The Late Quaternary biogeographic histories of some Great Basin mammals (western USA)

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Abstract

The Great Basin of arid western North America provides one of the most detailed late Pleistocene and Holocene mammal records available for any part of the world, though the record is by far strongest for small mammals. Of the 35 genera of now-extinct North American Pleistocene mammals, 19 are known to have occurred in the Great Basin, a list that is likely to be complete or nearly so. Of these 19, seven can be shown to have survived beyond 12,000 radiocarbon years ago, a proportion similar to that for North America as a whole. Horses, camels, mammoth, and helmeted musk-oxen appear to have been the most abundant of these genera. Pygmy rabbits (*Brachylagus idahoensis*), yellow-bellied marmots (*Marmota flaviventris*), and bushy-tailed woodrats (*Neotoma cinerea*) declined in abundance at the end of the Pleistocene, at about the same time as populations south of their current arid western distributional boundary were extirpated. Subsequent declines occurred during the hot/dry middle Holocene. Pygmy rabbits also declined as modern pinyon-juniper woodlands developed across the Great Basin. The Snake Range of eastern Nevada has seen the late Pleistocene or Holocene extinction of both northern pocket gophers (*Thomomys talpoides*) and pikas (*Ochotona princeps*). Coupled with the rarity of yellow-bellied marmots here, these histories make the Snake Range a biogeographic oddity. These and other Great Basin mammal histories provide significant insights into the possible responses of Great Basin small mammals to global warming.
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1. Introduction

The Great Basin is the vast area of internal drainage in the arid western United States (Fig. 1). Well-known to Quaternary scientists because it saw the development of massive pluvial lakes during the Pleistocene, this region has provided a rich record of now-extinct Pleistocene mammals and what is perhaps the most detailed late Pleistocene and Holocene small mammal record available for any place in the world. In recent years, thorough overviews of the later Pleistocene and Holocene histories of Great Basin glaciers (Osborn and Bevis, 2001), plants (Wigand and Rhode, 2002), and lakes (Lowenstein, 2002; Negrini, 2002; Oviatt and Thompson, 2002; Benson, 2004) have appeared. Over a decade has passed, however, since the later Pleistocene and Holocene histories of Great Basin mammals have been examined in detail (Grayson, 1993; see also Heaton, 1999). During that time, substantial progress has been made toward understanding the biogeographic history of a broad range of those mammals. Here, I review that progress, focusing on those mammals about which we have learned the most.

2. The Great Basin

The Great Basin spans about 10° of latitude (ca 34.5°N–44°N) and longitude (ca 111°W–121°W) and contains both the lowest point in North America (-86 m, in Death Valley, California) and one of the highest (4342 m, White Mountain Peak, California). Because much of the Great Basin is marked by tall and massive mountains separated by long and narrow valleys, elevational relief throughout the region tends to be substantial. Indeed, the average elevational difference between valley floor and mountain top across the central Great Basin is about 1770 m (Grayson, 1993).

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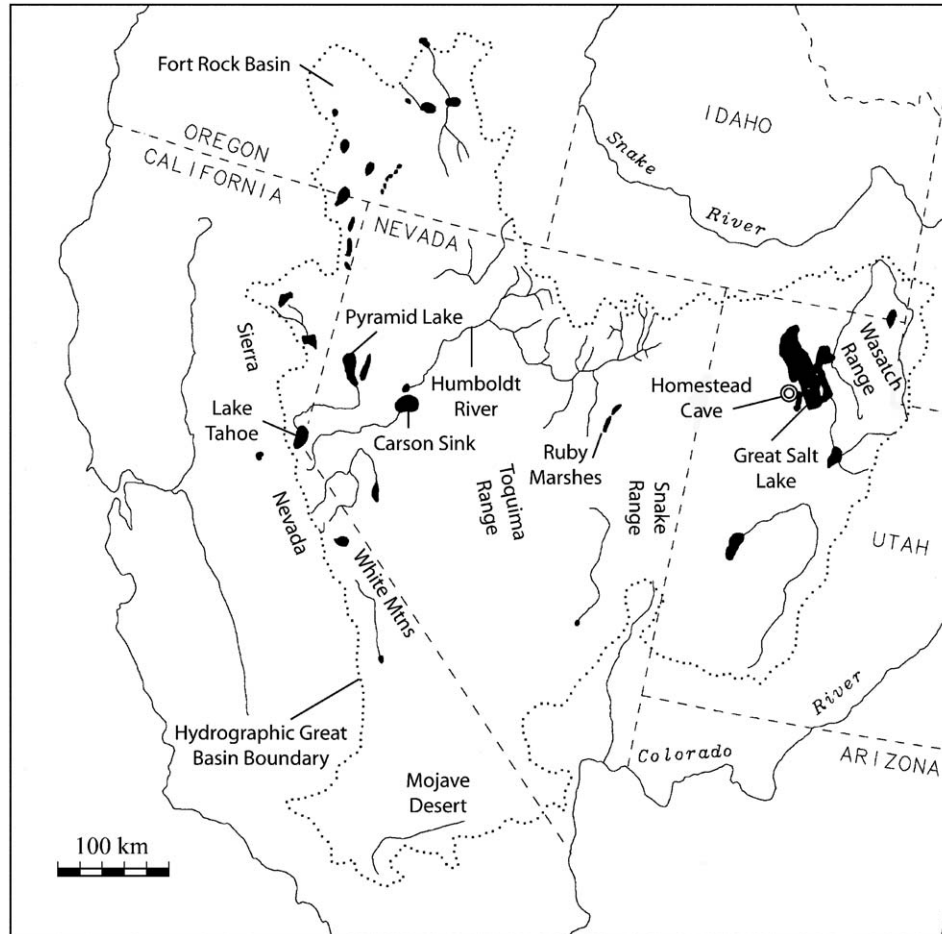*E-mail address:* grayson@u.washington.edu.

Fig. 1. The hydrographic Great Basin, with locations of selected areas mentioned in the text.

Lying in the rainshadow of the Sierra Nevada and Cascade Mountains, the Great Basin is arid, with valley-bottom precipitation (ca 10–20 cm yr^{-1}) far lower than average annual evaporation (ca 90–220 cm yr^{-1}). The adjoining mountains couple higher precipitation with far lower evaporation. Much of the precipitation received by these mountains falls as snow during the winter, which then feeds the region's streams and lakes during spring and summer. In the eastern and southern Great Basin, this source of summer moisture is augmented by monsoonal storm systems, which derive their moisture from the Gulfs of California and Mexico and enter the region from the south (Houghton, 1969). (Fig. 1).

Although the salt pans that mark some valley bottoms lack vegetation, most valleys are covered to one degree or another by grasses and such xeric-adapted shrubs as big sagebrush (*Artemisia tridentata*), saltbushes (*Atriplex* spp.), and, to the south, creosote bush (*Larrea divaricata*) and blackbrush (*Coleogyne ramosissima*). Throughout much of the Great Basin, mountain flanks are covered by woodlands composed of singleleaf pinyon (*Pinus monophylla*) and Utah juniper (*Juniperus osteosperma*), with higher elevations supporting a variety of subalpine conifers, including limber pine (*P. flexilis*), bristlecone pine (*P. longaeva*), Engelmann spruce (*Picea englemannii*), and

white fir (*Abies concolor*). Alpine tundra covers the uppermost reaches of the Great Basin's highest mountains (Billings, 1951).

The distribution of Great Basin mammals reflects this environmental diversity. For instance, some small mammals, including the chisel-toothed kangaroo rat (*Dipodomys microps*) and the dark kangaroo mouse (*Microdipodops megacephalus*), are so well-adapted to hot and dry settings that they do not need to drink. Others, such as the American pika (*Ochotona princeps*) and yellow-bellied marmot (*Marmota flaviventris*), cannot survive in these settings and are entirely or largely confined to Great Basin mountains. The complexity of small mammal distributions within the Great Basin have made this region the focus of innovative and influential biogeographic research (e.g., Brown, 1971; Lawlor, 1998; Rickart, 2001). Knowledge of the deeper histories of these mammals has been critical to understanding their modern distributions and to developing and refining the biogeographic models derived from them.

3. The Late Pleistocene: extinct mammals

Toward the end of the Pleistocene, North America saw the loss of some 35 genera of primarily large mammals, of

which six live on elsewhere (Table 1). While it is often assumed that all of these extinctions occurred between about 12,000 and 10,000 yr BP (unless otherwise indicated, all ages in this paper are in radiocarbon years), only 16 of the 35 have been dated to this interval, and it is possible that the North American extinctions were staggered in time and space, just as they were in Eurasia (Grayson, 2001, n press a; Grayson and Meltzer, 2002).

Of these 35 genera, 19 are known from the Great Basin (Table 1) and there are good reasons to think that the Great Basin list of extinct Pleistocene mammals is nearly complete. Of the 16 missing taxa, only one—the dhole (*Cuon*)—might reasonably be expected to be found here in the future. Today, dholes are widely distributed in southern and eastern Asia. During the later Pleistocene, their distribution extended deep into southwestern Europe (Crégut-Bonnoure, 1996) and into Alaska and the Yukon Territory (Youngman, 1993). They are also known from San Josecito Cave, Nuevo Léon, Mexico (Arroyo-Cabrales and Polaco, 2003). Since these canids were in both eastern

Table 1
The extinct late Pleistocene mammals of North America, including three extinct species of extant North American genera (*Canis dirus*, *Panthera leo*, and *Oreamnos harringtoni*); taxa known from the Great Basin are in bold

Order	Family	Genus	Illustrative Great Basin site and references
Xenarthra	Pampatheriidae	*Pampatherium*[a]	
		Holmesina	
	Glyptodontidae	*Glyptotherium*	
	Megalonychidae	**Megalonyx**	Orem, UT [1]
	Megatheriidae	*Eremotherium*	
		Nothrotheriops	Gypsum Cave, NV [2]
	Mylodontidae	**Paramylodon**[b]	Carson City, NV [3]
Carnivora	Mustelidae	**Brachyprotoma**	Crystal Ball Cave, UT [4]
	Canidae	*Cuon*[c]	
		Canis dirus	Silver Creek, UT [5]
	Ursidae	*Tremarctos*[c]	
		Arctodus	Huntington Dam, UT [6]
	Felidae	**Smilodon**	Black Rock Desert, NV [7]
		Homotherium	Fossil Lake, OR [8]
		Miracinonyx	Crypt Cave, NV (9)
		Panthera leo	Tule Springs, NV [10]
Rodentia	Castoridae	*Castoroides*	
	Caviidae	*Hydrochoerus*[c,d]	
		Neochoerus	
Lagomorpha	Leporidae	*Aztlanolagus*	
Perissodactyla	Equidae	**Equus**[c]	Long Valley, NV[11]
	Tapiridae	*Tapirus*[c]	
Artiodactyla	Tayassuidae	*Mylohyus*	
		Platygonus	Franklin, ID [12]
	Camelidae	**Camelops**	Hidden Cave, NV [13]
		Hemiauchenia	Crystal Ball Cave, UT [4]
		Palaeolama	
	Cervidae	**Navahoceros**	Mineral Hill Cave, NV [14]
		Cervalces	
	Antilocapridae	**Capromeryx**	Schuiling Cave, CA [15]
		Tetrameryx	Lark Fauna, UT [16]
		Stockoceros	
	Bovidae	*Saiga*[c]	
		Euceratherium	Falcon Hill Caves, NV [17]
		Bootherium	Logan City Cemetery, UT [18]
		Oreamnos harringtoni	Smith Creek Cave, NV [19]
Proboscidea	Mammutidae	**Mammut**	Mastodon Sinkhole, UT [20]
	Elephantidae	**Mammuthus**	Black Rock Desert, NV [7]

CA = California, ID = Idaho, NV = Nevada, OR = Oregon, UT = Utah.

[a]The single record for this genus may actually pertain to *Holmesina* and should be reanalyzed (Grayson, in press a).

[b]Harlan's ground sloth continues to be referred to as both *Glossotherium* (e.g., Yates and Lundelius, 2001) and *Paramylodon* (e.g., McDonald, 1995).

[c]Genus survives outside of North America.

[d]Classification and spelling of *Hydrochoerus* follow Wilson and Reeder (2005). References: (1) Gillette et al. (1999); McDonald et al. (2001); (2) Stock (1931), Harrington (1933); (3) Stock (1920, 1925, 1936b); (4) Heaton (1985); (5) Miller (1976); (6) Gillette and Madsen (1992), Madsen 2000a); (7) Dansie et al. (1988); Livingston (1992b); (8) Jefferson and Tejada-Flores (1993); (9) Orr (1969), Adams (1979); (10) Mawby (1967); (11) Huckleberry et al. (2001); (12) McDonald (2002); (13) Grayson (1985); (14) Hockett and Dillingham (2004); (15) Downs et al. (1959); (16) Gillette and Miller (1999); (17) Hattori (1982), Dansie and Jerrems, in press; (18) Nelson and Madsen (1978, 1980), Miller (2002); (19) Stock (1936a), Miller (1979); Mead et al. (1982); (20) Miller (1987).

Beringia and northeastern Mexico, they must also have been found in between these two places, and the Great Basin may have been within its range.

Nearly all other North American extinct Pleistocene mammals that are unknown from the Great Basin had distributions far to the north (for instance, the saiga, genus *Saiga*), or south and east of this region (for instance, the capybaras *Hydrochoerus* and *Neochoerus*, the pampathere *Holmesina*, the glyptodont *Glyptotherium*, and the long-nosed peccary *Mylohyus*). Late Pleistocene tapirs come close—Arizona and southeastern California—but there is no suggestion that they came close enough to have entered the Great Basin (Graham, 2003).

