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Mammalian responses to Middle Holocene climatic change in the Great Basin of the western United States

Donald K. Grayson *Burke Museum of Natural History and Culture and Department of Anthropology, University of Washington, Seattle, WA 98195, U.S.A. E-mail: grayson@u.washington.edu*

Abstract

In spite of decades of intense research directed toward understanding the climates and ecology of the Great Basin (western United States) during the past 10,000 years, the responses of mammals to the extreme aridity of the Middle Holocene (*c.* 8000–5000 years ago) in this region have been poorly understood. Using a well-dated small mammal sequence from Homestead Cave, north-central Utah, I show that the Middle Holocene small mammal faunas of this area underwent a decrease in species richness and evenness, driven largely by a series of local extinctions and near-extinctions coupled with a dramatic increase in the abundance of taxa well-adapted to xeric conditions. At the end of this period, some taxa that require relatively mesic habitats began to increase in abundance immediately, others did not rebound in abundance until several thousand years later, while still others have not returned at all. This suite of responses has been difficult to detect because climatic change at the beginning of the Middle Holocene was so much more substantial than that which occurred toward its end.

Keywords

Great Basin, Middle Holocene, global warming, climate change, biotic diversity.

INTRODUCTION

The Great Basin, that portion of the arid western United States which drains internally (Fig. 1), has been the focus of palaeoenvironmental research for over a century (e.g. Russell, 1885; Gilbert, 1890; Van Winkle, 1914; Gale, 1915; Antevs, 1938, 1948; Hansen, 1947). The past few decades, however, have seen enormous increases in our understanding of Great Basin late Pleistocene and Holocene climates and biotas, and of the relationships between the two (see the review in Grayson, 1993).

One of the most marked episodes of climatic change in this region during the past 10,000 years occurred during the Middle Holocene, between about 8000 and 5000 years ago. Although the Middle Holocene climates of the Great Basin were variable through time and across space, a variety of analyses show that this period was in general far warmer and drier than what came before or what followed, at least in part a response to the fact that summer precipitation decreased at the same time as temperatures increased (Grayson, 1993; Thompson *et al.*, 1993; Bartlein *et al.*, 1998).

Correspondence: Donald K. Grayson, Burke Museum of Natural History and Culture, Box 353010, University of Washington, Seattle, WA 98195 USA, E-mail: grayson@u.washington.edu

At the beginning of this episode, many lakes and marshes that had been in existence since the waning years of the Pleistocene either desiccated or shrank dramatically. Trees then grew in areas that are now beneath the waters of Lake Tahoe (Lindstrom, 1990; see Fig. 1 for location of places mentioned in the text), while Owens Lake (Benson *et al.*, 1997), Mono Lake (Benson *et al.*, 1997), and the marshes in Ruby Valley (Thompson, 1992) dried. Springs in the southern Great Basin ceased to flow after having been active for thousands of years (Quade *et al.*, 1998).

Changes in Great Basin Middle Holocene floras followed suit. In the White Mountains of south-eastern California, woodlands composed of singleleaf pinyon (*Pinus monophylla*; plant nomenclature follows Welsh *et al.*, 1987) and Utah juniper (*Juniperus osteosperma*) moved upslope some 250 m (Jennings & Elliot-Fisk, 1993) and the lower elevational limits of bristlecone pine (*P. longaeva*) climbed some 150 m (LaMarche, 1973); deuterium/hydrogen ratios from White Mountains bristlecones indicate that a thermal maximum was reached here at about 6800 years ago (Feng & Epstein, 1994). In the far southern Great Basin, thermophilous shrubs increased in abundance at the expense of mesophiles (Spaulding, 1991). To the north, vegetation dominated by shadscale (*Atriplex* spp.) replaced vegetation dominated by sagebrush (*Artemisia* spp.) in the lowlands of the Carson

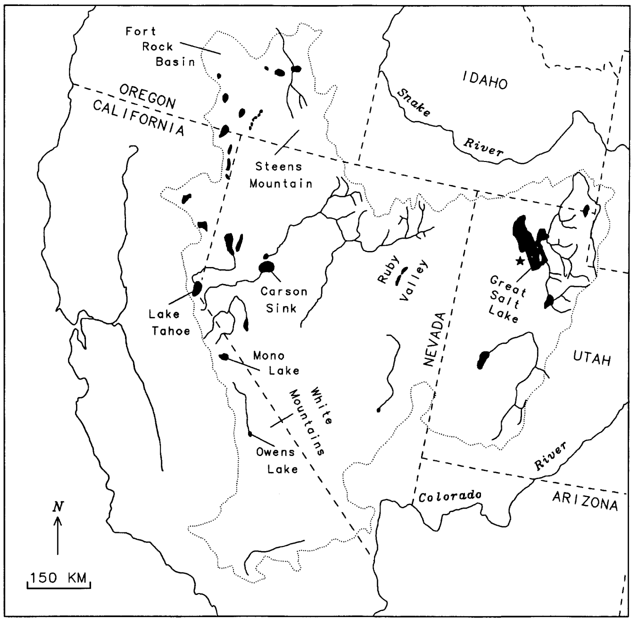

Figure 1 The Great Basin (indicated by dotted line), with locations of places mentioned in the text; the star marks the location of Homestead Cave.

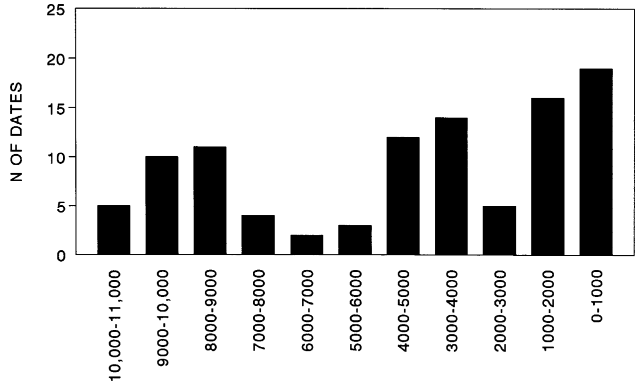

Figure 2 Changing numbers of radiocarbon dates from archaeological sites through time in the Fort Rock Basin, south-central Oregon (data from Bedwell, 1973 and Aikens & Jenkins, 1994). Sequences of this sort, with a Middle Holocene trough in archaeological site occupation, are common in the Great Basin.

