ~9.6 and 7.5 ka and may correlate with the early Holocene lake oscillation (Madsen and Currey, 1979). Water, possibly derived from groundwater sources, continued to flow in the Old River Bed until as late as 9 ka (Oviatt and Madsen, 2000).

Climatic modelers using the National Center for Atmospheric Research Community Climate Model (NCAR CCM) have suggested the early Holocene in the northern Great Basin was not only relatively moist, as has long been suggested by a wide variety of proxy paleoclimatic indicators, but that it was warm as well (e.g. Kutzbach et al., 1993; Thompson et al., 1993; Mock and Bartlein, 1995). The Homestead Cave small mammal record, on the other hand, along with other Great Basin records dating to the early Holocene, strongly implies that this period of time was moist and cool, not moist and warm (see discussion and references in Grayson, 1998). At Homestead Cave five radiocarbon age estimates place the deposition of Strata II–V between ~9 and 8 ka. In addition to the high relative abundances of arvicoline rodents (voles and sage voles) and pygmy rabbits in Stratum II (Fig. 8), the abundance of a variety of other mammals such as bushy-tailed wood rats, Great Basin mice (*Perognathus parvus*) and marmots also implies a cool and moist climatic regime during the early Holocene, albeit less so than during the latest Pleistocene (Fig. 9). Even the history of kangaroo rats within the Homestead Cave is consistent with this view. These animals comprise a relatively small fraction of the Stratum II mammal assemblage, and within the Stratum II kangaroo rat fauna, *D. ordii* is 2.4 times more common than *D. microps*. The implications are clear: during the time that Stratum II accumulated, the area surrounding the site was marked by fairly dense concentrations of *Artemisia*, presumably big sagebrush, with a significant grass understory. Vegetation and mammals alike existed in a climatic context that was both cool and moist, though not as cool and moist as during the period when Stratum I accumulated.

This conclusion is in sharp disagreement with the implications of the climatic models for this time and this area.

While conditions continued to be cooler and moister than at present, percentages of many species such as pygmy rabbit, Ord's kangaroo rat, the little pocket mouse, bushy-tailed woodrat, marmot and northern pocket gopher decrease in numbers throughout the period. The number of waterfowl decreases as well, but the variety of other birds increases, suggesting more diverse habitats were present near the cave. Hackberry (*Celtis reticulata*) endocarps are common in Strata II–V suggesting it grew in the outcrops around Homestead Cave from before 10 ka until ~8 ka or slightly later, after which time it disappeared from the local area. Hackberry prefers rocky substrates where it can absorb water trapped in cracks in outcrops (DeBolt and McCune, 1995). The area in the vicinity of Homestead Cave is presently too dry to support hackberry, although it is found at relatively low elevations in the more massive and better watered Oquirrh and Stansbury Mountains not far away, and occurs at higher elevations in the Lakeside Mountains (Albee et al., 1988). Early Holocene plant remains, specifically ratios of sagebrush vs. shadscale and greasewood vs. pickleweed, from Danger Cave, west of Homestead Cave, suggest the period began with relatively dry conditions, ~10.2 ka, then became cool and moist about 9.8 ka, and subsequently grew warmer and drier by about 8.5 ka (Harper and Alder, 1972).

The available midden record suggests that xerophytic sagebrush and shadscale scrub dominated on the margins of the Bonneville basin, but some records indicate the presence of relatively mesophilic shrubs in lowland settings as well. A low-elevation midden sample dating to ~9.3 ka, contains remains of shadscale, horsebrush and other arid desert shrubs, while another, also dating to ~9.3 ka, is dominated by sagebrush, with shadscale as a relatively minor component (both of these localities harbored limber pine 2500 years earlier). This contrast is still present at the two localities. We have only one upland midden from the Deep Creek Range, southwest of the Great Salt Lake Desert, from this time period, and it represents the very latest end of the early Holocene, at ~8.1 ka. It contains abundant Rocky Mountain juniper, skunkbush sumac (*Rhus aromatica*) and