In addition to the 19 extinct Pleistocene mammalian genera that are known from the Great Basin, there are also three well-defined extinct species of mammals belonging to extant genera that are known from here (Table 1). Harrington's mountain goat (*Oreamnos harringtoni*) was first described from Smith Creek Cave, Snake Range, eastern Nevada (Stock, 1936a). It is now known to have been distributed from at least the central Great Basin into northern Mexico and to have survived until shortly after 11,000 yr BP (Mead, 1983; Mead et al., 1986, 1987; Mead and Lawler, 1994). The other two extinct species, dire wolf (*Canis dirus*) and American lion (*Panthera leo*), seem to have been quite rare in the Great Basin. The dire wolf is known from sites scattered across the Great Basin, from the Mojave Desert in the south (identified as *Canis* cf. *dirus*: Jefferson, 2003) to Fossil Lake, Oregon in the north (Elftman, 1931; see the reviews in Nowak, 1979, Dundas, 1999). The American lion was also apparently widespread in the Great Basin, with sites scattered throughout much of Nevada (Jefferson et al., 2004).

I have mentioned that 16 of the 35 extinct late Pleistocene North American mammal genera have secure ^{14}C dates that fall between 12,000 and 10,000 yr BP (Grayson, in press a), the same general period of time that provides the first secure evidence for a human presence here (Meltzer, 2004). Of the 19 extinct genera known from the Great Basin, seven have ^{14}C dates from sites within the Great Basin that place them within the same terminal Pleistocene period (Table 2). This is similar to the fraction of taxa that has been dated to this period for North America as a whole (16 of 35; $\chi^2 = 0.40$, $p > 0.50$). This similarity does not result from the fact that the Great Basin has provided the only terminal Pleistocene dates for these seven taxa; all but the shrub-ox *Euceratherium* also have terminal Pleistocene dates from elsewhere in North America. Whether this similarity reflects the chronological structure of late Pleistocene extinctions in North America or instead reflects the fact that the most abundant of these mammals have, in general, been easiest to date to the end of the Pleistocene cannot currently be resolved (Grayson and Meltzer, 2002, 2003; Grayson, in press a).

There is no way to assess the absolute abundances of these animals on the late Pleistocene Great Basin landscape. In an important paper, Mack and Thompson (1982; see also Knapp, 1996), observed that the structure of the arid steppe plant communities of intermountain western North America, marked by (among other things) caespitose grasses and a widespread cryptogamic crust, is not consistent with the presence of substantial herds of large mammals of any sort. The native grasses of this region do not tolerate heavy levels of ungulate grazing (and were rapidly replaced by alien species after the introduction of livestock), and cryptogamic crusts are rapidly destroyed by trampling. The paleontological and archaeological records available for the Great Basin are fully consistent with this argument.

Even though the absolute abundances of late Pleistocene mammals cannot be measured, relative abundances can be assessed by tallying the number of stratigraphically and geographically separate locations from which each of the extinct genera has been reported. The results, compiled primarily from FAUNMAP (1994), Jefferson et al. (1994), Jefferson et al. (2002), Jefferson et al. (2004), Gillette and Miller (1999), and Miller (2002), are shown in Fig. 2. This figure strongly suggests that horses, camels, mammoth, and helmeted muskoxen were the most abundant now-extinct mammals in the Great Basin during the late Pleistocene. These relative abundances are fairly similar to those for North America as a whole (Grayson and Meltzer, 2002), which suggest the most common now-extinct Pleistocene mammals to have been horse, mammoth, mastodon, and camel, in that order.

These numbers, however, ignore the fact that not all of these animals were distributed throughout the Great Basin during the late Pleistocene. The helmeted muskox, for

Table 2
Extinct mammal genera from the Great Basin with secure ^{14}C ages < 12,000 yr BP

| Genus	Illustrative site	^{14}C age	Reference
Nothrotheriops	Gypsum Cave, NV	$11,360 \pm 260$	Long and Martin (1974)
Arctodus	Huntington Mammoth Site, UT	$10,870 \pm 75$	Madsen (2000a)
Equus	Fishbone Cave, NV	$11,210 \pm 50$	Dansie and Jerrems (in press)
Platygonus	Franklin Peccary, ID	$11,340 \pm 50$	McDonald (2002)
Camelops	Sunshine, Long Valley, NV	$11,390 \pm 60$	Huckleberry et al. (2001)
Euceratherium	Falcon Hill, NV	$11,950 \pm 50$	Dansie and Jerrems (in press)
Mammuthus	Huntington Mammoth Site, UT	$11,220 \pm 110$	Madsen (2000a)

ID = Idaho, NV = Nevada, UT = Utah.
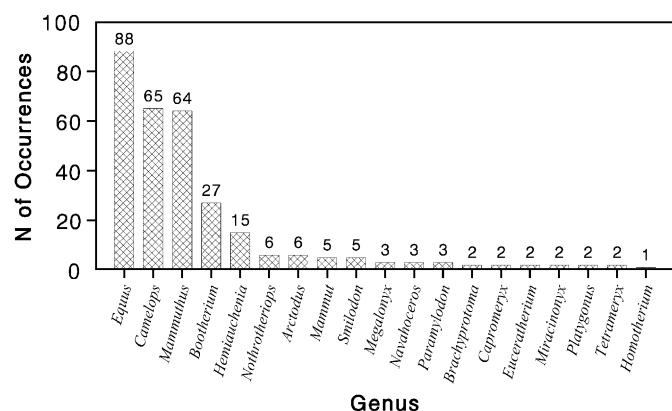
Fig. 2. The relative abundances of extinct Pleistocene mammals in the Great Basin; an "occurrence" refers to a stratigraphically or geographically distinct record for the taxon involved.

instance, has been reported only from the edges of Pleistocene Lake Bonneville, while the long-nosed peccary is known only from the far northern parts of the Great Basin—from Fossil Lake, Oregon (Elftman, 1931) and southern Idaho (McDonald, 2002). Similarly, ground sloths appear to have entered the Great Basin only along its edges: *Nothrotheriops* in southeastern California and southern Nevada and *Megalonyx* in southern Nevada and along the eastern edge of Pleistocene Lake Bonneville (McDonald, 1996, 2003; Gillette et al., 1999; McDonald et al., 2001). Horses, camels, and mammoth, on the other hand, seem to have been widespread throughout much of the region. Indeed, mammoths are known from elevations as high as 2740 m, and mastodon as high as 3000 m, on the Wasatch Plateau, Utah (Miller, 1987; Gillette and Madsen 1993; Madsen, 2000a).

Our understanding of the causes of late Pleistocene extinctions in the Great Basin is no more secure than it is for any other part of North America. There is, however, no reason to think that the demise of the Great Basin's late Pleistocene mammals was related to human hunting (e.g., Martin and Steadman, 1999). While people were most certainly living in the Great Basin between 12,000 and 10,000 yr BP (Beck and Jones, 1997), there is not a single secure association between artifacts and the remains of any extinct Pleistocene mammal here (Grayson and Meltzer, 2002; Huckleberry et al., 2001). Once the extinctions were over, the region was left with only five genera of large herbivores: bison (*Bison*), deer (*Odocoileus*), elk (*Cervus*), mountain sheep (*Ovis*), and pronghorn (*Antilocapra*).

4. The extant small mammals of the late Pleistocene and Holocene

As I have mentioned, the Great Basin probably has the most detailed late Pleistocene and Holocene small mammal record available for any place in the world. There are

multiple reasons for this. First, the general aridity of the Great Basin provides a superb setting for the preservation of fossil accumulations in sheltered settings. Second, the region has an abundance of caves with stratified deposits rich in vertebrate remains, the careful excavation and analysis of which has provided exquisite data on small mammal histories. Open sites have provided such information as well (e. g., Huckleberry et al., 2001; Mawby, 1967), but these sites provide far shorter chronological sequences and reduced chances for organic preservation. Third, the Great Basin is dotted with woodrat (*Neotoma*) middens, organic accumulations amassed by these rodents and cemented together by their urine (Betancourt et al., 1990). Because these accumulations can endure on the landscape for tens of thousands of years and because they may contain mammal bones, teeth, and fecal pellets, analyses of these middens have contributed remarkably precise data about the history of Great Basin mammals (e.g, Rhode and Madsen, 1995).

While our knowledge of late Pleistocene and Holocene small mammal history in the Great Basin is extensive, equivalent knowledge is not available for larger mammals, including ungulates. Unlike many other parts of the world, the Great Basin has not provided well-stratified cave sites that contain rich assemblages of large mammal remains. This situation may indicate that ungulates were not particularly abundant on Great Basin landscapes during the past 11,000 years or so. However, since human hunters provide the most obvious mechanism for introducing the remains of large mammals into Great Basin caves, the paucity of ungulate-rich cave sites here may also result from the fact that these animals were more often processed and utilized in open sites. Unless previously unknown sources of information on large mammal history in the Great Basin become available, building a detailed history of extant large mammals for this region will have to depend on accumulating separate records from disparate sites (e.g., Grayson (in press b) for bison).

4.1. Homestead Cave

The most detailed record of small mammal history in the Great Basin has been provided by Homestead Cave, northwestern Utah (Grayson, 2000a, b; Madsen, 2000b; see Figs. 1 and 3). Overlooking the Bonneville Salt Flats (the basin of Pleistocene Lake Bonneville) at an elevation of 1406 m, some 100 m above the valley floor, this site provided a finely stratified, extraordinarily rich vertebrate record. A total of ca 184,000 mammal bones and teeth were identified to at least the genus level from 15 of the 18 Homestead strata (strata XIII, XIV, and XV were not analyzed and only the kangaroo rat [*Dipodomys*] fraction from stratum X was identified). Raw data on the abundances of the mammals from Homestead Cave are presented in Grayson (2000b). Since the assemblages primarily reflect owl foraging, and secondarily the collecting activities of woodrats, nearly all specimens are of small

Fig. 3. The location of Homestead Cave (arrow) on Homestead Knoll; the linear features are terraces of Pleistocene Lake Bonneville.

mammals. The chronology of the site, discussed elsewhere (Madsen, 2000b), was initially based on 21 ^{14}C dates, and has now been augmented by an additional 12 dates (D.B. Madsen, pers. comm.). The following discussion begins with the history of five small mammals that are either particularly well-represented at Homestead Cave or for which the Homestead record has provided novel biogeographic insights.

4.2. Pygmy Rabbits (Brachylagus idahoensis)

North America's smallest leporid (mean body weight- < 500 g), pygmy rabbits are today discontinuously distributed throughout the botanical Great Basin and parts of immediately adjacent areas; there is also a disjunct population in southeastern Washington (Hall, 1981). These animals are heavily dependent on tall, dense stands of big sagebrush. Up to 99% of their winter diet may be drawn from this plant, they burrow in the friable substrate found beneath these stands, and they use the stands to escape from predators (Green and Flinders, 1980; Weiss and Verts, 1984; Dobler and Dixon, 1990; Verts and Carraway, 1998). As pygmy rabbit habitat has declined in abundance during recent decades, so has the abundance of the animals themselves. The Washington state populations are now listed as Endangered on the US Fish and Wildlife Service's Threatened and Endangered Species list and all Great Basin states list them as species of special concern (but see Sequin and Brussard, 2004). The prehistoric record for pygmy rabbits in the Great Basin documents that their history in this region since the end of the Pleistocene has been one of strong declines in abundance through time. This history is documented in detail at Homestead Cave and, with less precision, at a number of other sites in arid

western North America (see Supplementary Table 1 for data; see also Table 3).

At Homestead Cave, pygmy rabbits declined in abundance dramatically as the Pleistocene came to an end (Fig. 4). This decline was associated with the declining abundance of sagebrush habitat on the landscape, as is indicated by the histories of other small mammals in the Homestead fauna. For instance, as pygmy rabbits declined across the Pleistocene/Holocene boundary here, the abundances of the chisel-toothed kangaroo rat *Dipodomys microps* increased substantially (Grayson, 2000b). The specialized teeth of this xeric-adapted rodent allow it to thrive in vegetation dominated by saltbush (*Atriplex* spp.; see Kenagy, 1972, 1973), strongly suggesting that the decline in pygmy rabbit abundance in the Homestead area was associated with the replacement of sagebrush-dominated habitat by that dominated by *Atriplex*. Although there is a dearth of paleobotanical information for the Bonneville Basin for the 11,000–10,000 yr BP interval (Rhode, 2000; Wigand and Rhode, 2002), the mammals themselves speak plainly enough about the rise in *Atriplex* during this period.

The decline in pygmy rabbit abundance at the end of the Pleistocene at Homestead Cave is matched by the sequence available from Danger Cave, located across the Bonneville Salt Flats approximately 100 km to the west. The Danger Cave faunal assemblage, obtained from excavations conducted during the 1950s (Jennings, 1957), is not nearly as rich as that available from Homestead Cave, but it does contain 37 specimens of pygmy rabbit. Of these, 35 were recovered from stratum DI, which was deposited between ca 10,600 and 10,100 yr BP (Grayson, 1988; Rhode et al., 2005, in press).