Sink (Wigand & Mehringer, 1985) and in Ruby Valley (Thompson, 1992), and sagebrush increased at the expense of grasses in the upper elevations of Steens Mountain (Mehringer, 1985).

The human occupants of the Great Basin appear to have been greatly affected as well. The earliest well-dated archaeological sites in this region are of latest Pleistocene age, and while sites that predate 8000 years ago are notoriously difficult to date accurately in the Great Basin (Beck & Jones, 1997), both they, and sites dated to the Late Holocene, are far more common than sites that have been dated to the Middle Holocene (Fig. 2; see also Grayson, 1993 and Kelly, 1997).

With the end of Middle Holocene aridity, effective precipitation did not return to the high levels that had marked the first few thousand years of the Holocene, but lake levels increased, southern Great Basin springs began to flow again, timberlines descended, sagebrush recolonized some of the lower elevations settings it had occupied before, and human population densities increased (Grayson, 1993).

Although Middle Holocene responses in Great Basin lake levels, spring discharge, floral composition, and, to a lesser degree, human population densities are now reasonably well-understood, the same cannot be said about our understanding of the contemporary responses of nonhuman mammals.

It has been clear for some time that a number of mammal species were dramatically affected by the onset of Middle Holocene climatic conditions here. For instance, as sagebrush declined in abundance in Great Basin valley bottoms, so did the abundance of pygmy rabbits (*Brachylagus idahoensis*; mammalian nomenclature follows Wilson & Reeder, 1993), an animal that is typically associated with dense stands of big sagebrush (*Artemisia tridentata*) growing in deep, easily excavated substrates (Green & Flinders, 1980a, 1980b; Katzner & Parker, 1997). Pikas (*Ochotona princeps*) seem to have been extirpated from lower elevation settings in at least most parts of the Great Basin by or during the Middle Holocene (Grayson, 1993), and Great Basin small mammal faunas deposited between 11,000 and 8300 years ago seem to have been richer in species than those deposited later (Grayson, 1993, 1998).

Although mammalian responses to the onset of Middle Holocene aridity have been detected, there have been no compelling, detailed records that shed much light on the responses of mammals during, and at the end of, this episode in the Great Basin. As I noted a number of years ago (Grayson, 1993), the fact that palaeoecologists had not detected such responses probably simply reflected the fact that sufficiently detailed faunal sequences had yet to be discovered and analysed. As a result, some of the more pronounced changes in mammalian distributions and abundances that occurred at the beginning of the Middle Holocene had been detected, but the less pronounced changes that must have followed had not.

Here, I report just such changes from a well-stratified and well-dated set of faunal assemblages from a recently excavated cave site located in the Bonneville Basin of north-central Utah.

HOMESTEAD CAVE

The Lakeside Mountains lie a few km west and south of Great Salt Lake in north-central Utah. The north-westernmost spur of these mountains is formed by Homestead Knoll, a low (maximum elevation = 1625 m), rocky promontory devoid of active springs and permanent streams. The barren playa of Pleistocene Lake Bonneville lies to the immediate west and north-west. The vegetation of the knoll is dominated by shrubs and grasses, although there are a few scattered Utah junipers on its highest reaches.

Figure 3 The location of Homestead Cave (arrow) on Homestead Knoll; the obvious benches on the knoll are terraces left by Pleistocene Lake Bonneville.

Most prominent among the shrubs are shadscale (*Atriplex confertifolia*), shortspine horsebrush (*Tetradymia spinosa*), and littleleaf horsebrush (*T. glabrata*). *Artemisia tridentata* is present along seasonally moist drainages, while bud sagebrush (*Artemisia spinescens*), rabbitbrush (*Chrysothamnus* sp.), and greasewood (*Sarcobatus vermiculatus*) are present but uncommon above the flanks of the knoll. Greasewood becomes increasingly abundant as the valley floor is approached and, along with *A. confertifolia*, is common on that floor itself, as are introduced Eurasian cheatgrasses (*Bromus* spp.).

Homestead Knoll is dotted by a number of caves, one of which, Homestead Cave, sits on the northern edge of the Knoll at an elevation of 1406 m, some 100 m above the valley floor (Fig. 3). Approximately 17 m deep and 4.5 m wide at the mouth, this cave was the focus of stratigraphic excavations, directed by D. B. Madsen of the Utah Geological Survey, in 1993. During those excavations, a 1 m × 1 m column sample was excavated to bedrock, encountered at a depth of about 2.7 m. Deposits were removed according to 18 separate strata, passed through 1/4″ (0.64 cm), 1/8″ (0.32 cm), and 1/16″ (0.16 cm) mesh screen, and organic remains removed from the screen residues. A total of twenty-one radiocarbon dates have been obtained on material taken directly from the excavated column (Table 1). The fish, bird, and mammal remains retrieved from the column sample have each been identified by different specialists. The results I report here are based on the mammal remains extracted from the 1/4″ and 1/8″ sample fractions.

The Homestead Cave deposits proved to be extraordinarily rich in bone. This richness stems not only from the excellent preservation provided by this arid and sheltered setting, but also from the fact that the cave served as a roosting site for owls throughout its depositional history. The sediments of the column sample contain owl pellets in all states of decay and many specimens, especially skulls, have owl pellet debris adhering to them regardless of their antiquity. While some animals may have died on the site on their own, and some specimens were likely brought to the site by woodrats (*Neotoma* spp.), the great abundance of bone has resulted from the foraging activities of owls.