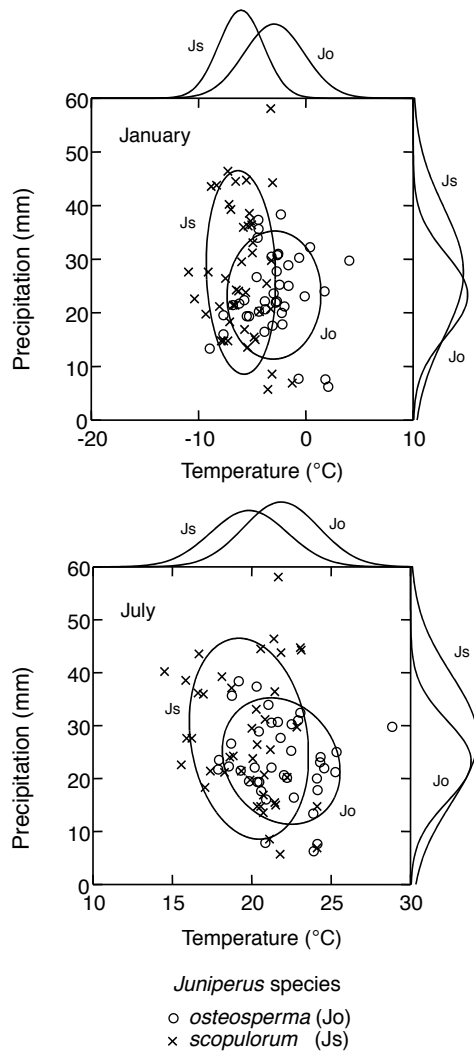


Fig. 10. Average January and July temperature and precipitation values (1961–1990) of weather stations in the western USA that lie within the distribution of Utah juniper (*J. osteosperma*) and Rocky Mountain juniper (*J. scopulorum*), as mapped by Little (1971). Climate data are from the U.S. Department of Commerce, National Oceanographic and Atmospheric Administration, and National Climatic Data Center.

hackberry, with smaller quantities of mesophilic shrubs including chokecherry and elderberry (*Sambucus* sp.). A mesophilic montane juniper-shrub community is indicated, quite different from the singleleaf pinyon–Utah juniper woodland extant today. The midden record from the southwestern Bonneville basin (Wells, 1983; Thompson, 1984,

1990) is more montane than lowland in distribution, but it too is very sparse. This record suggests that lower montane settings were dominated by a mosaic of mesophilic shrubs and a sparse woodland dominated by Rocky Mountain juniper and the newly immigrant Utah juniper. Conifers such as bristlecone pine, limber pine and common juniper, retreated to higher sub-alpine altitudes, persisting at lower elevations only on shaded north-facing slopes.

The widespread occurrence of Rocky Mountain juniper in upland settings, and the more restricted distribution of Utah juniper to southerly latitudes, also suggest that early Holocene climates were cooler than today, and possibly (though not necessarily) somewhat wetter. Comparison of weather station data from the present distribution of Rocky Mountain juniper vs. Utah juniper (Fig. 10) indicates that the two taxa differ most significantly in their preferred temperature regimes: Utah juniper typically requires warmer winters and tolerates warmer summers than Rocky Mountain juniper. The two taxa do not differ greatly in the seasonal abundance of precipitation required, though weather stations in the range of Rocky Mountain juniper do have significantly greater annual precipitation and somewhat higher summer precipitation than those found in Utah juniper habitat.

It seems most likely, therefore, that the early Holocene climate that fostered the dominance of Rocky Mountain juniper was cooler and had possibly wetter summers than the present climate which supports Utah juniper. How much cooler and wetter is harder to say because climate may not have been the main limiting factor in the distribution of Utah juniper. Another possible factor could be rate of population expansion. Both taxa also tolerate a rather wide latitude of climatic conditions with broad overlap, rendering precise estimates difficult. Further, climatic tolerances may be affected by competitive relationships within plant communities, which can change over time. Despite these interpretive difficulties, if weather station data can be applied, it appears that a transition from exclusively Rocky Mountain juniper to exclusively Utah juniper would require a warming of at least 3–5°C overall, helping to confirm the faunal data discussed above.