The general history of pygmy rabbits in the arid west also documents a significant decline in the abundance of

Table 3
Southwestern extralimital records for *Brachylagus idahoensis* (Bi), *Marmota flaviventris* (Mf), and *Neotoma cinerea* (Nc)

Site	Age	Bi	Mf	Nc	Reference
Algerita Blossom Cave, NM	LW			X	Harris (1993a)
Anthony Cave, NM	LW			X	Harris (1977, 1984)
Baldy Peak Cave, NM	LW/H?		X	X	Harris (1984, 1990)
Big Manhole Cave, NM	LW		X	X	Harris (1984, 1993a)
Burnet Cave, NM	ND		X	X	Murray (1957), Schultz and Howard (1936)
Conkling Cavern, NM	ND			X	Harris (1977, 1984, 1993a)
Cylinder Cave, AZ	ND		X		Lange (1956)
Dark Canyon Cave, NM	LW		X	X	Harris (1977, 1984, 1990), Lundelius (1979)
Dry Cave, NM	LW		X	X	Harris (1970, 1977, 1984, 1985, 1987, 1990, 1993a,b)
Dust Cave, TX	LW		X		Harris (1990)
Fowlkes Cave, TX	LW		X		Dalquest and Stangl (1984)
Government Cave, AZ	ND		X		Lange (1956)
Hermit's Cave, NM	LW		X		Schultz et al. (1970)
Howell's Ridge, NM	ND			X	Harris (1977, 1984, 1985)
Isleta Cave 1, NM	ND			X	Harris (1984, 1985); Harris and Findley (1964)
Isleta Cave 2, NM	ND	X	X	X	Harris (1984, 1985, 1993a); Harris and Findley (1964)
Jimenez Cave, Chihuahua, Mexico	ND			X	Harris (1984), Messing (1986)
Keet Seel, AZ	LH		X		Lange (1956)
Lower Sloth Cave, TX	ND		X	X	Logan (1983)
Manzano Mountains Cave, NM	ND		X		Harris (1993a); Howell (1915)
Muskox Cave, NM	ND		X	X	Logan (1981)
New La Bajada Hill, NM	ND		X		Stearns (1942)
Papago Springs, AZ	LW		X		Czaplewski et al. (1999)
Pendejo Cave, NM	LW		X	X	Harris (2003)
Pratt Cave, TX	ND		X	X	Lundelius (1979); Lundelius, pers. comm. (2005)
Rampart Cave, AZ	LW		X		Mead and Phillips (1981); Van Devender et al. (1977)
San Josecito Cave, Mexico	LW		X		Arroyo-Cabrales and Polaco (2003)
Sheep Camp Shelter, NM	ND	X	X	X	Gillespie (1984); Harris (1990, 1993a)
Shelter Cave, NM	ND			X	Harris (1977, 1984, 1993a)
Tse'An Kaetan Cave, AZ	ND		X		Lange (1956)
Tse'An Olje Cave, AZ	ND		X		Lange (1956)
Tularosa River Cave, NM	ND		X		Harris (1993a)
U-Bar Cave, NM	LW		X	X	Harris (1987)
Upper Sloth Cave, TX	ND		X	X	Logan and Black (1979)
Vulture Cave, AZ	LW/H?		X		Mead (1981); Mead and Phillips (1981)
Woodchuck Cave, AZ	LH		X		Lange (1956); Lockett and Hargrave (1953)

AZ = Arizona; NM = New Mexico; TX = Texas; LW = Late Wisconsinan; ND = No Secure Age Known; LW/H? = Late Wisconsinan and possibly Holocene; LH = Late Holocene.

these animals as the Pleistocene came to an end. Fig. 5 shows the location of all archaeological and paleontological records for pygmy rabbits from within and near the Great Basin that can be placed within at least a general chronological framework (late Wisconsinan, ca. 40,000–10,000 yr BP; early Holocene, 10,000–7500 yr BP; middle Holocene, 7500–4500 yr BP; late Holocene, 4500 – latest prehistoric). Fig. 6 eliminates the late Pleistocene assemblages (the latest of which dates to ca 11,500 yr BP). Once these assemblages are removed, all pygmy rabbit records in the intermountain area south of Washington state are from within the current distributional range of the species (ca 12% of the records from the sites depicted in Fig. 6 are early Holocene in age).

Pygmy rabbits have also been identified from Isleta Cave 2, in west-central New Mexico (Findley et al., 1975; Harris, 1985, 1993a) and from Sheep Camp Shelter, northwestern New Mexico (Gillespie, 1984; Harris, 1993a; see Table 3). Although the age of these specimens is not known (both sites contain a combination of Pleistocene and Holocene material), they do document that the range of the species once extended far to the south and east of its current distribution. Given the fate of other southern extralimital pygmy rabbit populations, it seems most likely that the pygmy rabbit specimens from these sites are Pleistocene in age, but only by directly dating the specimens themselves can their ages be known.

Although my focus here is on the Great Basin, it is worth noting that much remains to be learned about the history of the disjunct and endangered pygmy rabbit population of eastern Washington state. Lyman (1991, 2004) has reviewed that history and documented that the prehistoric distribution of pygmy rabbits in eastern Washington was far broader than it is today. However, there are no records for this species between their current northern Great Basin boundary and the Columbia River. A full understanding of the history of this disjunction will not be possible until such records become available.

Fig. 4. Changing relative abundances of pygmy rabbits through time at Homestead Cave. Relative abundances calculated as the number of pygmy rabbit specimens divided by the total number of mammal specimens. NISP = number of identified specimens; numbers above bars provide the number of identified pygmy rabbit specimens per stratum.

While pygmy rabbit abundance in the Homestead Cave area declined dramatically at the end of the Pleistocene, they were still present during the early Holocene (Fig. 4). It is not possible to know from the Homestead Cave sequence when they were finally extirpated from the area, but it was clearly during the middle Holocene, between about 7500 and 4500 yr BP.

This local extinction event is matched by similar changes elsewhere in the Great Basin. At the Connley Caves, southcentral Oregon, 7.7% of all mammal specimens deposited before 7200 yr BP were of pygmy rabbits; 1.49% of those deposited after 4200 yr BP were of this species, a difference that is highly significant ($\chi^2 = 6.93$, $p < .01$; these sites lack deposits that date to between 7200 and 4200 yr BP: Grayson, 1979). Camels Back Cave, located 120 km south of Homestead Cave, does not have a rich record for pygmy rabbits, but all specimens of this species here were deposited prior to 8000 yr BP, even though the deposits at the site span the past 12,000 years or so (Schmitt et al., 2002; Schmitt and Lupo, 2005).

Thus, multiple sites show that the onset of the middle Holocene in the Great Basin was in general accompanied

Fig. 5. The distribution of dated archaeological and paleontological sites with identified pygmy rabbit remains in and near the Great Basin. The solid line represents the boundary of pygmy rabbit distribution in the Great Basin. A = Bechan Cave; see Table 4 for key to other sites.

Table 4
Key to Site Locations on Maps

Map number	Site
1	12640, White Mountains, CA
2	42Wb32, Great Salt Lake Valley, UT
3	Alta Toquima Village, Toquima Range, NV
4	Amy's Shelter, Snake Range, NV
5	Antelope Cave, Ivanpah Mountains, CA
6	Avocado Shelter, Quinn Canyon Range, NV
7	Bear River 1, eastern Great Salt Lake Valley, UT
8	Bear River 2, eastern Great Salt Lake Valley, UT
9	Bowling Dune, Fort Rock Basin, OR
10	Camels Back Cave, Camels Back Ridge, UT
11	Civa Shelter II, Golden Gate Range, NV
12	Conaway Shelter, Echo Canyon, NV
13	Connley Caves 3, 4, 5, 6, Fort Rock Basin, OR
1	Corral North, White Mountains, CA
1	Corral South, White Mountains, CA
14	Council Hall Cave, Snake Range, NV
1	Crooked Forks, White Mountains, CA
1	Crooked Forks 2, White Mountains, CA
15	Crystal Ball Cave, Snake Valley, UT
16	Danger Cave, Silver Island Range, UT
17	Deer Creek Cave, Jarbidge Mountains, NV
18	Devil Peak, Spring Mountains, NV
19	Dirty Shame Rockshelter, Owyhee Plateau, OR
1	Enfield, White Mountains, CA
20	Ephraim, Sanpete Valley, UT
21	Evans Mound, Parowan Valley, UT
22	Ezra's Retreat, Little Humboldt Valley, NV
23	Five Finger Ridge, Clear Creek Canyon, UT
24	Garrison 1, 2, Snake Valley, UT
25	Gatecliff Shelter, Toquima Range, NV
26	Hanging Rock Shelter, Hanging Rock Canyon, NV
27	Hidden Cave, Eetza Mountain, NV
28	Hogup Cave, Hogup Mountain, UT
29	Homestead Cave, Homestead Knoll, UT
30	Humboldt Lakebed Site, Humboldt Basin, NV
31	Hunt's Canyon Shelter, Monitor Valley, NV
32	Injun Creek, eastern Great Salt Lake Valley, UT
33	James Creek Shelter, Eagle Rock, NV
34	Jeans Spring Shelter, Toquima Range, NV
35	Kokoweef Cave, Ivanpah Mountains, CA
36	Last Supper Cave, Hell Creek Canyon, NV
37	Lead Mine Hills Cave, Lead Mine Hills, NV
38	Lovelock Cave, West Humboldt Mountains, NV
39	Mercury Ridge, Spotted Range, NV
40	Mescal Cave, Mescal Range, CA
1	Midway, White Mountains, CA
41	Mineral Hill Cave, Sulphur Spring Range, NV
42	Mitchell Caverns, Providence Mountains, CA
43	Mormon Mountain Cave, Mormon Mountain, NV
44	Nawthis Village, Fishlake Plateau, UT
45	Newark Cave, Newark Valley, NV
46	Newberry Cave, Newberry Mountains, CA
47	O'Malley Shelter, Clover Valley, NV
48	Owl Caves 1, 2, Snake Valley, NV
49	Pharo Village, Scipio Valley, UT
50	Pie Creek Shelter, Tule Valley, NV
51	Pintwater Cave, Pintwater Range, NV
52	Potosi Mountain Midden 2, Spring Range, NV
1	Pressure Drop, White Mountains, CA
53	Pyramid Lake Fishway, 26Wa1016 and 1020, Truckee River Valley, NV
1	Rancho Deluxe, White Mountains, CA

Table 4 (*continued*)

Map number	Site
1	Raven Camp, White Mountains, CA
54	Remnant Cave, Grouse Creek Range, UT
55	Rock Springs Bison Kill, Curlew Valley, ID
56	Serendipity Cave, Roberts Mountains, NV
1	Shooting Star, White Mountains, CA
1	Shortstop, White Mountains, CA
57	Silver Creek, Wasatch Range, UT
58	Slivovitz Shelter, Quinn Canyon Range, NV
59	Smith Creek Cave and Smith Creek Cave Packrat Midden SC1, Snake Range, NV
60	Snake Creek Burial Cave, Snake Valley, NV
61	South Fork Shelter, South Fork, Humboldt River, NV
62	Sunshine Locality, Long Valley, NV
63	Swallow Shelter, Goose Creek Mountain, UT
64	Toquima Cave, Toquima Range, NV
65	Triple T Shelter, Toquima Range, NV
66	Tule Springs, Las Vegas Valley, NV
67	Utah Lake, NV
68	Vista, Truckee Meadows, NV
69	Wagon Jack Shelter, Edwards Valley, NV

CA = California, ID = Idaho, NV = Nevada, OR = Oregon, UT = Utah.

by a decline in pygmy rabbit abundance, with Homestead Cave providing our most precise view of that decline. The reason for the decline is clear: the middle Holocene was a time of elevated temperatures and decreased effective precipitation in the Great Basin.

A wide variety of data documents this substantial climate change. The pollen profile from Hidden Cave (Carson Sink, western Nevada) shows that chenopod pollen increased substantially between 9000 and 8000 yr BP, suggesting the replacement of sagebrush steppe by saltbush-dominated desert shrub vegetation at this time (Wigand and Mehringer, 1985; Wigand and Rhode, 2002). To the northwest, the middle Holocene saw a substantial decline in the levels of Pyramid Lake, a decline that is associated in part with an estimated 3–7°C estimated increase in late summer or fall temperatures (Benson et al., 2002; Mensing et al., 2004). The Pyramid Lake decline is also associated with a significant drop in the level of Lake Tahoe, the source of the Truckee River, which in turn feeds Pyramid Lake. The Lake Tahoe decline is well-documented by the discovery of drowned pine trees rooted up to ca 12 m beneath the current surface of the lake and radiocarbon dated to between 5500 and 4240 yr BP (Harding, 1965; Lindström, 1990; Benson et al., 2002; Mensing et al., 2004).