A total of *c.* 184,000 mammalian bones and teeth have been identified to at least the genus level from fifteen of the eighteen Homestead Cave strata (Table 2; there are no plans to identify the mammals from the remaining three strata and only the kangaroo rats, genus *Dipodomys*, have been identified from stratum X). Since these assemblages primarily reflect owl foraging, the vast majority of the specimens are

Table 1 Radiocarbon and calibrated ages from Homestead Cave (yr BP = years before the present, measured from 1950).

Stratum	Age (^{14}C year BP)	Lab. No.	Age* (cal year BP)
XVII	1020 ± 40	Beta 101877	925–961
XVI	1200 ± 50	Beta 66940	1058–1216
XIV	2850 ± 50	Beta 103962	2873–3056
XIII	3480 ± 40	Beta 101878	3328–3689
XII	3400 ± 60	Beta 63179	3572–3695
X	5330 ± 65	AA 14822	5993–6266
VII	6160 ± 85	AA 14824	6906–7208
	6185 ± 105	AA 14825	6908–7248
VI	7120 ± 70	AA 14826	7865–8003
V	8230 ± 69	AA 16810	9033–9399
IV	8195 ± 85	AA 14823	9097–9397
II	8520 ± 80	AA 14821	9474–9547
	8790 ± 90	AA 14820	9808–10,146
	8830 ± 240	Beta 63438	9544–10,221
I (Upper 5 cm)	10,160 ± 85	AA 14819	11,706–12,105
	10,350 ± 80	AA 14818	11,948–12,600
I (General)	10,910 ± 60	Beta 72205	12,878–13,005
I (Lower 5 cm)	11,065 ± 105	AA 14817	12,919–13,160
	11,181 ± 85	AA 16808	13,018–13,187
	11,263 ± 83	AA 16809	13,142–13,397
	11,270 ± 135	AA 14816	13,039–13,431

*Calibration from Stuiver *et al.* (1998) at one standard deviation (Madsen, 2000).

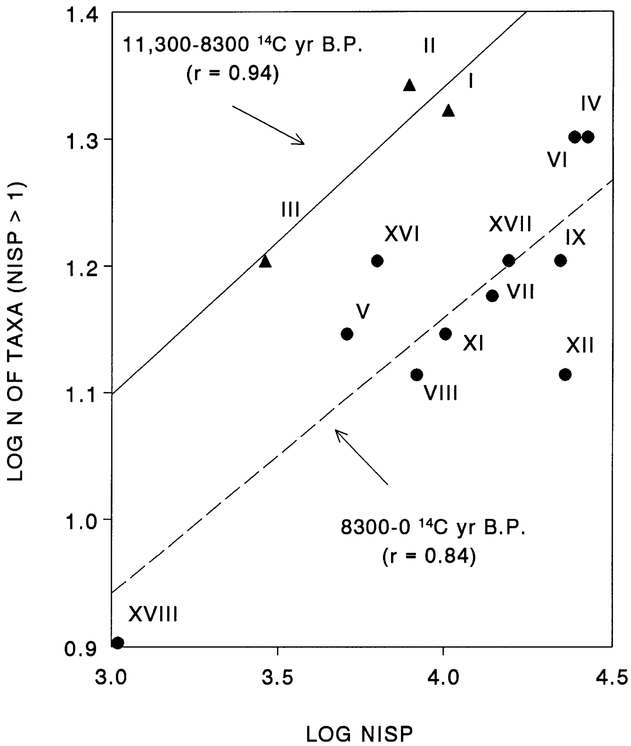

Figure 4 The relationships between number of identified specimens (NISP) and taxonomic richness at Homestead Cave (Grayson, 1998).

Table 2 Numbers of identified specimens (NISP) for all mammalian taxa by stratum at Homestead Cave.

Stratum	NISP
XVIII	1047
XVII	15,548
XVI	6296
XII	22,860
XI	10,096
X	6601*
IX	22,088
VIII	8289
VII	13,905
VI	24,330
V	5109
IV	26,615
III	2884
II	7855
I	10,275
Total	183,798

*Only the kangaroo rat component of the Stratum X assemblage was identified.

from lagomorphs and rodents (99.9%, excluding stratum X), and the analysis that follows examines only these two groups. The raw data on which these analyses are based are to be published separately (Madsen, 2000).

MIDDLE HOLOCENE MAMMAL HISTORY

Mammal community richness

As I have discussed elsewhere (Grayson, 1998), the end of the Early Holocene at Homestead Cave is marked by a significant reduction in the taxonomic richness of the mammalian assemblages incorporated into the sediments of the site. This reduction reflects a decrease in the richness of the small mammal community in the area surrounding the cave as the cooler and moister climatic regime that prevailed between 11,300 and 8300 years ago gave way to the warmer/drier regime that marked the Middle Holocene (Fig. 4; in this and later figures, NISP stands for the number of identified specimens).

There is no corresponding change in taxonomic richness across the Middle Holocene/Late Holocene boundary at *c.* 5000 years ago, even though Middle Holocene richness values are lower than those that mark the Late Holocene. This asymmetry in the taxonomic richness response is consistent with other evidence, noted above, suggesting that changes in climate and vegetation at the end of the Early Holocene in the Great Basin were far more substantial than were such changes at the end of the Middle Holocene.

The responses of individual species

Also consistent with this asymmetrical richness response is the fact that the Middle Holocene saw the last local occurrence of several small mammals that are today found only in