## 2.6. 8000–7000 BP

At or slightly before 8 ka, a major shift to warmer

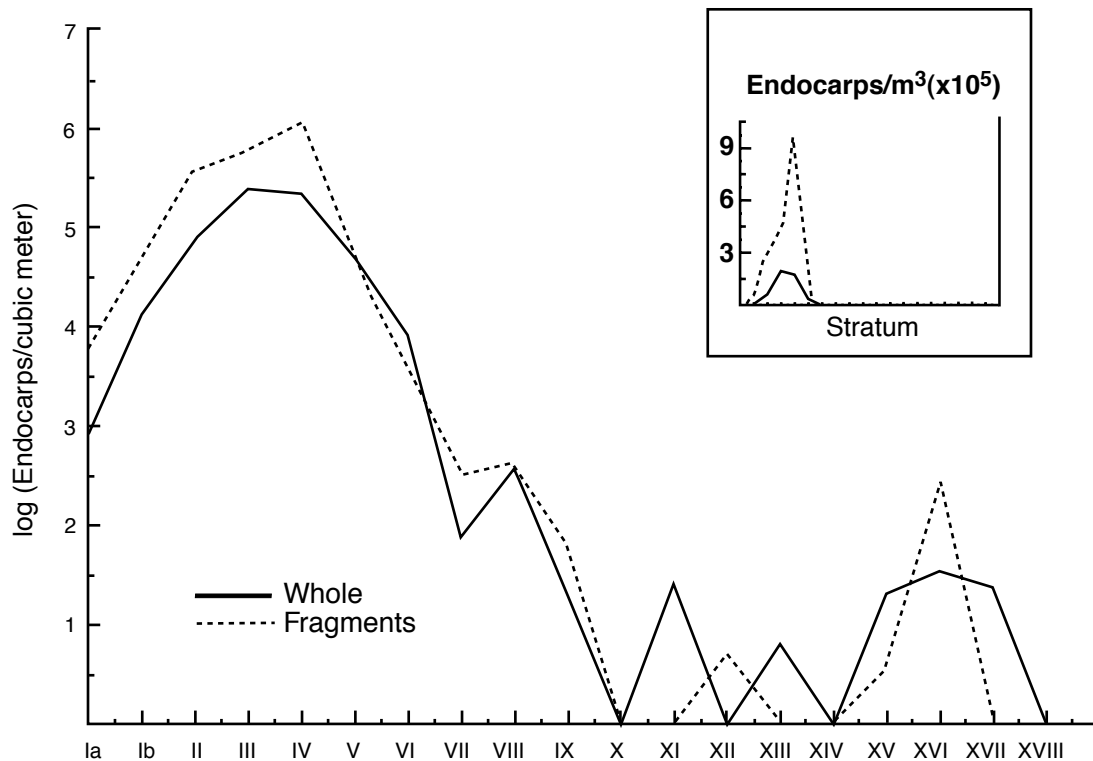


Fig. 11. Distribution of hackberry endocarps in strata from Homestead Cave. Note that the main graph is a logarithmic scale; inset is graphed on a linear scale.

conditions in the Bonneville basin appears to have occurred rather rapidly. By the end of the period Little Cottonwood Canyon was fully deglaciated. A ratio of conifer pollen to all other pollen at Snowbird Bog used as a gauge of temperature shows a rapid transition from maximum Holocene cool temperatures to maximum warm levels shortly before 8 ka (Madsen and Currey, 1979). The pollen record from Swan Lake, north of the Bonneville basin, shows a marked change after  $\sim 8.4$  ka (Bright, 1966). Increased warming toward the end of the early Holocene is also reflected in the pollen sequence from Grays Lake on the margins of the Snake River Plain, where a transition from sagebrush steppe to sagebrush/shadscale steppe is dated to  $\sim 8.5$  ka (Beiswenger, 1991). A similar sequence is found at Ruby Marsh,  $\sim 120$  km west of the Bonneville basin, where the transition dates from 8.5 to 8.0 ka (Thompson, 1992). At least one and possibly two oscillations of Great Salt Lake

levels occurred during this period, but these are well within the elevation of modern short-term fluctuations (Murchison, 1989). Murchison and Mulvey (2000), for example, report a date of  $7650 \pm 90$  yr BP on marsh deposits associated with a lake rise to 1283 m, an elevation well within the envelope of the historical record.