To the southwest, in the White Mountains, pinyon (*Pinus monophylla*)-juniper (*Juniperus osteosperma*) woodland moved upslope some 250 m during this period (Jennings and Elliot-Fisk, 1993), at the same time as bristlecone pines (*Pinus longaeva*) were moving as much as 150 m upslope at higher elevations on the same mountain range (LaMarche, 1973). Far to the northeast, the Ruby
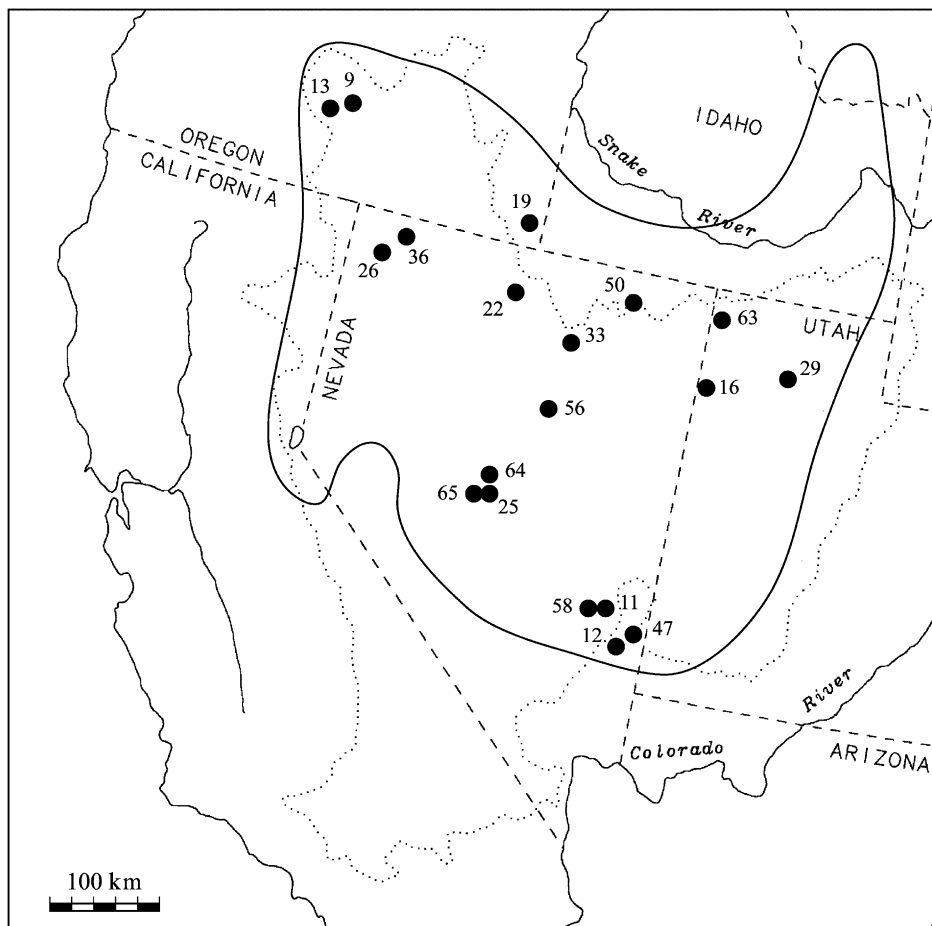
Fig. 6. The distribution of dated Holocene-aged archaeological and paleontological sites with identified pygmy rabbits in and near the Great Basin. See Table 4 for key to sites.

Marshes of northeastern Nevada shrank dramatically, and may have dried entirely, between ca 6800 and 4420 yr BP, a decline that followed a decrease in sagebrush pollen and an increase in the pollen of such plants as saltbush that began about 7700 yr BP (Thompson, 1992). Evidence of this sort, for a very warm and dry middle Holocene, is found throughout the Great Basin (Grayson, 1993; Feng and Epstein, 1994; Benson et al., 2002; Wigand and Rhode, 2002; Gu et al., 2005), and is tightly associated with the decline in pygmy rabbit abundance. This, in turn, was almost certainly caused in large part by a decline in the abundance of big sagebrush.

While current information suggests that late Pleistocene and middle Holocene declines in pygmy rabbit abundance were Great Basin-wide, there are strong reasons to believe that there were also time-transgressive declines in the abundances of these animals. In particular, the local abundance of pygmy rabbits may track the history of pinyon-juniper woodlands in the Great Basin, which today cover the flanks of many Great Basin mountains. Vegetation dominated by sagebrush and grasses is found below, above, and within the pinyon-juniper zone. Billings (1951, p. 117) observed long ago that this woodland appears to be

"merely superimposed upon a large sagebrush-grass zone which has wide elevational tolerances." We now know that he was right.

Utah juniper has a lengthy history in much of the Great Basin (Nowak et al., 1994; Wigand and Rhode, 2002), but *P. monophylla* was confined to the southern edges of the region until the latest Pleistocene (Thompson, 1990). As the Pleistocene ended, the species began to move differentially northward, reaching parts of the western Bonneville Basin by at least 6700 yr BP (Rhode and Madsen, 1998). Across the Great Basin, in the Carson Sink area, pinyon pine did not become an important part of the local vegetation, and may not even have arrived, until after 1500 yr BP (Wigand et al., 1995; Wigand and Rhode, 2002). Indeed, it may have reached its current distributional limits in northwestern Nevada only during the past few hundred years (Wigand and Nowak, 1992; Nowak et al., 1994).

As pinyon pine expanded across the Great Basin and combined with Utah juniper to form pinyon-juniper woodlands, the extent of sagebrush-grass habitat was vastly reduced. Given that sagebrush provides the habitat required by pygmy rabbits, it is extremely likely that the

time-transgressive formation of pinyon-juniper woodland also caused a time-transgressive decline in the abundance of pygmy rabbits.

Gatecliff Shelter, located in pinyon-juniper woodland in the Toquima Range, central Nevada, at an elevation of 2319 m (Thomas, 1983), has provided a faunal sequence that spans the past ca 7100 years and that seems to document this process in action. Thompson and Kautz (1983) analyzed pollen from the sediments of this well-stratified site and observed a sharp increase in both pinyon and juniper pollen shortly after 6000 yr BP. The earliest pinyon pine macrofossil from the site dates to 5350 yr BP (Rhode and Thomas, 1983). Together, these data indicate the formation of pinyon-juniper woodland in this part of the Toquima Range at ca 5500 yr BP.

Fig. 7 plots the relative abundances of pygmy rabbit specimens through time at Gatecliff from all strata with more than 150 identified specimens (data from Grayson, 1983) and shows that these abundances declined dramatically between 5350 and 5000 yr BP. Within a few hundred years of the deposition of the first pinyon pine macrofossil at Gatecliff, pygmy rabbit relative abundances had declined by some 80%. They never recovered.

Thus, the establishment of pinyon-juniper woodland in this part of the Toquima Range was tightly associated with the decline of pygmy rabbits, a decline that is best explained by the loss of sagebrush-grass habitat. As other detailed sequences of this sort become available from the Great Basin, it is reasonable to suspect that similar declines will be discovered, with the timing of the decline dependent on the timing of the local formation of pinyon-juniper woodland. This process likely occurred wherever woodland replaced lower-elevation sagebrush-grass vegetation in the Great Basin, no matter what the composition of that woodland.
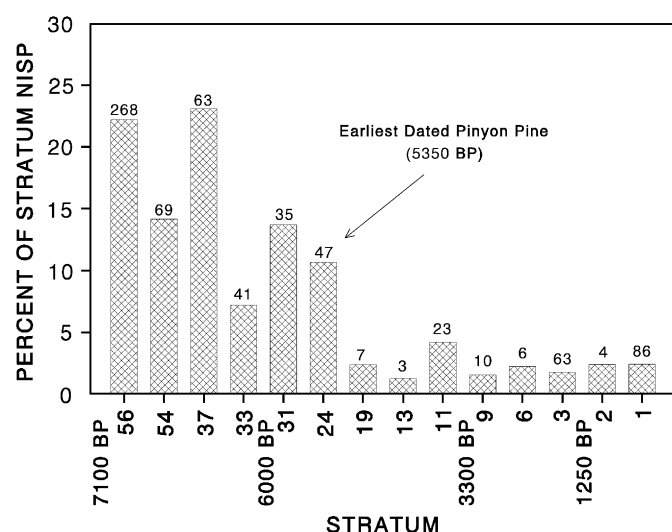
In short, there appear to have been at least three distinct types of decline in pygmy rabbit abundance in the prehistoric Great Basin, all associated with the loss of sagebrush habitat. Two of these seem to have been roughly synchronous across the Great Basin: one at the end of the Pleistocene, and one associated with the middle Holocene. The third decline, less fully substantiated, was time-transgressive, associated with the development of pinyon-juniper woodland within the region.

4.3. Yellow-bellied Marmots (Marmota flaviventris)

Yellow-bellied marmots are widely, but also discontinuously, distributed across intermountain western North America, reaching as far north as central British Columbia (Hall, 1981). Within the Great Basin, they are primarily confined to the higher elevations of mountains, though they descend into relatively low elevations in the northernmost reaches of this area. They are, however, absent from the southern Great Basin, most likely a result of the intense summer temperatures and dryness of this area.

The history of marmots at Homestead Cave is similar to that of pygmy rabbits (Fig. 8). Their numbers plummeted at the end of the Pleistocene but they remained locally present until sometime during the middle Holocene, when they became locally extinct. The extinction event was, presumably, causally related to middle Holocene heat and aridity.

Aspects of this history are replicated by other sites within the Bonneville Basin. At Danger Cave, marmots were present only in stratum DI, ca 10,600–10,100 yr BP

Fig. 7. Changing relative abundances of pygmy rabbits through time at Gatecliff Shelter in strata with more than 150 identified specimens. Relative abundances calculated as the number of pygmy rabbit specimens divided by the total number of small mammal specimens. NISP = number of identified specimens; numbers above bars provide the number of identified pygmy rabbit specimens per stratum.
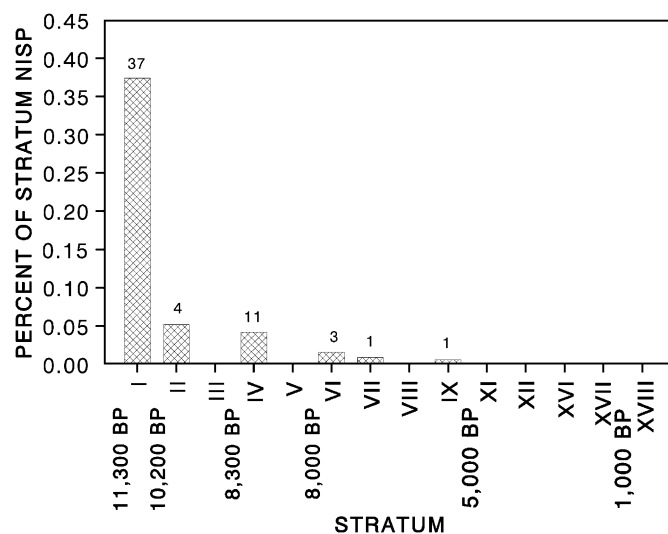
Fig. 8. Changing relative abundances of yellow-bellied marmots through time at Homestead Cave. Relative abundances calculated as the number of marmot specimens divided by the total number of mammal specimens. NISP = number of identified specimens; numbers above bars provide the number of identified marmot specimens per stratum.

(Grayson, 1988; Rhode and Madsen, 1998; Rhode et al., 2005, in press). At Camels Back Cave, they are represented in stratum IIA, deposited at ca 8800 yr BP (Schmitt et al., 2002; Schmitt and Lupo, 2005), but not after that time.

A third Bonneville Basin record for these animals is provided by Hogup Cave, located about 30 km to the northwest of Homestead Cave. Deposition at this site began about 8400 yr BP and continued through the rest of the Holocene. Unfortunately, the site had been sufficiently disturbed, to judge by reversals in the radiocarbon record, that little faith can be placed in much of the stratigraphy that it provided (Aikens, 1970, p. 27). The site does, however, document that marmots were locally present between 8400 and 6200 yr BP and that they have been absent for the past 3000 years and perhaps longer (Aikens, 1970; Durrant, 1970). Marmots do not occur in the lower elevations of the Bonneville Basin today; the full set of records from this area suggests that their disappearance here may have been time-transgressive, occurring between 10,000 and 6,000 yr BP.

I have already observed that the decline in pygmy rabbit abundance at the end of the Pleistocene at Homestead Cave and elsewhere in the Great Basin is associated with the loss of pygmy rabbit populations south of their current distributional boundary. The same is true for marmots (Figs. 9 and 10; ca 13% of the records from the sites depicted in Fig. 10 are early Holocene in age [Supplementary Table 1]).