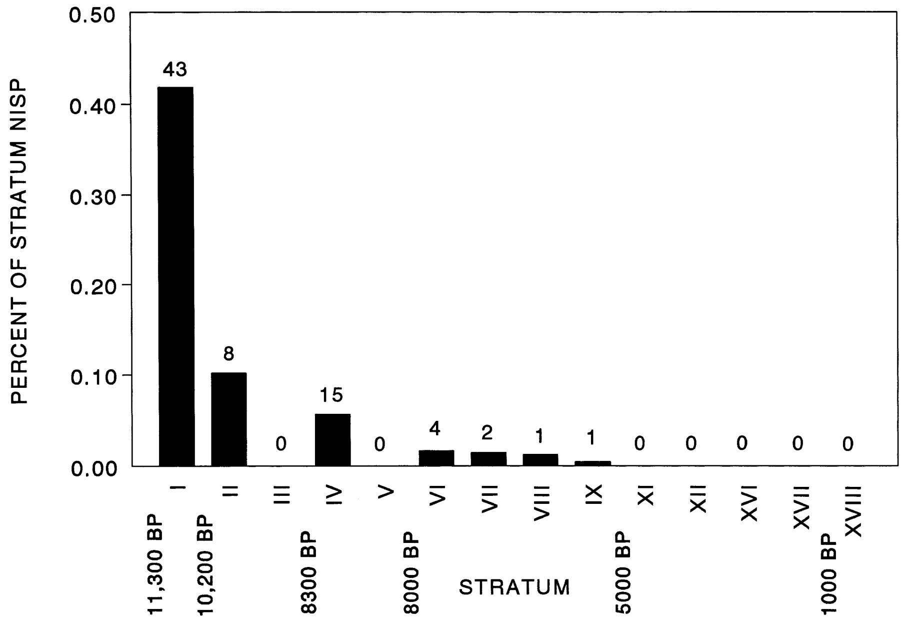

Figure 5 Changing abundances of yellow-bellied marmots at Homestead Cave; numbers above the bars provide the total number of identified *Marmota flaviventris* specimens in each stratum.

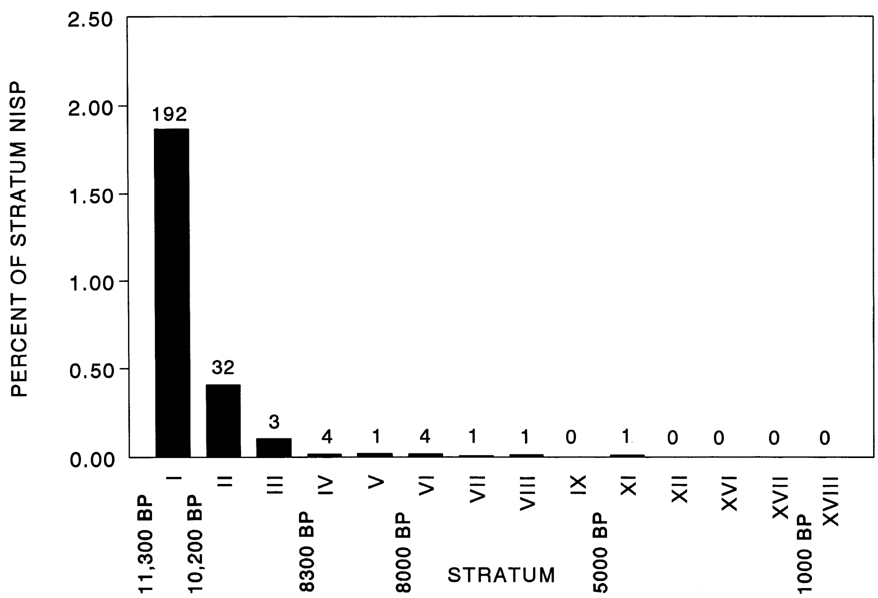

Figure 6 Changing abundances of pygmy rabbits at Homestead Cave; numbers above the bars provide the total number of identified *Brachylagus idahoensis* specimens in each stratum.

cooler, moister parts of the Great Basin. These include yellow-bellied marmots (*Marmota flaviventris*; Fig. 5) and pygmy rabbits (Fig. 6).

In addition, several species became locally extinct during the Middle Holocene and did not reappear until well into the Late Holocene. Those species include the bushy-tailed woodrat (*Neotoma cinerea*; Fig. 7), which is present on Homestead Knoll today (Grayson *et al.*, 1996) but which is most abundant in far cooler and moister settings, and the Great Basin pocket mouse (*Perognathus parvus*; Fig. 8), whose modern Great basin abundance is positively correlated with both degree of ground cover and winter precipitation (Verts & Carraway, 1998). Sage voles (*Lemmiscus curtatus*), often associated with habitats dominated by big sagebrush and grasses (Maser, 1974; Carroll & Genoways, 1980), show a similar response (Fig. 9).

Other species responded to both the onset and termination of the Middle Holocene. Western harvest mice (*Reithrodontomys megalotis*; Fig. 10) are common in the Early Holocene faunal assemblages of Homestead Cave, become

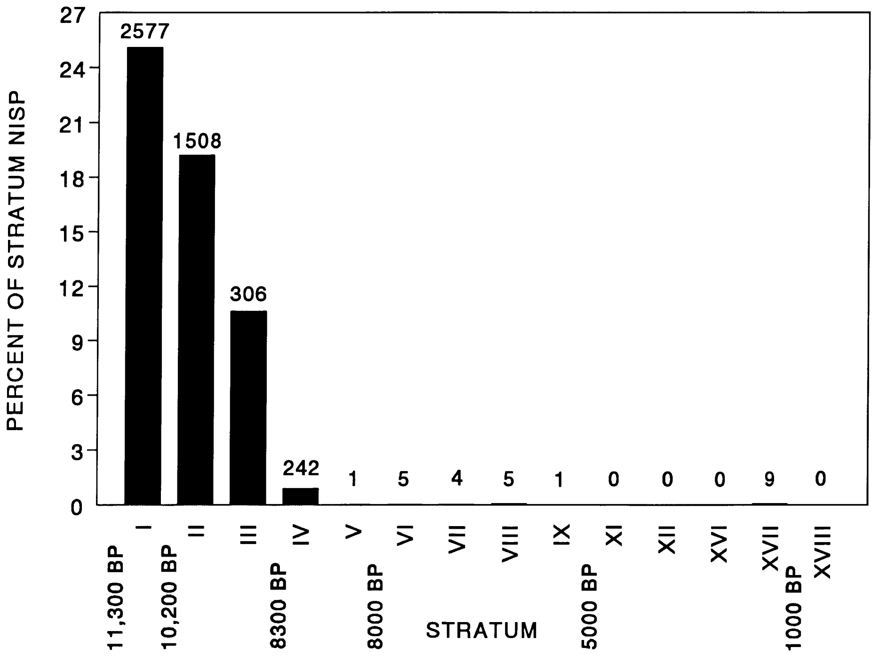

Figure 7 Changing abundances of bushy-tailed woodrats at Homestead Cave; numbers above the bars provide the total number of identified *Neotoma cinerea* specimens in each stratum.