The lowland midden record for the middle Holocene is practically non-existent. One midden suggests that by 7.5 ka, *Atriplex* dominated an association containing other shrubs such as sagebrush, greasewood, rabbitbrush, boxthorn (*Lycium* sp.), cliff rose (*Cowania stansuriana*) and desert snowberry (*Symphoricarpos longiflorus*). No other middens from lowland settings that date to the middle Holocene are known from the northern Bonneville basin, and middens from upland areas are confined to mountains to the west. These records suggest that lower montane woodlands were still dominated by Rocky

Mountain juniper. It is during this climatic cycle that singleleaf pinyon first makes its appearance in the Bonneville basin. Its migration may, in part, be related to its use by people, as the earliest record is from Danger Cave where pinyon nut hulls first appear in the cave's archaeological record between ~7.4 and 6.7 ka (Rhode and Madsen, 1998). In a few protected settings limber pine was a minor component of the lower woodlands, but the main populations of these conifers were probably located at higher elevations than the midden record presently reaches. Limber pine nut hulls also occur in sediments of Danger Cave dating between 7 and 8 ka (Rhode and Madsen, 1998), suggesting limber pine may have grown at relatively low elevations in nearby mountains.

At Homestead Cave, the number of hackberry endocarps drops off markedly after ~8.2 ka suggesting a marked drying trend occurred at that time (Fig. 11). This is associated with a reduction in the number of avian species caused primarily by the disappearance of waterfowl. Gulls (*Larus* sp.) also disappear from the record after Stratum IV. Upland small mammal species such as Ord's kangaroo rat, pygmy rabbit, bushy-tailed woodrat and marmot virtually disappear from the record. Trees may have been restricted to small riparian stands of deciduous species at medium to high elevations. Greasewood and horsebrush replaced sagebrush around Homestead Cave. The dominant juniper in the northern Bonneville basin continued to be Rocky Mountain juniper rather than Utah juniper and a number of species, such as Mormon tea, had not yet made their appearance.

Overall, perhaps the greatest environmental change in the Homestead Cave record takes place between this period and the preceding one. After ~8.2 ka, there is a significant reduction in the diversity of animals, and probably plants as well. Since small mammal richness in this area declined as moisture declined, it appears likely that the positive richness response model (e.g. Brown 1973, 1975) applies to all low-elevation settings in the Great Basin. The "unimodal" small mammal species-response model (e.g. Rosenzweig, 1992, 1995; Rosenzweig and Abramsky, 1993) does not appear to apply to the Great Basin, and does not appear to have done so since at least the latest Pleistocene (Grayson, 1998).

## 2.7. 7000–5300 BP

Environmental records for the middle Holocene in the Bonneville basin are relatively sparse. During this period Great Salt Lake may have dried almost completely, with desiccation polygons forming at what is now the deepest area of the lake (Currey, 1980), but appears to have rebounded ~5.9 ka to an elevation of ~1283 m (Murchison, 1989; Murchison and Mulvey, 2000). A sudden surge in conifer pollen at Curelom Cirque in the Raft River Mountains of northwestern Utah may be related to this 6 ka lake peak (Mehring et al., 1971). A change in sagebrush/saltbush ratios at Hogup Cave dated to about 6 ka also suggests a period of greater effective moisture (Harper and Alder, 1970). At Potato Canyon Bog, in central Nevada, a pronounced increase in the abundance of pine occurred approximately 6.5–6.0 ka, significantly different from the "period of possibly lower effective moisture that preceded it" (Madsen, 1985). The Ruby Marsh's record suggests shadscale replaced sagebrush in many low-elevation areas (Thompson, 1992) and maximum Holocene warm temperatures continued to be recorded at the high-elevation Snowbird Bog locality, although here too a brief, slightly cooler period is recorded (Madsen and Currey, 1979). Both Utah juniper and pinyon pine began to expand their range in the Bonneville basin during this time, but a paucity of middens containing these species suggests their distribution was spotty at best. North of 40° north latitude we have a single record from the Onaqui Mountains, dating to 6.6 ka. Limber pines were eliminated from all low-elevation areas, including cold-air drainages.