It has long been known that marmots had once existed far to the south and east of their modern range (e.g., Schultz and Howard, 1936). Today, the southernmost extralimital record for these animals is from San Josecito Cave, Mexico (Arroyo-Cabrales and Polaco, 2003), with numerous occurrences known from Arizona, New Mexico, and Texas (Table 3). Unfortunately, most of the southern extralimitals are very poorly dated and it is often impossible to know even whether a given occurrence is Pleistocene or Holocene in age. However, in nearly all cases, those that can be placed in time are of Pleistocene age. The Pratt Cave (Guadalupe Mountains, western Texas) specimen was initially reported as being late Holocene in age (Lundelius, 1979), but it is now recognized that it may owe its stratigraphic position to post-depositional disturbance of Pleistocene deposits (Lundelius, pers. comm.) The most recent of the dated southern Pleistocene extramilimitals is from Dry Cave, New Mexico, and falls at $14,470 \pm 250$ yr BP (Harris, 1985), but so few of the Pleistocene occurrences have been precisely dated that
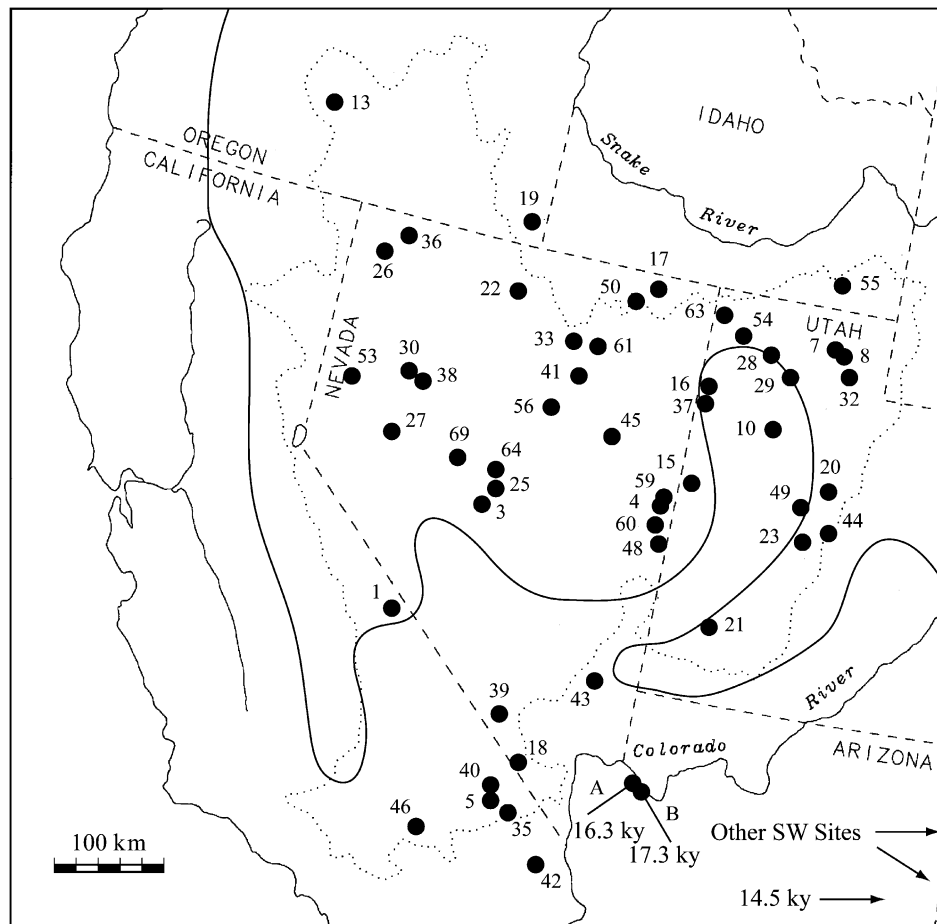

Fig. 9. The distribution of dated archaeological and paleontological sites with identified yellow-bellied marmot remains in and near the Great Basin. The solid line represents the distributional boundary of marmots in the Great Basin. A = Rampart Cave; B = Vulture Cave; see Table 4 for key to other sites.
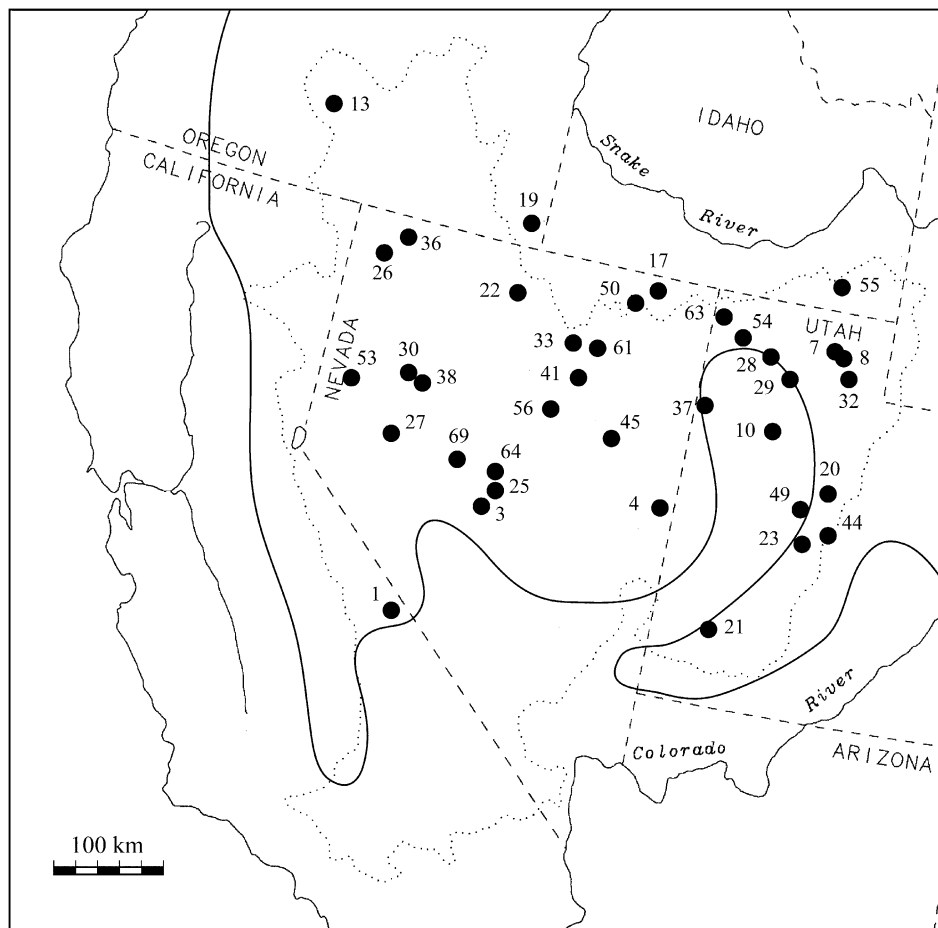
Fig. 10. The distribution of dated Holocene-aged archaeological and paleontological sites with identified yellow-bellied marmot remains in and near the Great Basin. See Table 4 for key to sites.

there is no reason to think that they did not survive later than this. Of the extralimitals shown in Fig. 9, only those from Rampart Cave (16,330±270 yr BP: Van Devender et al., 1977) and Vulture Cave (17,290±240: Mead and Phillips, 1981) have associated chronometric dates. All the others extralimitals on Fig. 9 are certainly late Wisconsinan in age, but that is all that can be said.

Removing the late Wisconsinan records also removes nearly all of the southern extralimitals, much as was the case with pygmy rabbits (Fig. 10). Unlike the situation with pygmy rabbits, however, there are Holocene southern extralimital records for marmots, though their meaning is unclear. All of these records are from the Tsegi Canyon area of far northeastern Arizona, approximately 125 km southwest of the closest known modern populations of *M. flaviventris* (Hall, 1981). Kidder and Guernsey (1919) reported the presence of "*Marmota* sp." in archaeological sites they excavated here, but they did not indicate which site or sites had provided this material. All of the possibilities, however, are very late Holocene in age. Lange (1956) reported the presence of a single *M. flaviventris* mandible from excavations that had been conducted in 1934 at the Puebloan site of Kiet Seel, dated to AD

950-1300 (Dean, 1969). The precise location from which the specimen came within this very large site is unknown (Lange, pers. comm.). Finally, Lockett and Hargrave (1953) reported the presence of "*Marmota*" from Woodchuck Cave, dated to ca AD 200. This site contained a number of human burials, nearly all of which were accompanied by grave offerings. Two of these burials contained marmot mandibles that seem to have been grave goods. Since the Woodchuck Cave burials also included materials that had been transported long distances—*Olivella* and *Conus* shells, for instance—it is very possible that the marmot mandibles had also been brought in from afar.

The curation of small mammal mandibles in western North America is well-described ethnographically and archaeologically. Lagomorph mandibles, for instance, were used as pressure flakers in stone tool manufacturing (Echlin et al., 1981), marmot teeth were used as dice in gambling games (DeBoer, 2001), and carefully detached marmot mandibles have been described from prehistoric Great Basin archaeological sites (Grayson, 1988). Since this is the case, and since the contexts from which the Kidder and Guernsey (1919) and Kiet Seel specimens came

is unknown, none of these records can be taken as providing secure evidence of the presence of extralimital late Holocene marmots in northeastern Arizona.

In short, the abundance of yellow-bellied marmots in the Great Basin declined dramatically at the end of the Pleistocene. This decline appears to have coincided with the northward retreat of marmots to within their current distributional boundary. Clearly, though, additional chronometric dates are needed to determine the precise timing of this retreat. The only Holocene marmot specimens known from south of their current boundary are those from northeastern Arizona and these may represent long-distance transport by people. In at least some parts of the Great Basin, local populations of marmots were extirpated during the middle Holocene, and it seems very likely that the final disappearance of marmots from most of the area that was once covered by the waters of Lake Bonneville dates to this time period.

4.4. Bushy-tailed Woodrats (Neotoma cinerea)

Bushy-tailed woodrats are widely distributed in western North America, from northern New Mexico northwest to the Pacific Coast, and northwards to the Northwest Territories (Hall, 1981). They are widespread within much, though not all, of the Great Basin. As with the other mammals discussed here, bushy-tailed woodrats are found discontinuously within those parts of the Great Basin that fall within their general range. Toward the northern parts of the Great Basin, they can be found at nearly all elevations but they become increasingly restricted to higher elevations toward the south. For many years it had been assumed that bushy-tailed woodrat populations in the

mountains of the hotter and drier portions of the Great Basin were isolated by the valleys that separate them (e.g., Brown, 1971), but recent work strongly questions this assumption (Lawlor, 1998), including that which is discussed below.

The Homestead Cave record for *N. cinerea* differs in some significant ways from that for pygmy rabbits and marmots at this site. Given that bushy-tailed woodrats are animals of fairly cool environments, it is not surprising that they are common in late Pleistocene deposits here (Fig. 11). In fact, they are the most abundant mammal in deposits of this age (Grayson, 2000 a,b). Their numbers decline across the Pleistocene/Holocene transition, but much less dramatically than the declines seen for pygmy rabbits and marmots at this time (Figs. 4 and 8). Instead, their steepest decline occurs at 8300 yr BP. Sometime after that date, they, too, become a local victim of middle Holocene heat and aridity.

They did not, however, remain locally extinct. Stratum XVII at Homestead Cave, which was deposited shortly before 1000 yr BP, contains nine specimens of this animal, suggesting that *N. cinerea* recolonized this hot and dry region at about that time (the absence of *N. cinerea* specimens in stratum XVIII means little, since this stratum contained only a very small sample of vertebrate material). Confirmation that this was likely the case is provided by the fact that, in 1995, *N. cinerea* was discovered living within the cave itself (Grayson et al., 1996; Grayson and Madsen, 2000). In addition, a review of unpublished data available in the archives of the Utah Museum of Natural History by E. Rickart documented additional historic records for this animal in nearby low-elevation areas (Grayson et al., 1996).

Thus, the Homestead Cave record shows that bushy-tailed woodrats were extremely abundant in this area at the end of the Pleistocene; that they declined, though not precipitously, at the very end of the Pleistocene; that they remained fairly common here during the early Holocene; and, that they were extirpated sometime during the middle Holocene. Then, perhaps shortly before 1000 yr BP, they recolonized the area and remain here today. Given the general perception that *N. cinerea* is an animal of much cooler and moister habitats, the discovery of this recolonization event, and of their current presence in the area, was a surprise.

Other stratified histories for *N. cinerea* within the Bonneville Basin parallel the Homestead Cave record reasonably well. At Danger Cave, bushy-tailed woodrats were common in stratum DI (10,600–10,100 yr BP: Grayson, 1988; Rhode and Madsen, 1998; Rhode et al., 2005, in press). Unlike the situation at Homestead Cave, however, their abundance at Danger Cave dropped sharply at the end of the Pleistocene, though local extinction occurred during the middle Holocene here also. There were three specimens of *N. cinerea* in late Holocene deposits at Danger Cave but these may reflect disturbance in the site (Rhode et al., in press). These animals have not been
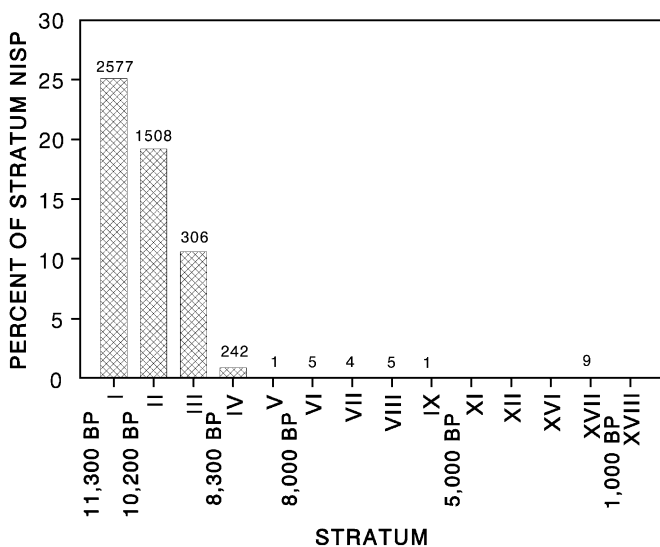
Fig. 11. Changing relative abundances of bushy-tailed woodrats through time at Homestead Cave. Relative abundances calculated as the number of *N. cinerea* specimens divided by the total number of mammal specimens. NISP = number of identified specimens; numbers above the bars provide the number of identified *N. cinerea* specimens per stratum.

reported from the Silver Island Mountains, though they are present in the nearby Pilot range (Rickart, 2001).

Camels Back Cave, to the south of Homestead Cave, has a bushy-tailed woodrat record that is quite similar to that provided by Homestead Cave. They are common in Camels Back stratum I, which appears to span the Pleistocene/Holocene transition and dates to as late as 9560 yr BP (Schmitt et al., 2002; Schmitt and Lupo, 2005). They decline during the early Holocene, dropping dramatically in abundance at about 8800 yr BP, about the same time as the similar decline at Homestead Cave. Then, and just as at Homestead, they become locally extinct during the middle Holocene. Between 7600 yr BP and latest prehistoric times, only two specimens of *N. cinerea* were deposited in the site; they are not known to exist in the area today.