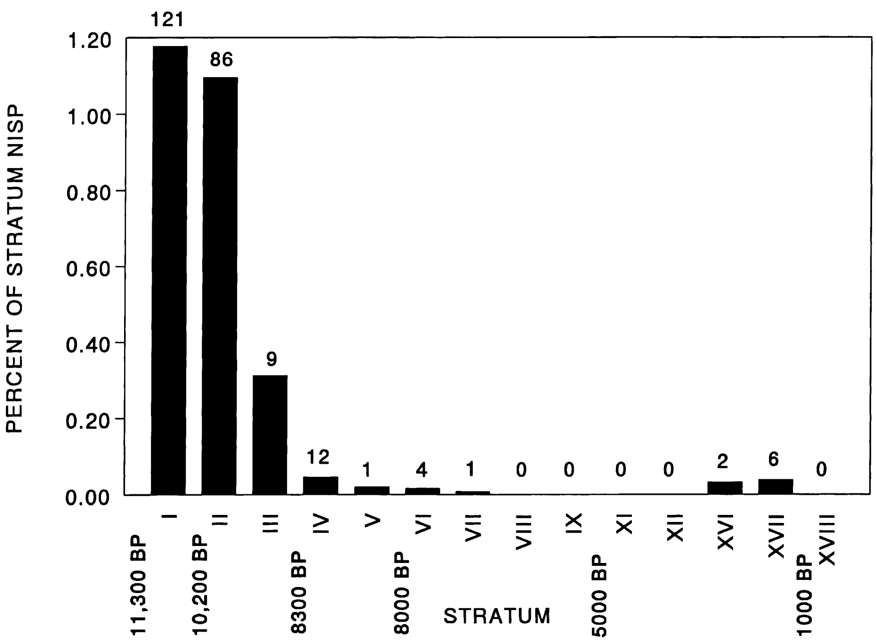

Figure 8 Changing abundances of Great Basin pocket mice at Homestead Cave; numbers above the bars provide the total number of identified *Perognathus parvus* specimens in each stratum.

rare in the Middle Holocene assemblages, and then return as this period ends. Today, these animals are most common in well-watered parts of the Great Basin and may undergo population reductions in response to drought (Whitford, 1976).

Kangaroo rats also show a marked response to Middle Holocene climates. There are two species of this genus represented at Homestead Cave, Ord's (*Dipodomys ordii*) and the chisel-toothed (*D. microps*) kangaroo rat. Both are common in the Great Basin today since both are well-adapted to arid settings, as are kangaroo rats in general (French, 1993). Neither species is abundant in late Pleistocene Stratum I at Homestead Cave, but they become increasingly common during the Early Holocene, and dominate all assemblages once the Middle Holocene begins (Fig. 11).

Dipodomys ordii and *D. microps* tend to occupy different kinds of habitats in the modern Great Basin. The chisel-toothed kangaroo rat is exquisitely adapted to utilizing habitats dominated by shadscale, using its distinctive incisors to shave off the external and highly saline faces of shadscale leaves to expose the palatable, moister inner parts of these leaves, which it then consumes (Kenagy, 1972, 1973). Ord's kangaroo rat, on the other hand, is primarily a granivore and is often

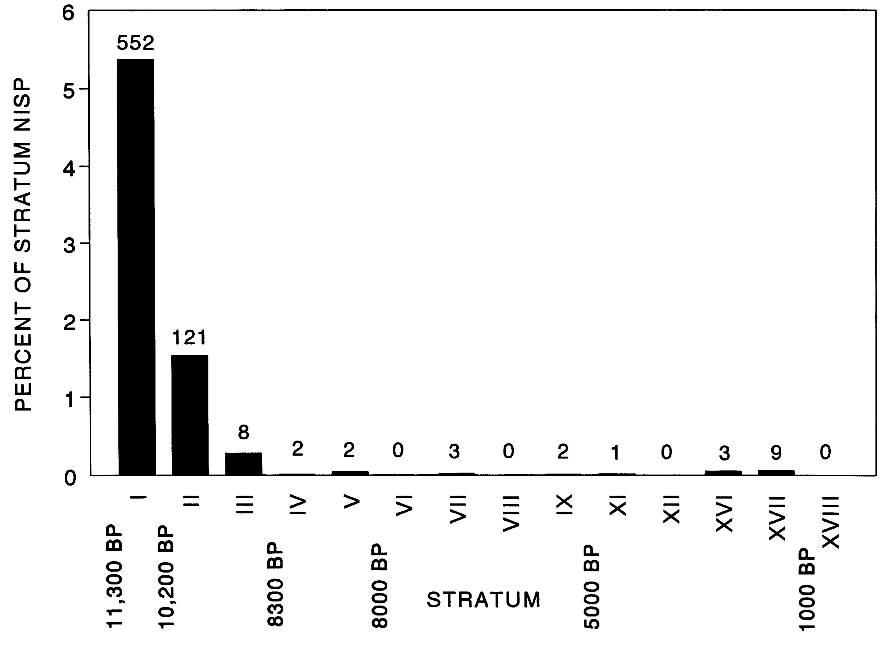

Figure 9 Changing abundances of sage voles at Homestead Cave; numbers above the bars provide the number of identified *Lemmiscus curtatus* specimens in each stratum.