Strata VII–X were likely deposited at Homestead Cave during this climatic cycle. Beginning in Stratum VII, horned larks (*Eremophila alpestris*), which prefer open shrub habitats with sparse vegetation, along with other passerine birds with similar adaptations, increase in frequency. The frequency of ducks and shorebirds is also at its lowest during this and the following period. Woodrat fecal pellets are completely absent from the deposits in Strata VI–XI, suggesting their extirpation from the immediate vicinity of the cave, but desert woodrats continued to be collected from elsewhere in the Lakeside Mountains and deposited in the cave by raptors. Artiodactyl fecal

pellets show a marked cyclicity in frequency suggesting they may be related to the relative abundance of forage locally. An increase in frequency in Stratum VII dating to ~6.1 ka may be related to the lake-level and pollen changes noted above which also occurred at this time.

The proportion of the chisel-toothed kangaroo rat to Ord's kangaroo rat is extremely high in Strata VII–X, suggesting that shadscale largely replaced sagebrush around Homestead Cave during this period. A small deviation in that trend dating to ~6 ka may correspond to the shift in the Hogup Cave record noted by Harper and Alder (1970). The number of harvest mice is also extremely low throughout the period, indicating there was a marked reduction in grass cover and other herbaceous vegetation. Great Basin pocket mice become locally extinct. Together the small mammal and bird record suggests sagebrush/grass communities in the northern Lakeside Mountains were largely replaced by open shadscale scrub communities with little ground cover.

#### 2.8. 5300–4400 BP

Environmentally, this middle Holocene period is almost indistinguishable from the period that preceded it. Isotope records from Great Salt Lake cores suggest an oscillation event occurred during the period (McKenzie and Eberli, 1987), but there is as yet no shoreline evidence for such a cycle (Murchison, 1989). However, an increase in artiodactyl fecal pellets in Stratum X at Homestead Cave may correspond to such an event. Murchison and Mulvey (2000) interpret a Holocene sequence on Antelope Island to indicate a mean lake-level elevation of 1280 m or lower during this period. At Snowbird Bog, conditions get markedly cooler after ~5.3 ka, but the upper part of the sequence is poorly dated and it is unclear to what climatic cycle this cooling event may be related (Madsen and Currey, 1979).

At other localities, such as Ruby Marsh and Swan Lake, there is little record of environmental change during this climatic cycle. The period is poorly represented in the Homestead Cave faunal sequence, but what is there also shows little change from the preceding period. However, both pinyon pine and Utah juniper

per continued to expand towards their modern woodland distributions. Utah juniper was apparently absent in the northwestern Bonneville basin region until after 5.1 ka, near the end of the middle Holocene, where it occurs in small quantities in a single midden from the Toana Range. Rocky Mountain juniper was still present at lower elevations in the north, but in the southern Bonneville basin it had largely been replaced by Utah juniper. The direction of this replacement seems to have been from southeast to northwest. The migration route followed by singleleaf pinyon is not yet clear, and it appears to have continued to expand its territory into historical times. By the end of this climatic cycle, however, pinyon was likely present on all the major mountain ranges where it occurs at present.