Finally, at Pintwater Cave, on the eastern edge of the hydrographic Great Basin in the northern Mojave Desert, small numbers of bushy-tailed woodrats were deposited between 32,000 and 8300 yr BP (Hockett, 2000). Their regional extirpation here thus seems to have occurred at about the same time as it occurred in the Bonneville Basin far to the north.

There are not many records for bushy-tailed woodrats directly south of their southern Great Basin distributional boundary: only Mescal and Kokoweef caves in the Mojave Desert of southeastern California have, to date, provided them (Fig. 12: see Supplementary Table 1 for data). This is somewhat surprising, since bushy-tailed woodrats were found throughout much of New Mexico and into at least western Texas during the Pleistocene (e.g., Harris, 1984, 1985, 1993a; see Table 3). A possible late Pleistocene specimen has also been reported from Cueva Jimènez, Chihuahua, northern Mexico, but the identification is not secure (Messing, 1986; Arroyo-Cabrales and Polaco, 2003).

The chronology for these southern extralimitals is fairly weak, but none has been reliably dated to the Holocene (Table 3). Late Holocene *N. cinerea* has been reported from Pratt Cave but, just as with the *Marmota* specimen discussed earlier, these specimens may owe their position to disturbance (Lundelius, 1979, pers. comm.). Some years ago, Harris (1984, pp. 173-174) observed that in New Mexico, "*Neotoma cinerea* apparently was absent from . . . deposits that are surely Holocene", a statement that remains true 20 years later. Indeed, with the marginal exception of Pintwater Cave, today on the edge of
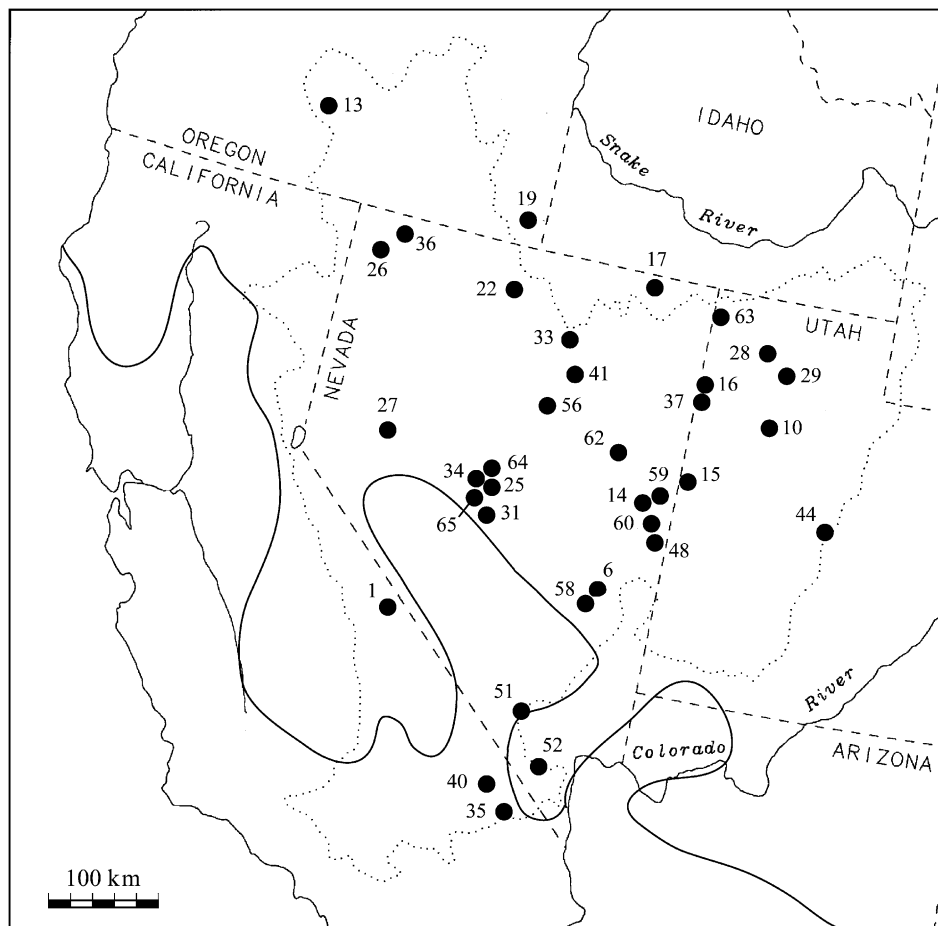

Fig. 12. The distribution of dated archaeological and paleontological sites with identified bushy-tailed woodrat remains in and near the Great Basin. The solid line represents the southern distributional boundary of bushy-tailed woodrats in the Great Basin. See Table 4 for key to sites.

N. cinerea range, that statement remains true of all southern extralimitals for this animal. The youngest such record falls at 10,730±150 (Harris, 1984, p. 170). All dated records that fall after that time are within (or just on the edge of) the southern modern boundary of the distribution of this animal. The extirpation of southern bushy-tailed woodrat populations mirrors the situation we have seen for pygmy rabbits and marmots.

4.5. Northern Pocket Gophers (Thomomys talpoides)

Four species of pocket gophers are currently found within the Great Basin, of which one, the northern pocket gopher, is confined either to the northern, cooler parts of this region, or, in the more southerly parts of its range, to higher, montane settings. When restricted to mountains within its general range, *T. talpoides* is routinely replaced in adjoining valleys by the larger Botta's pocket gopher *T. bottae*.

Aspects of the distribution of these two rodents have long been recognized as curious. In 1946, E. R. Hall observed that the pocket gopher of the tall and massive Snake Range of eastern Nevada (maximum elevation = 3982 m) is not *T. talpoides*, but instead the valley-bottom species, *T. bottae*. "I suppose," Hall (1946, p. 437) wrote, *T. bottae* "was the only kind of pocket gopher around the bases of Wheeler Peak and Mount Moriah [on the Snake Range] when the higher elevations of these peaks became available for gopher-occupancy" and, in the absence of *T. talpoides*, "worked slowly upward, developing populations adapted to living at these higher elevations as it went." Much the same can be said for the Toquima Range of central Nevada (maximum elevation = 3640 m). Here, Hall (1946) observed, *T. bottae* is also present, even though *T. talpoides* is the only gopher in the Toiyabe Range to the west and in the Monitor Range to the east. In both cases, Hall (1946) suggested, the absence of *T. talpoides* allowed *T. bottae* to occupy elevations and habitats it otherwise could not have occupied.

Recent work has documented that Hall's hypothesis concerning the ability of *T. bottae* to occupy higher elevations in the absence of *T. talpoides* is correct. Rickart (2001) has shown that in the absence of northern pocket gophers in the Stansbury Mountains, central Utah, Botta's pocket gopher extends 400 m higher than it does in the Uinta Mountains, where *T. talpoides* does occur; in the Deep Creek Range just east of the Utah–Nevada border, that figure is 1160 m; in the Snake Range, it is 1280 m. Rickart (2001) notes that this expansion in elevational range apparently reflects competitive release, just as Hall (1946) suggested.

When Hall (1946) made his insightful suggestions concerning the possible history of *Thomomys* in the Great Basin, nothing was known of that history. He could conclude that the "antiquity of a species, a presence of one species and absence of another, seems to have been one factor responsible for present occurrence" (Hall, 1946,

p. 437). He could not, however, turn to the fossil record to support or refute this supposition.

Although the prehistoric record for *T. talpoides* in the Great Basin is not as rich as that available for the other small mammals discussed to this point, it is rich enough to suggest that Hall's suggestions concerning the deeper history of this species were incorrect (Fig. 13; see Supplementary Table 1 for data).

Today, northern pocket gophers are found as far east as the North American Plains and as far south as northern New Mexico and Arizona. During the late Pleistocene, they were found as far east as Wisconsin and Missouri, and as far south as Texas and southern New Mexico (Harris, 1993a; FAUNMAP, 1994).

The late Pleistocene record for *T. talpoides* directly south of its modern Great Basin distributional limit is sparse but informative (Fig. 13). At Homestead Cave, northern pocket gophers are the only gophers present in stratum I, ca 11,300–10,200 yr BP (represented by only two specimens). All later gopher specimens from this site that could be identified to the species level are of *T. bottae* ($N = 967$). This was the first sequence from the Great Basin to suggest that Botta's pocket gopher replaced northern pocket gophers in a low elevation setting, presumably in response to climate change. This sequence also suggests that the montane distributional oddities noted by Hall (1946), involving the presence of *T. bottae* in mountains where *T. talpoides* would otherwise be expected, may not be due to the fact that *T. talpoides* never colonized these areas.

Pintwater Cave, southern Nevada, has provided a generally similar sequence. Here, northern pocket gophers are found in deposits that date to between 32,000 and 9000 yr BP but not after that time. All later pocket gophers from the site are *T. bottae* (Hockett, 2000). Unlike Homestead Cave, however, *T. bottae* is also present in strata that contained *T. talpoides*, documenting that both mammals were living close enough to this low-elevation (1270 m) site for their remains to have been incorporated into it. The animals overlap in distribution in some areas today (Durrant, 1952).

While there are no Pleistocene faunal sequences from in or near the Toquima Range, central Nevada, such data do exist for the Snake Range of eastern Nevada. Owl caves 1 and 2, in the Snake Valley just east of the Snake Range, contain *T. talpoides* (or *T.* cf. *talpoides*) of late Pleistocene age. Owl Cave 2 does not contain *T. bottae*, but Owl Cave 1 does, and all *T. bottae* remains from this site are from excavation levels higher than, and thus presumably younger than, those that provided *T. talpoides* (Turnmire, 1987). Not far to the south, Smith Creek Cave, on the eastern edge of the Snake Range, also provided *T. talpoides*, but not *T. bottae*, of late Pleistocene age; there are no stratigraphically secure records for either species from later deposits at the site (Bryan, 1979; Miller, 1979; Mead et al., 1982). Excavations at the Lehman Caves, in the southern Snake Range, have also provided the remains of
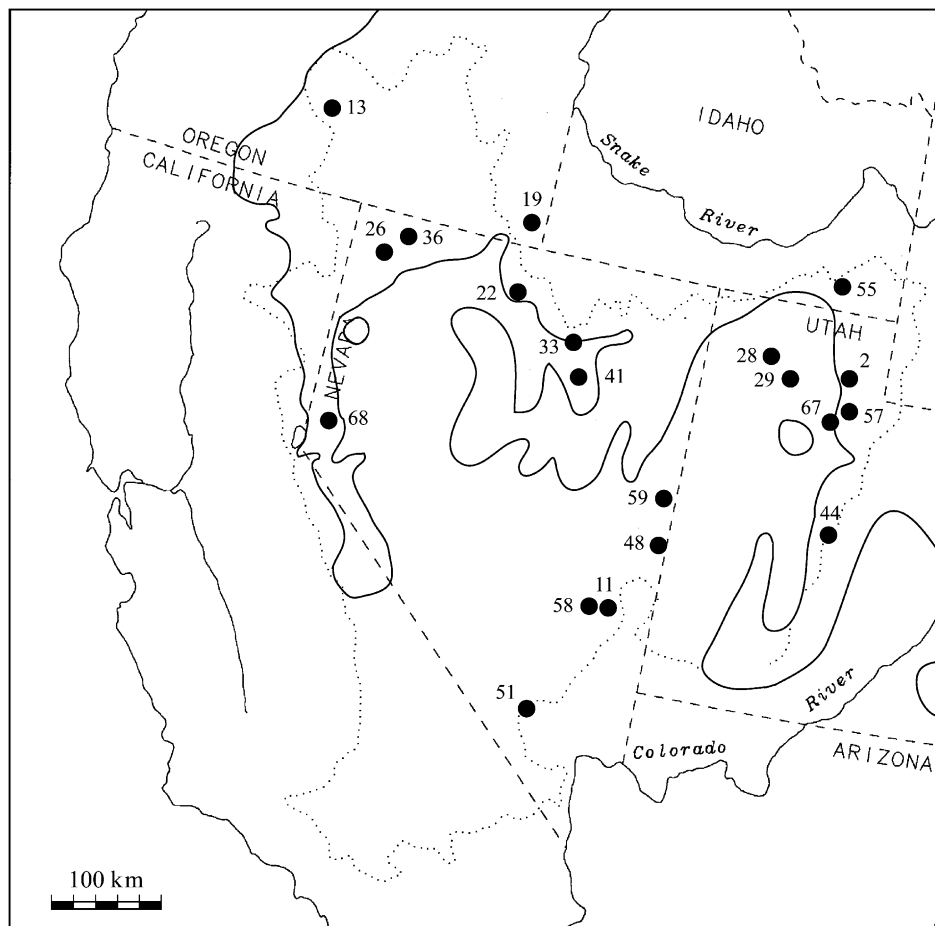
Fig. 13. The distribution of dated archaeological and paleontological sites with identified northern pocket gopher remains in and near the Great Basin. The solid line represents the southern distributional boundary of northern pocket gophers in the Great Basin. See Table 4 for key to sites.

northern pocket gophers but the age of these specimens is unknown (Rozaire, 1964; Ziegler, 1964).

It is this set of records from the general vicinity of the Snake Range that shows that Hall's intriguing speculations on the history of *T. talpoides* and *T. bottae* here cannot be correct. *T. talpoides* occupied at least the eastern edge of the Snake Range during the late Pleistocene, only to become extinct here, much as it was extirpated from the Mojave Desert in the vicinity of Pintwater Cave and from that part of the Bonneville Basin in which Homestead Cave sits. While it is no surprise that northern pocket gophers occupy neither the Mojave Desert nor the lower reaches of the Bonneville Basin, it is not at all clear why they do not inhabit the Snake Range. I return to this issue below.