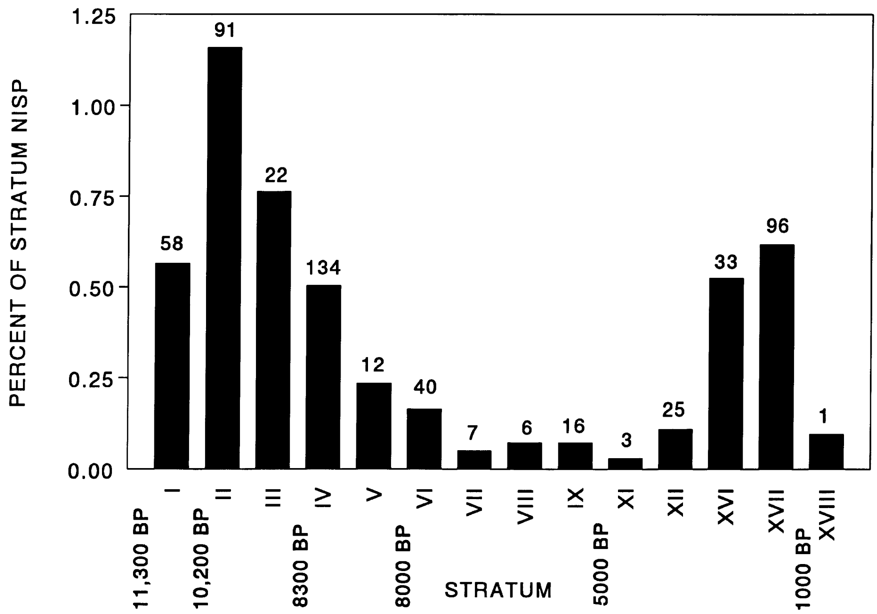

Figure 10 Changing abundances of western harvest mice at Homestead Cave; numbers above the bars provide the number of identified *Reithrodontomys* specimens in each stratum (because all harvest mice that could be identified to species are *R. megalotis*, specimens that could be identified only as *Reithrodontomys* are included in these counts).

common in sagebrush habitats (Hayssen, 1991). Where the two overlap in distribution, *D. microps* is primarily found in shadscale-dominated settings (O'Farrell, 1980).

Figure 12 displays the ratio of *D. microps* to *D. ordii* through time at Homestead Cave. As I mentioned, kangaroo rats are not abundant here during the late Pleistocene and Early Holocene, but among those that are present, *D. ordii* is far more common than it has been at any time since (in Stratum I, forty-three of the fifty specimens identified to the species level are of *D. ordii*). As the Middle Holocene is approached, the relative abundance of *D. microps* increases, presumably reflecting the increasing dominance of shadscale vegetation in the area, then peaks during the heart of this episode. As the Middle Holocene ends, *D. microps* declines in relative abundance, though *D. ordii* never becomes as common in the fauna as it was prior to this interval.

In short, most small mammals in the Homestead Cave faunal assemblages that are both abundantly represented

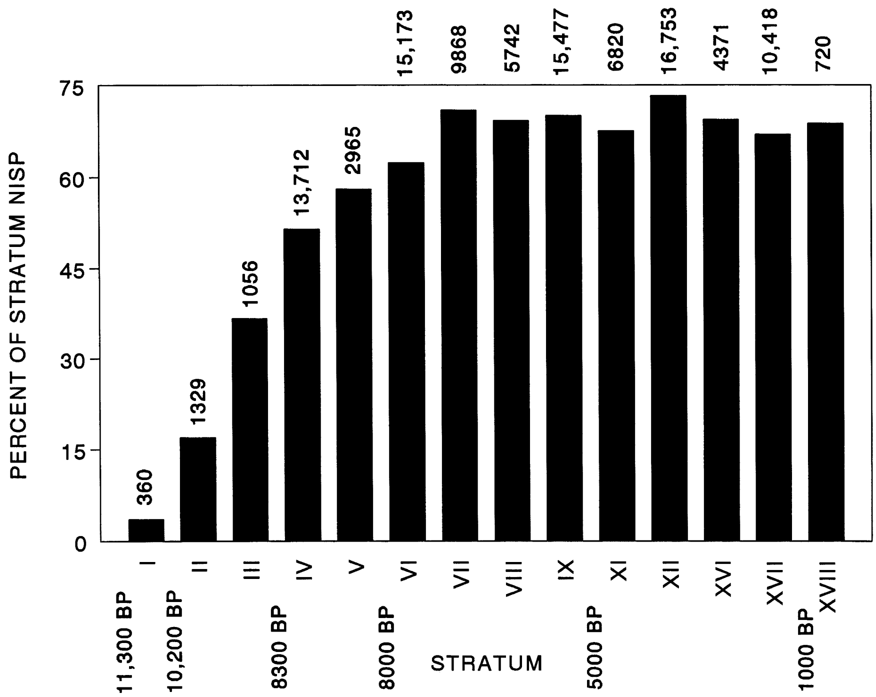

Figure 11 Changing abundances of kangaroo rats at Homestead Cave; numbers above the bars provide the number of specimens identified as *Dipodomys* in each stratum.

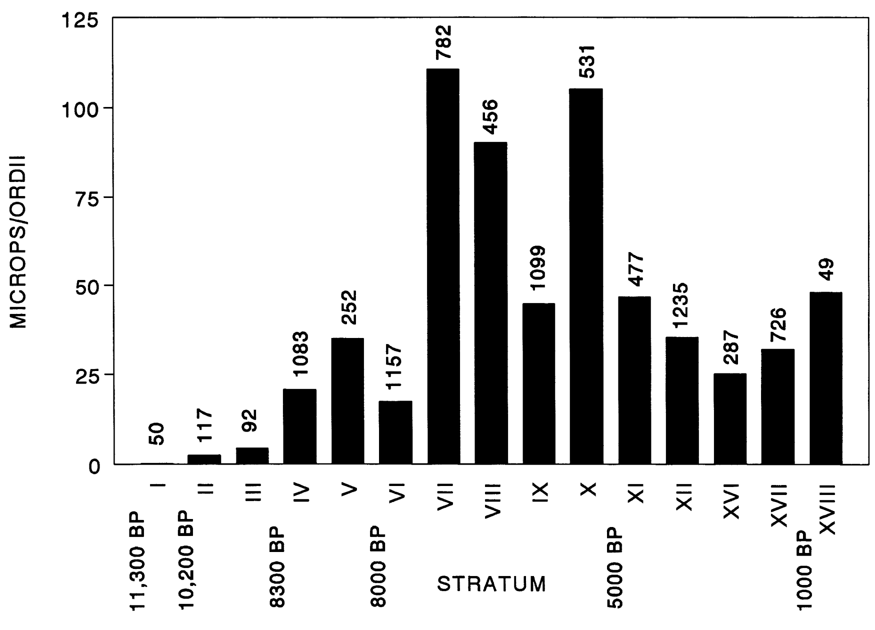

Figure 12 The ratio of *Dipdomys microps* to *D. ordii* through time at Homestead Cave; the numbers above the bars provide the total number of specimens identified as either *D. microps* or *D. ordii* in each stratum.