#### 2.9. 4400–2950 BP

A gradual return to cooler temperatures was initiated during this period. After ~4.4 ka in Ruby Marsh shadscale was reduced at the expense of sagebrush and the water depth increased (Thompson, 1992). At Crescent Springs, on the northern margin of the Great Salt Lake Desert, conifer and sagebrush pollen increase at the expense of shadscale and other xeric desert scrub vegetation (Mehring, 1985). Towards the end of this period, at ~3.1 ka in the Swan Lake record, advancing conifer tree lines edged lower into sagebrush steppe (Bright, 1966). Isotope records from Great Salt Lake suggest this period started with a warming period, but grew increasingly colder (McKenzie and Eberli, 1987), with a lake cycle peaking at ~1284 m dating to ~3.4 ka (Murchison, 1989). Pollen records from a number of other locations around the Bonneville basin are also indicative of a marked increase in greater effective moisture (e.g. Madsen and Currey, 1979; Thompson, 1984; Madsen, 1985).

The midden record representing the first part of the late Holocene is more abundant than that representing the previous several thousand years. Twelve of our midden samples date between 2 and 4 ka in the northern Bonneville basin and vicinity. Several midden records indicate that Utah juniper grew at elevations at least 50–100 m lower than it occurs today during this interval. Records of juniper below its present distribution are found at five localities in

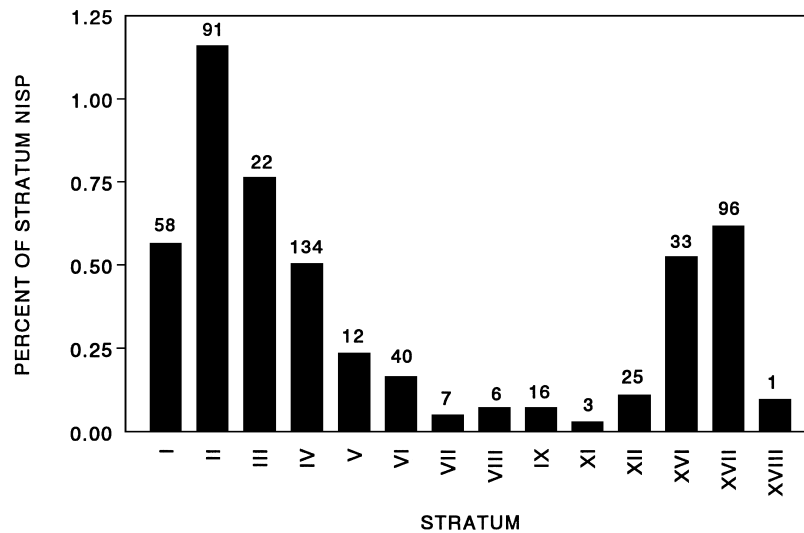


Fig. 12. Relative abundance of harvest mice at Homestead Cave. Harvest mice are most abundant in grassy habitats and provide a measure of grass cover through time in the northern Lakeside Mountains. NISP equals number of identified specimens. The numbers above the bars provide the total number of specimens of *Reithrodontomys* sp.

the Bonneville basin dating to between  $\sim 3.7$  and 2.5 ka.

At Homestead Cave, these cooler conditions are marked by the reappearance of small amounts of ducks and shorebirds, and by the return of woodrats to the cave itself. If woodrat fecal pellet diameters are useful in identifying body size, and, hence, woodrat species (Smith et al., 1995; Smith and Betancourt, 1998), the presence of pellets exceeding 5.0 mm in diameter suggests that at least some of these may have been bushy-tailed woodrats, although no skeletal remains occur. The endocarps of hackberry also reappear in the record, although only in small numbers. In Stratum XI and later there is an increase in taxonomic richness in the avian fauna, suggesting an increased diversity of local habitats. However, the change in the overall composition of local plant communities was probably relatively minor, as horned larks and other passerines continue to dominate the avian record. A midden from the Lakeside Mountains dating to  $\sim 3.0$  ka contains vegetation much like that found locally at present, but also contains Utah juniper which may have been growing at slightly lower elevations.