As I have discussed, the end of the Pleistocene seems to have seen the extirpation of pygmy rabbits, marmots, and bushy-tailed woodrats from those parts of the Great Basin and immediately adjacent areas that are today south of their modern distributional boundary. The record is not quite so clear for northern pocket gophers. At Pintwater Cave, they are present in early, but not middle, Holocene deposits. In addition, there are three other Great Basin

sites that have provided the remains of *T. talpoides* south of their modern range in Holocene-aged deposits.

Two of these sites—Slivovitz Shelter, Quinn Canyon Range, southern Nevada, and Civa Shelter II in the nearby Golden Gate Range—are of late Holocene age. These records are potentially very important, given that the Quinn Canyon Range today supports only *T. bottae* and that the specimens are of relatively recent age. Unfortunately, the analysts indicate neither which skeletal elements formed the basis of the identifications nor how those specimens were identified (Kobori, 1979; Northey, 1979). As a result, the identifications cannot be evaluated and they should be revisited. Until this is done, the identifications should be held in abeyance.

There is, however, no reason to question the identification of *T. talpoides* from Hogup Cave (Aikens, 1970; Durrant, 1970). Although, as I have discussed, parts of the Hogup Cave depositional sequence were disturbed, both early and middle Holocene deposits here contain *T. talpoides* (there are no Pleistocene-aged sediments in the site), while later deposits contain only *T. bottae*. The sequence coincides well with pollen evidence for substantially decreased effective moisture during the

middle Holocene at Crescent Spring, which supported a small marsh just beneath the site (Mehringer, 1985). The absence of comparable water sources in the Homestead Cave area may explain the difference between the two sequences.

The prehistoric record for *T. talpoides* in and near the Snake Range shows that Hall's hypothesis for the presence of *T. bottae* in this range is incorrect. As I have mentioned, the Toquima Range presents a similar biogeographic mystery, since it is also marked by the presence of *T. bottae*, not *T. talpoides*. Unfortunately, the fossil record available for this region does not shed much light on the histories of these mammals here. The one deep sequence has been provided by Gatecliff Shelter (Thomas, 1983; Grayson, 1983). It documents that the only pocket gopher in the vicinity of the site during the past 7100 years or so was *T. bottae*. In the absence of a sequence that extends back into the Pleistocene, it is not possible to know whether *T. talpoides* occurred in this area, only to be replaced by *T. bottae*, perhaps at the end of the Pleistocene or during the early Holocene. Given the sequences in the southern and eastern Great Basin, however, this now seems more likely than Hall's initial hypothesis.

4.6. Dark Kangaroo Mice (Microdipodops megacephalus)

The kangaroo mouse genus *Microdipodops* is the only genus of mammal that is virtually confined to the Great Basin (Hall, 1981). Of the two species within the genus, only the dark kangaroo mouse *M. megacephalus* has a prehistoric record and even it is quite sparse.

Today, *M. megacephalus* is found on substrates ranging from the sandy edges of dunes to gravelly soils, and in vegetation ranging from sagebrush to greasewood (*Sarcobatus* spp.) and saltbush. With diets heavily dependent on seeds and insects, these generally bipedal mammals are found throughout much of the lower elevations of the central Great Basin but also occupy two disjunct locations, one along the California-Nevada border, the other in the Bonneville Basin of western Utah (Hall, 1946, 1981; O'Farrell and Blaustein, 1974; Verts and Carraway, 1998; see Fig. 14).

Five sites have provided prehistoric records for *M. megacephalus*, four of which are within, or on the edge of, its current range. Camels Back Cave, within the modern range of the animal, has provided records for *M. megacephalus* that are scattered throughout the sequence and
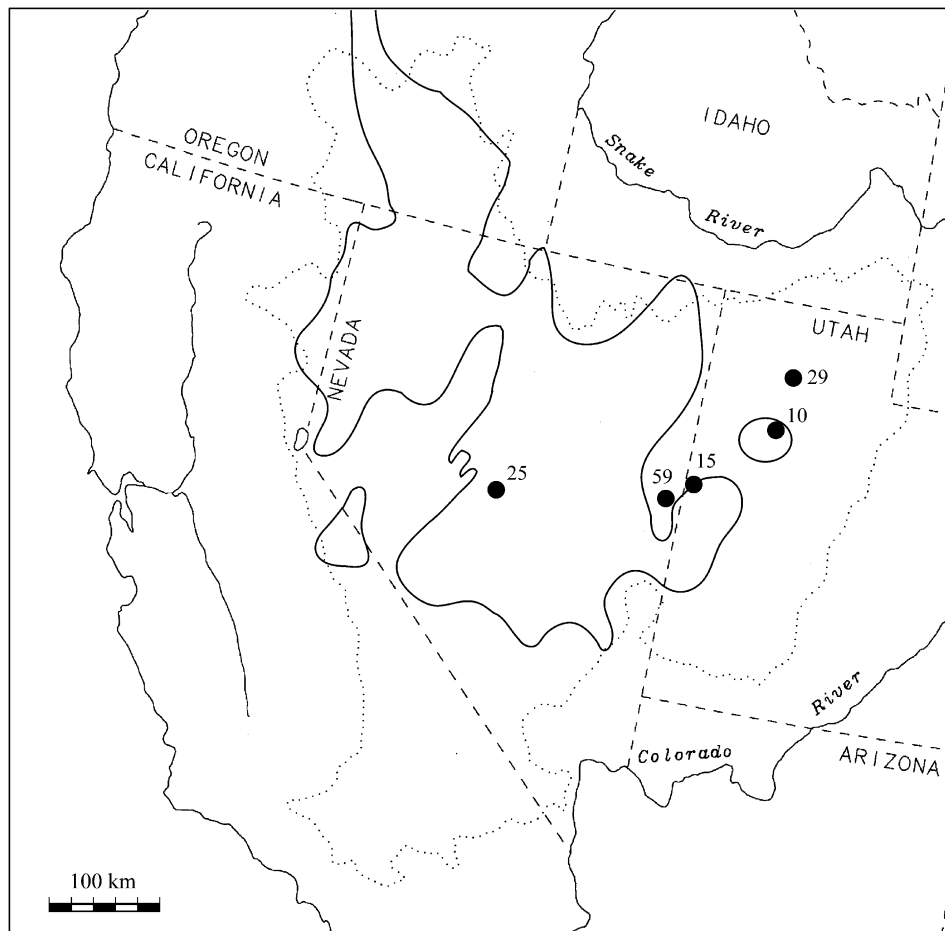

Fig. 14. The distribution of dated archaeological and paleontological sites with identified Great Basin kangaroo mouse remains in and near the Great Basin. The solid lines represent the distributional boundaries of Great Basin kangaroo mice. See Table 4 for key to sites.

that date to between the latest Pleistocene and the last few hundred years (Schmitt et al., 2002; Schmitt and Lupo, 2005). The temporal depth of these records suggest that the Utah disjunct is a true relict, as opposed to reflecting relatively recent colonization (but see also Schmitt and Lupo, 2005).

Homestead Cave may reveal when the Utah disjunction occurred. Dark kangaroo mice have never been reported from this part of Utah but Homestead Cave contains their remains in strata I and II, ca 11,300–8500 yr BP (Grayson, 2000b). They are not in any of the later, faunally rich deposits at the site. These animals thus seem to have become locally extinct here toward the end of the early Holocene, suggesting that this may also have been the period of time that saw the disjunction of the now-isolated Bonneville Basin populations of this animal. Although there are no prehistoric records that shed light on the disjunct population that occurs along the California-Nevada border, it would not be surprising to learn that this disjunction dates to the same period.

Thus, the Camels Back Cave record suggests the long-term existence of the disjunct Utah kangaroo mice, while the Homestead Cave sequence suggests that this disjunction occurred toward the end of the early Holocene.

4.7. American pikas (Ochotona princeps)

Small diurnal herbivores closely related to rabbits and hares, American pikas are today found across the mountains of western North America, from the southern Sierra Nevada and Rocky Mountains to central British Columbia. Within this general range, pikas are today tightly restricted to talus slopes adjacent to the vegetation that provides their diet. The paleontological record clearly documents that both the geographic and habitat restrictions are fairly recent. Pikas were found as far east as Ontario, Canada as recently as 9000 yr BP, though the species involved was larger than *O. princeps*. *Ochotona princeps* itself lived in the eastern United States until some 30,000 yr BP and perhaps later (Mead, 1987; Mead and Grady, 1996). In addition, American pika remains from woodrat middens in western North America show that at ca 12,000 yr BP, these animals were living at relatively low elevations in areas devoid of talus (Mead, 1987; Mead and Spaulding, 1995; Rhode and Madsen, 1995). Thus, one cannot infer from the geographic and habitat restrictions of today's American pikas where they may have lived in the past.
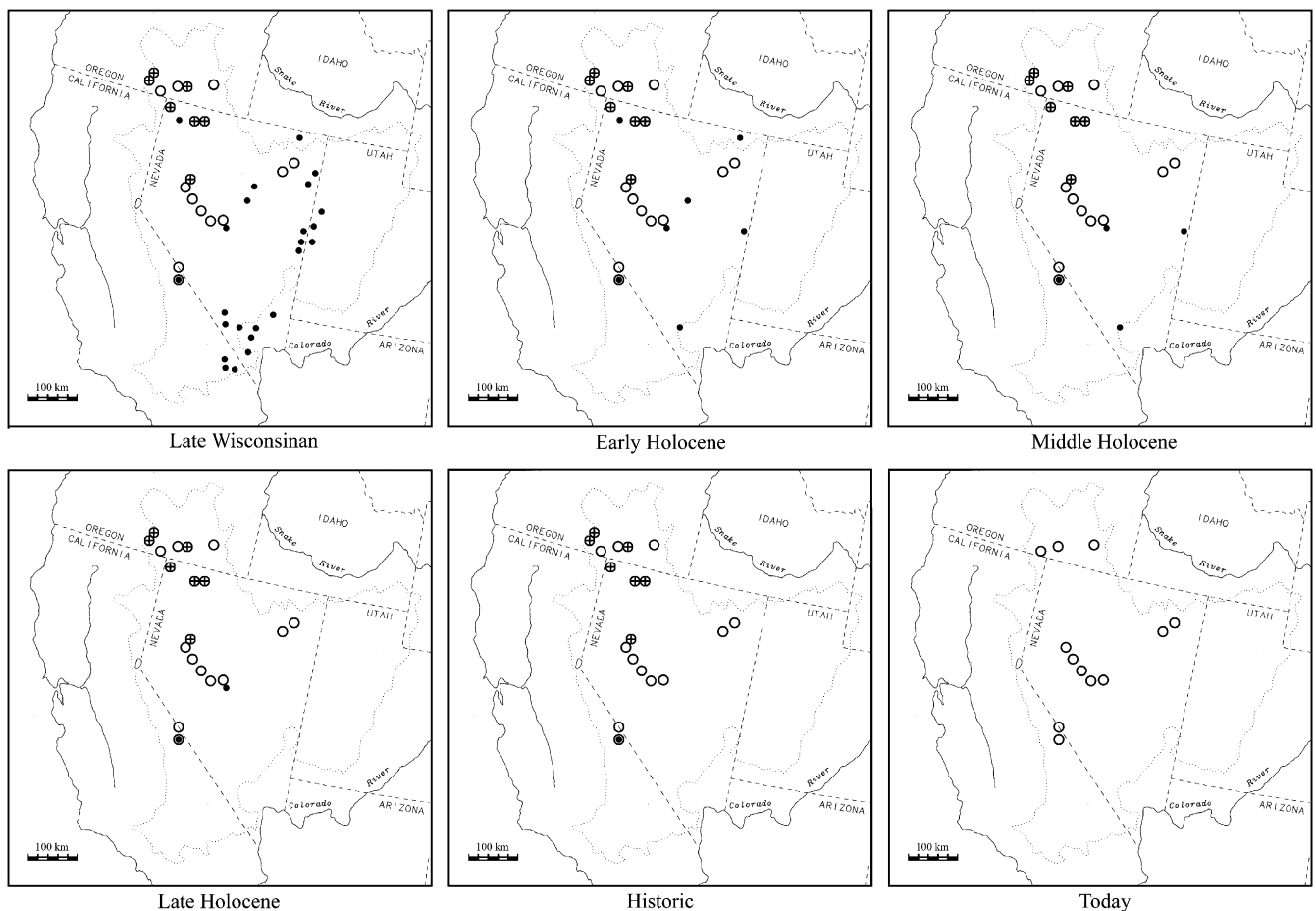

Fig. 15. The changing distribution of pikas through time in the Great Basin (from Grayson, 2005).

I have recently reviewed the history of Great Basin pikas in some detail (Grayson, 2005). Here, I repeat only one of the salient points that emerged from that review.

During the late Wisconsinan, pikas were far more widespread in the Great Basin than they are today. The sites that contain them occur at an average elevation of ca 1750 m, nearly 800 m lower than they now occur in this region. Since that time, the history of pikas in the Great Basin has been one of nearly relentless extinction, a process that has continued in recent decades (Beever et al, 2003; Grayson, 2005). Fig. 15 displays these losses. The data that lie behind this figure are presented and discussed in Grayson (2005), but that paper does not discuss one intriguing aspect of the pattern of pika extinction so evident in this figure.