and that can be securely identified to the species level responded to the increasing aridity that marks the onset of the Middle Holocene here. Responses to the end of this interval, however, vary from species to species. Some, including *Marmota flaviventris* and *Brachylagus idahoensis*, became locally extinct during this episode and have never recolonized. Others, including *Dipodomys ordii* and *Reithrodontomy megalotis*, became extremely uncommon, if not locally extinct, but rebounded in numbers as the Middle Holocene ended. Still others, including *Perognathus parvus* and *Neotoma cinerea*, were extirpated during this episode and did not recolonize until long after the Middle Holocene. These varied histories may represent individual responses to the varying nature of Late Holocene climates, but they may also reflect distance to source areas for recolonizers, or some combination of the two.

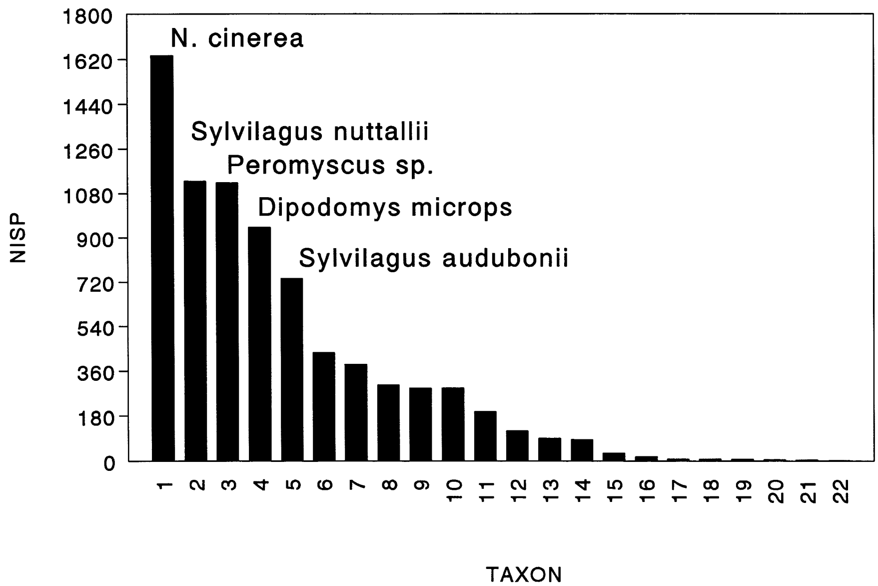

Figure 13 The distribution of abundances in Homestead Cave Early Holocene Stratum II; the five most abundant taxa are identified.

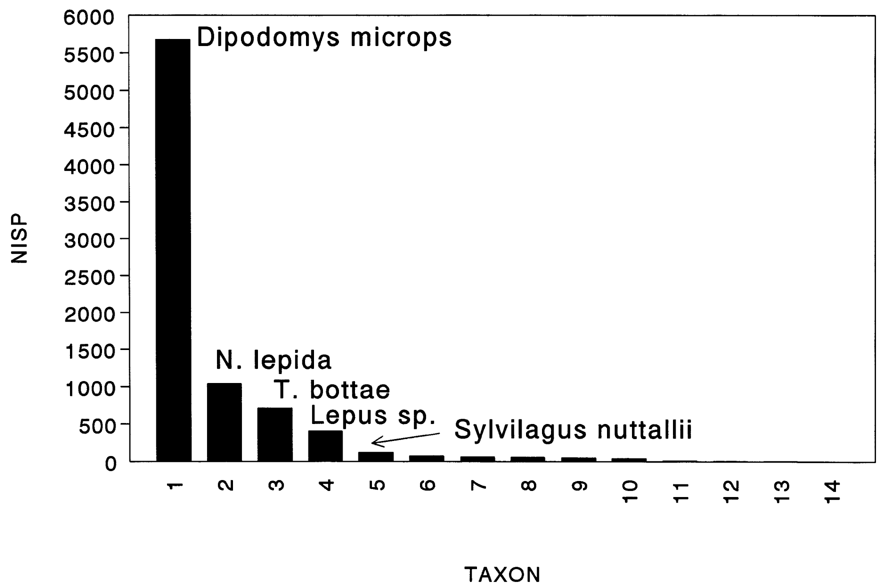

Figure 14 The distribution of abundances in Homestead Cave Middle Holocene Stratum VIII; the five most abundant taxa are identified.

Evenness

As aridity increased at the end of the Early Holocene in the Homestead Knoll area, kangaroo rats became increasingly dominant in the Homestead Cave faunal assemblages at the same time as species requiring relatively mesic habitats declined in abundance. As a result, Homestead Cave faunal assemblage evenness, or the degree to which taxa are equally represented in those assemblages, also changed dramatically.

This change in evenness can be seen subjectively by comparing histograms of taxonomic abundances of Early and Middle Holocene faunal assemblages (e.g. Figures 13 and 14), which make clear the heavy dominance of Middle Holocene assemblages by *Dipodomys* (and in particular, by *D. microps*). It can best be seen, however, by plotting quantitative evenness values for all assemblages through time (Fig. 15).