Rosenfeld (1991) has suggested that during wetter periods of the Holocene, Great Salt Lake may have

become sufficiently diluted in places to support populations of the moderately saline tolerant Utah chub, a hypothesis which appears to be confirmed by the Homestead Cave record. Utah chub occurs in large enough numbers in Strata XII–XIII to suggest these fish may have been able to survive in the waters of Great Salt Lake, particularly where fresh water springs and rivers created slightly fresher conditions. Utah chub presently inhabit springs of widely varying salinity (fresh water to 2.5% NaCl) in the Great Salt Lake Desert. In addition, laboratory experiments conducted on these fish indicate they can readily tolerate waters with salt contents as high as 213 mM/l (Westenfelder et al., 1988).

Waterfowl also return to the Homestead Cave record in Stratum XIII and increase in relative abundance thereafter. These are primarily shallow-water ducks, however, suggesting lake waters were not very deep in the vicinity of the northern Lakeside Mountains. The small-mammal record is limited for this period, since the Stratum XIII materials were not analyzed, but species such as harvest mice return to the record in Stratum XII and the proportion of chisel-toothed kangaroo rats to Ord's kangaroo rats is lower in Stratum XIV than anytime during the last 8000 years. Together these species suggest a return of

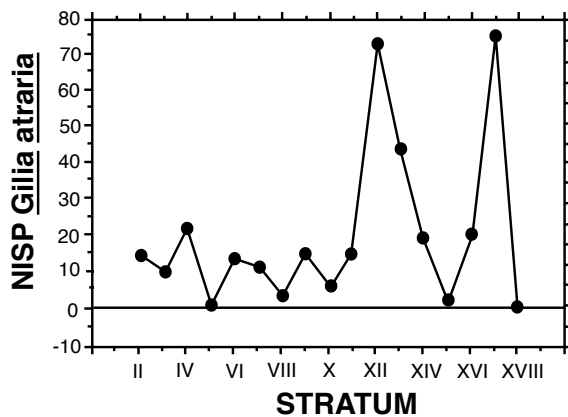


Fig. 13. The number of identified specimens (NISP) of Utah chub through time at Homestead Cave. The peaks in frequency at  $\sim 3.5$ – $3.4$  and  $\sim 1.2$ – $1.0$  ka suggest Utah chub were present in Great Salt Lake within the 5 km foraging radius of raptors at the cave.

sagebrush–grass communities to the Homestead Cave foraging area (Fig. 12).

#### 2.10. 2950–2400 BP

The degree of change associated with this climatic cycle is one of the most dramatic of any in the Bonneville basin during the Holocene. A major cooling event is evident in virtually all the biotic records and in both shoreline and core records from Great Salt Lake. Middens from Antelope Island, the northern Promontory and Cricket Mountains all suggest Utah juniper tree lines continued to be lower during this period. Isotope records (McKenzie and Eberli, 1987) indicate a freshening of lake waters between  $\sim 3$  and 2 ka, and shoreline data (Currey, 1990) suggest the lake reached a maximum of  $\sim 1287$  m and flooded the Great Salt Lake Desert as far west as the Utah/Nevada border.

Unfortunately, distinguishing between climatic cycles during the late Holocene is difficult due to the poor chronological controls associated with many biotic records. At Crescent Spring, for example, the pollen record (Mehringer, 1985) suggests several periods of greater effective moisture are separated by intervals of warmer and dryer conditions over the course of the last 4000 years, but when these periods occurred is not clear. For the most part it appears that modern plant communities were well established by

3.0 ka, with Mormon tea possibly being the last major taxon to be added (Wigand and Rhode, 2001). The last climatic cycles of the Holocene are marked by variations in proportion, but not in kinds, of plant and animal species. An exception is Rocky Mountain juniper, which continued to be a major component of woodland communities in some areas until after  $\sim 2.0$  ka.

#### 2.11. 2400–550 BP

Previous research suggests lake-level oscillations associated with this climatic cycle were modest, with the lake reaching elevations of  $\sim 1283$  m following an initial regression (Murchison, 1989; Currey, 1990). At Swan Lake, warmer conditions  $\sim 1.7$  ka are suggested by increasing levels of sagebrush pollen relative to that of conifers. However, after Utah juniper finally replaced Rocky Mountain juniper in the Silver Island Mountains after  $\sim 1.9$  ka, the few Bonneville basin middens dating to this period suggest vegetation patterns were essentially modern in character. Together these other data suggest overall temperature and moisture changes likely fluctuated within the envelope of modern weather patterns.