The evenness values in Fig. 15 were calculated as $-\Sigma\, p_i \ln p_i / \ln T$, in which p_i represents the proportion of individuals in the *i*th taxon in a given assemblage, and T the number of taxa in that assemblage; an evenness value of 1.0 represents the situation in which all taxa are equally common (Pielou, 1975; Magurran, 1988). To produce these values, taxonomic abundances were counted using the protocol described in

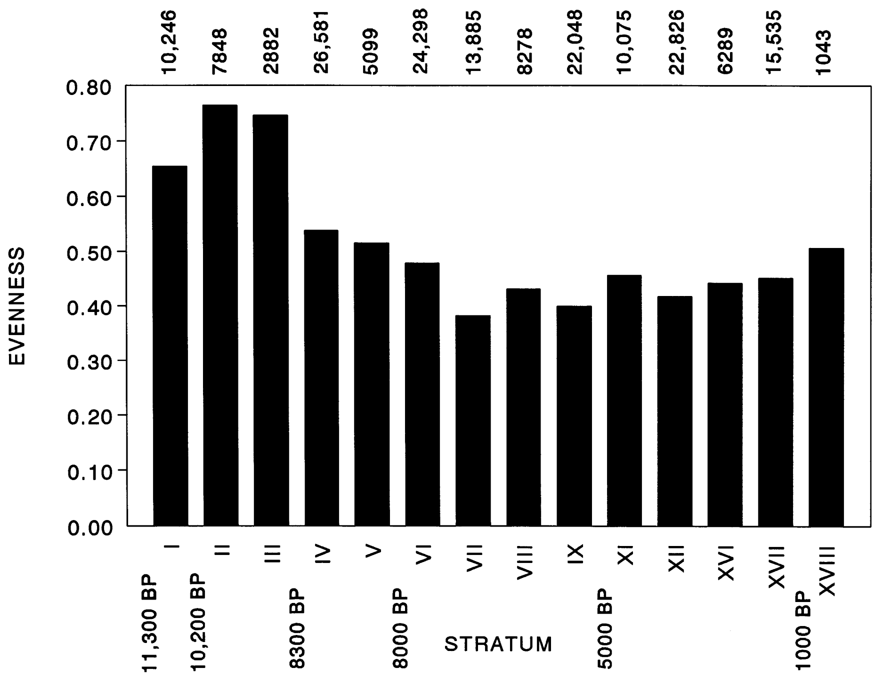

Figure 15 Evenness values for the Homestead Cave lagomorph and rodent assemblages; the numbers above the bars provide the total number of identified lagomorph and rodent specimens in each stratum.

Grayson (1998); the results are not significantly correlated with sample size ($r = -0.39$, $P > 0.15$). The highest evenness values mark late Pleistocene and Early Holocene strata I, II, and III; the lowest mark Middle Holocene strata VII and IX. The variable nature of these values during the Middle Holocene matches independent evidence, discussed above, that the Middle Holocene of the Great Basin was climatically variable, not monolithically arid.

CONCLUSIONS

The Middle Holocene has at times been used as a rough analogue for conditions that might pertain under modern global warming in the arid west (e.g. Murphy & Weiss, 1992). If the analogy is appropriate, then the Homestead Cave faunal assemblages suggest that a significant increase in summer temperatures in this region will see the loss of a number of mammals, including *Neotoma cinerea*, *Perognathus parvus*, and *Reithrodontomys megalotis*. We would also expect certain xeric-adapted species, including *Dipodomys microps*, to increase sharply in abundance, and community evenness to decline.

It is not clear, however, that the Middle Holocene provides an appropriate analogue for mammalian responses under conditions that might be caused by modern global warming. First, such modern warming is thought to be driven not by the changing nature of solar insolation, but by the accumulation of greenhouse gasses, including CO_2, in the atmosphere (Crowley, 1990; Mitchell, 1990). Second, while Middle Holocene warming in the south-western United States was accompanied by strengthened monsoonal incursions and thus by increased summer precipitation (Van Devender, 1990), those incursions do not seem to have penetrated significantly into the Great Basin (Spaulding, 1991). It is unknown whether the Great Basin would see increased monsoonal precipitation under conditions of global warming, and we have no detailed palaeontological analogues from the Great Basin that would pertain to hotter and wetter, as opposed to hotter and drier, conditions. Third, the 11,000 year small mammal history recorded by Homestead Cave is almost entirely prehistoric in age. The exotic plants, most notably cheatgrass, that are an integral part of the local vegetation today were not present prehistorically, yet it is within this altered biotic context that mammalian responses to global warming will take place.

As a result, we cannot as yet draw secure inferences concerning small mammal responses to global warming conditions in the Great Basin from the Homestead Cave faunal assemblages. Nonetheless, those assemblages do provide our first detailed understanding of mammalian reponses to Middle Holocene warmth and aridity in this region.

As the Early Holocene ended in the Homestead Knoll area, local rodent and lagomorph faunas underwent dramatic changes. Mammalian community richness and evenness declined substantially, and mammals that are today most abundant in relatively cool and moist habitats in the Great Basin either became locally extinct or decreased dramatically in abundance. As the Middle Holocene ended, species richness remained low, but evenness increased as species that are well-adapted to demanding xeric conditions declined in abundance and a subset of those requiring more mesic settings became more common. This latter increase, in fact, mirrors the response made by the human occupants of this region at the same time (compare, for instance, Figs 2 and 10). Some species, however, have not returned, while others did not return until long after the Middle Holocene ended. These later Holocene changes have not previously been detected because they are far more subtle than those that occurred at the end of the Early Holocene, and because faunal sequences adequate for the task have until now been unavailable.

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BIOSKETCH

Donald K. Grayson is Professor of Anthropology, Department of Anthropology, and Adjunct Curator of Environmental Archaeology, Burke Museum of Natural History and Culture, in the University of Washington, Seattle. His research focuses on the paleoecology and human prehistory of the Great Basin, and on the nature of human interactions with the faunal landscape during the Pleistocene of western Europe. He is the recipient of the Fryxell Award for Interdisciplinary Research from the Society for American Archaeology; his latest book is *The desert's past: a natural prehistory of the Great Basin* (Smithsonian Institution, 1993).