The Homestead record, on the other hand, suggests much more dramatic changes occurred during this period. An initial warm period, with concomitant lower lake levels, is reflected in the virtual absence of fish remains in Stratum XV. Utah chub returns in number in Stratum XVII, however, and in proportions slightly higher than in the earlier late Holocene period (Fig. 13). Since Stratum XVII is dated to  $\sim 1.2$  ka, the relatively fresher lake water in which these fish thrived may have exceeded 1283 m. Alternatively, a subsequent lake rise to elevations sufficient to flood the Great Salt Lake Desert, is currently undated and may relate to this period. Hackberry endocarps are common in Strata XV–XVII indicating significantly moister conditions in the Homestead Cave vicinity. Voles return in small numbers in Strata XVI and XVII and the ratio of Great Basin pocket mice to little pocket mice in these same strata increases to levels not seen since the early Holocene. Bushy-tailed woodrat faunal remains make a significant return to the record in Stratum XVII. Harvest mice also reach their Holocene peak in Strata XVI and XVII, although



the faunal assemblage in the latter stratum is small. This may be related to an increase in grass pollen at stratified Bonneville basin archaeological sites dating to this period. Wigand and Rhode (2001) suggest this may be related to an increase in summer moisture which promoted growth of ephemeral plant species. A single midden from the southern Bonneville basin dating to ~1 ka suggests lower Utah juniper treelines were depressed 50–100 m.

### 2.12. 550–50 BP

The final Holocene period is characterized by a transgression of Great Salt Lake to what is called the “late prehistoric high” (Currey, 1990). Sometime during this period the lake expanded well into the Great Salt Lake Desert, reaching an elevation of ~1285 m. There is no evidence of any significant change in the kinds and distribution of plant and animal species, and modern communities seem to be firmly established at this time. Between ~0.7 and 0.6 ka, widespread drought caused dramatic changes in the distribution and subsistence focus of prehistoric peoples in the region, with farmers dependent on corn, bean and squash crops shifting to full-time foraging (Madsen and Simms, 1998). Harper and Alder (1970, 1972), using plant remains from Bonneville basin cave sites, suggest the last 600–1000 year period may have been one of the warmest and driest of the Holocene.

## 3. Summary

The Homestead Cave faunal materials, together with the plant macrofossil record from woodrat middens, provides an unusually coherent, comprehensive and consistent picture of environmental change in the eastern Great Basin during the late Pleistocene and Holocene. In large measure this is due to three factors: (1) an extensive testing program designed to identify and excavate a deeply stratified cave site relatively uncontaminated by human foragers; (2) the tight stratigraphic controls employed during the cave excavations; and (3) the extensive use of radiocarbon dating (more than 100 samples were analyzed over the course of the project) to provide a chronological framework into which the collected data could be fitted. This project structure helped to significantly

reduce the contradictions that often appear when disparate types of biotic and physical terrestrial records are brought together.

The dating of this environmental record is not tightly controlled, particularly at the local level, and testing of the sequence described above is necessary. Moreover, some apparent conflict in proxy indicators of climate is also to be expected since these data are differentially sensitive to climate change. For example, mature limber pines may be able to tolerate changes associated with abrupt climate events that seedlings and younger trees may not, and evidence of the change may be delayed until these mature trees eventually die. Despite the current ambiguity about the timing of these events and about the extent of change during any particular period, it is becoming increasingly apparent that there is an episodic aspect to the paleoecological record of the Bonneville basin, which adds to the already complex interpretation of environmental change. The data presented here, together with existing information from in and around the Bonneville basin, suggest that modern plant and animal communities are part of a long trajectory of a constantly changing species matrix. Within this trajectory, however, lies a recurring pattern of environmental change.

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Smith, R. Thompson, S. Tolentino, A. Ugan, D. Weder, and G. Woodbury.

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