Many of the losses shown in Fig. 15 are in the southern Great Basin or along the Utah–Nevada border. The southern Great Basin losses are easy to understand: the Mojave Desert simply became too hot and dry to support these animals. Much the same is certainly the case for the losses along the Utah-Nevada border. Some of the losses, however, are in the Snake Valley just east of the Snake Range, and on the east flank of the Snake Range itself (Thompson and Mead, 1982; Mead et al., 1982). They thus raise the same question that is raised by the late Pleistocene presence, and modern absence, of *T. talpoides* in the Snake Range. Pikas were present along the eastern edge of this range during the late Pleistocene and into the middle Holocene, the latest record falling at ca 6900 yr BP (Thompson, 1984, pers. comm.). Since this is the case, why are they not found in the Snake Range today? It is perhaps not coincidental that although yellow-bellied marmots are present in this range, they are vanishingly rare there (Floyd, 2004).

Mead et al. (1982) suggested that middle Holocene warmth may have reduced the size of Great Basin montane habitats sufficiently to drive higher-elevation extirpations, including those in the Snake Range (see also McDonald and Brown, 1992). This certainly remains a viable hypothesis (see Section 5.2), but it does not seem likely that it could also account for the absence of *T. talpoides* and the rarity of *M. flaviventris* in the Snake Range. I return to this issue in Section 5.1.

4.8. Mammals on mountaintops: a note on J. H. Brown's model of Great Basin montane mammal biogeography

Pikas were not present at Homestead or Camels Back caves although they are currently found in the Rocky Mountains to the east and are known from a series of Pleistocene localities along the Utah–Nevada border just to the west of the Bonneville Basin. Indeed, there are no prehistoric records at all for pikas in the Bonneville Basin except for those along its far western edge, nor do any mountains within the Bonneville Basin support them today. It now seems possible that *O. princeps* either did not colonize the Bonneville Basin during the Pleistocene,

or, if it did, did not survive into the latest Pleistocene and early Holocene, when fossil records become thicker on the landscape.

If this were the case, it may be related to the fact that of the 46 species of mammals found in the Uinta Mountains of northeastern Utah and surveyed by Rickart (2001), pikas are one of only four species that do not today descend to elevations of less than 2300 m. The other three—the water vole *Microtus richardsoni*, snowshoe hare *Lepus americanus*, and western heather vole *Phenacomys intermedius*—are also unknown from within the Bonneville Basin. All four, Rickart (2001) observed, today appear to be obligate montane species in this part of the world.

Pikas were one of a series of mammals used by J. H. Brown in 1971 to produce what soon became the most important analysis of Great Basin mammal biogeography to have ever appeared (Brown, 1971; see also Brown, 1978, Lomolino et al., 2006). Using concepts drawn from equilibrium island biogeographic theory, Brown (1971) examined the distribution of 15 species of "boreal" mammals—mammals that "occur only at high elevations in the Rockies and Sierra Nevada and are unlikely to be found below 7500 feet at the latitudes of the Great Basin" (1971, p. 469)—across 17 Great Basin mountains. His quantitative analyses of this distribution led him to conclude that these mammals reached the mountains during the Pleistocene, that the opportunities for colonization ended when the Pleistocene ended, and that since then, montane mammals have become differentially extinct across the ranges.

As Lomolino (2001, p. 5) has suggested, Brown's Great Basin analysis helped to revitalize the study of montane biogeography on a global basis. As part of this, it either directly spurred, or strongly influenced, a wide variety of detailed analyses of the past and present distributions of montane mammals in arid western North America (e.g., Grayson, 1977, 1987; Mead et al., 1982; Thompson and Mead, 1982; Davis and Dunford, 1987; Davis and Callahan, 1992; Grayson and Livingston, 1993; Lomolino and Davis, 1997; Lawlor, 1998; Grayson and Madsen, 2000; Rickart, 2001).

The end result of this work was to show that Brown's model was incorrect, and that it was so for two prime reasons. First, and necessarily unknown to him, the distribution of montane mammals across Great Basin mountains was inadequately known during the 1970s (e.g., Grayson and Livingston, 1993; Lawlor, 1998). As Lawlor (1998) has elegantly shown, as those distributions became better understood, quantitative support for Brown's model dissolved. At the same time, and as both Lawlor (1998) and Rickart (2001) have documented, it became clear that the Holocene history of Great Basin mountain faunas has been a dynamic one, shaped by both colonization and extinction events—some of which may have been quite recent.

Second, as Grayson et al. (1996), Lomolino and Davis (1997), Lawlor (1998), Rickart (2001) and others have observed, rather than acting as a homogeneous unit, each of the species within Brown's set of montane mammals can

be expected to have its own independent history. To use an example from Lawlor (1998), Nuttall's cottontails *Sylvilagus nuttallii* are routinely found below elevations of 2300 m (7500') in the Great Basin, but pikas are not. Different environmental tolerances of this sort can be expected to lead to differential colonization and extinction histories. As Rickart (2001) has noted, the relative influence of immigration and extinction can be expected to have varied through time, and across both mountain ranges and taxa.

Homestead Cave provides an example of these processes in action, since it provides histories for a number of the taxa included in Brown's initial analysis, including northern pocket gophers, yellow-bellied marmots, and bushy-tailed woodrats. Each has a distinctly different history here. Northern pocket gophers appear to have been extirpated at the end of the Pleistocene, and marmots and bushy-tailed woodrats at the end of the early Holocene. Marmots have not returned, but bushy-tailed woodrats have and they must have done so by colonization across very low-elevation settings (Grayson et al., 1996; Grayson and Madsen, 2000). Such individualistic species responses are well-known paleontologically (e.g., Graham, 1985, 1988, 1992). Because they are the rule rather than the exception, I suspect that every paleoecologist would agree with Brown's conclusion that "with the notable exception of rare obligate interdependencies, each kind of organism tends to shift its abundance and distribution individualistically as environmental changes affect its unique tolerances and requirements" (2004, p. 364; see also Brown and Lomolino, 2000).

5. Some unsolved problems

As does any part of the world, the Great Basin abounds in questions posed by both the histories and the current distributions of its mammals. Why did so many large mammals become extinct here toward the end of the Pleistocene and, not unrelated, when did those extinctions occur? Why did the survivors survive? What is the relationship between the genetic diversity shown by particular species of Great Basin small mammals and the known late Pleistocene and Holocene histories of those mammals? How common were recolonization events of the sort shown by *Neotoma cinerea* at Homestead Cave; which species were involved in those events; and, what is the relationship between those events and the ecologies of the species involved? Is it true, as now seems very likely, that only woodland species (sensu Lawlor, 1998) participated in such events while such subalpine species as pikas did not? Rather than pursuing these and related matters here, I am instead going to address two other issues raised by the review I have presented.

5.1. The Snake Range Conundrum

The small mammal histories available for the Snake Range appear odd in several ways. Pikas are not present on the range today but were there as recently as 6900 yr BP. Northern pocket gophers were there during the latest Pleistocene, only to be replaced by Botta's pocket gopher. The same general sequence—the replacement of *T. talpoides* by *T. bottae*—is evident at Homestead, Hogup, and Pintwater caves but in these cases upslope movement of *T. talpoides* was not possible since these sites are not located at the base of a massive mountain range. Although marmots are present on the Snake Range today, they are surprisingly uncommon there, a situation that has existed since at least the early years of the last century (Floyd, 2004).

Quantitative measures of Great Basin mountain range habitat diversity rank the Snake Range at the top of the list (Johnson, 1975; Lawlor, 1998). As a result, the distributional and abundance oddities that this range presents cannot be explained by the depauperate nature of the Snake Range landscape. Indeed, Floyd (2004, p. 477) observed that in Great Basin National Park, which includes nearly all of the southern Snake Range, marmots were "surprisingly" absent in habitat that often supports them elsewhere. That "elsewhere" includes the Deep Creek Mountains to the immediate north, where Floyd (1994) found marmots to be common, though pikas and northern pocket gophers are absent there as well (Lawlor, 1998, Rickart, 2001).

It is possible that the situation in the Snake Range reflects the results of stochastic processes and thus simply seems odd without actually being so. At the moment, however, there are no answers to the questions posed by the historic biogeography of small mammals in and near these mountains.

5.2. Global Warming and Great Basin small mammals

Deep Great Basin mammal histories can explain not only how present-day mammal distributions came about but can also be taken as predictive analogs if those histories occurred under conditions expected to recur in the future. Pygmy rabbits provide a prime example. As I have discussed, the late Pleistocene and Holocene histories of these animals in the Great Basin strongly confirm their dependence on *Artemisia tridentata* as inferred from studies of contemporary populations. In the past, declines in pygmy rabbit abundance were tightly tied to declines in *A. tridentata* abundance. Since analyses of the impact of global warming on Great Basin vegetation predict that increases in the mean temperature of the coldest month may cause creosote bush (*Larrea tridentata*) to expand northwards into the Great Basin at the expense of *A. tridentata*, historic and prehistoric analyses combine to suggest that significant declines in the abundance of pygmy rabbits in the Great Basin are to be expected under conditions of global warming (Shafer et al., 2001). Much the same outcome can be expected if, as some global warming models imply, woodland expands into sagebrush habitat in this region (Wagner et al., 2003).

Most attention has been paid to the possible implications of global warming for mammals that now tend to be confined to Great Basin mountains. Building on the conceptual basis of Brown's model of Great Basin mammal history, McDonald and Brown (1992) built a quantitative model to predict the number and identity of montane species that might be lost from 19 Great Basin mountain ranges given a 3 °C temperature increase. They explicitly recognized that the relatively simplistic nature of their model might limit its accuracy, but that did not make its results any less unsettling. Their model predicted that those mountains could be expected to lose between 9% (White-Inyo ranges) and 62% (Desatoya Range) of their montane mammal species. In addition, three species (*Zapus princeps*, *Spermophilus beldingi*, and *Lepus townsendii*) were predicted to become extinct across the entire Great Basin, while *Ochotona princeps* was predicted to survive only on the Toiyabe Range.

One of the explicit assumptions of the McDonald and Brown (1992) model is that there is "virtually no contemporary migration of these boreal species across the desert valleys separating mountain ranges." As I have discussed, we now know that, for these species as a group, this assumption is incorrect (Grayson et al., 1996, 2000b; Lawlor, 1998), even if it is almost certainly correct for some of these species (for instance, *Ochotona princeps*: see Lawlor, 1998; Rickart, 2001; Beever et al., 2003). Because this is the case and because other aspects of the original Brown model are now known to have been wrong, the predictions made by McDonald and Brown (1992) on the basis of this model are also likely to be wrong. The same is true for the simpler approach taken by Murphy and Weiss (1992), which used projected species-area curves to predict that 44% of montane mammal species across the Great Basin mountain ranges they analyzed would be lost with a temperature increase of 3 °C.

The question is how wrong these earlier analyses might be. In stark contrast to McDonald and Brown (1992), Lawlor concluded that Great Basin montane mammals may be "extinction-proof survivors" (Lawlor, 1998, p. 1126) and that "virtually no extinctions can be expected from a projected 3°C rise in temperature with global warming" (Lawlor, 1998, p. 1127). That nearly 30% of known Great Basin pika populations have been lost within the past century does not mean that Lawlor's assertion must be incorrect, since these losses may have been driven by such direct anthropogenic landscape modification as grazing pressure (Beever et al., 2003).

Both McDonald and Brown (1992) and Lawlor (1998) recognized that the impact of a hot and dry middle Holocene on Great Basin montane mammals might be relevant for understanding the future impact of global warming on extant populations of those mammals. McDonald and Brown (1992, p. 413) observed that "such a warm period might already have caused the extinction of the most susceptible species on each mountain range" but concluded that other factors, including the current small and localized nature of some montane mammal populations, implied that those populations would be highly vulnerable to future climate change. Lawlor (1998, p. 1126) argued that middle Holocene climates "must have culled vulnerable montane species" and used this observation to bolster his argument that global warming might have only modest impact on Great Basin montane faunas. The two sets of authors thus made very similar observations about the possible impact of middle Holocene climates on Great Basin montane mammals but drew very different conclusions concerning that impact.

Perhaps surprisingly, there is almost no direct empirical support for the argument that montane mammals were culled from high elevation settings in the Great Basin during the middle Holocene. This is because almost no early and middle Holocene high elevation archaeological and paleontological sites have provided relevant faunas from this area. Lawlor (1998) adopted the 2135 m contour to approximate the modern lower treeline on Great Basin mountains. If this lower boundary is used to define the minimum elevation of a high elevation site, then only Gatecliff Shelter (Toquima Range, 2319 m) and Serendipity Cave (Roberts Mountains, 2134 m) qualify. Unfortunately, while these sites record the prehistoric presence of species now absent from the mountains in which they are located, they do not tell us about the timing of these disappearances.

Serendipity Cave (Livingston, 1992a) contains two montane mammals—*Ochotona princeps* and *Mustela erminea*—that have not been reported historically from the Roberts Mountains (Lawlor, 1998). Pikas are represented by eight specimens, seven of which were deposited prior to the deposition of Mazama Ash (ca 6850 yr BP). *Mustela* cf. *erminea* is represented by a single specimen, also deposited prior to Mazama ashfall. The chronology available for Serendipity Cave, however, does not indicate whether the extinctions of these mammals occurred during or after the middle Holocene.

Gatecliff Shelter has the advantage of being finely stratified and very well-dated, and of having a sequence that begins during the middle Holocene (Grayson, 1983). It also contains a diverse variety of montane mammals, including, among other species, pikas, yellow-bellied marmots, and the western jumping mouse *Zapus princeps*. Of these montane mammals, two are unreported historically from the Toquima-Monitor ranges (Lawlor, 1998), the white-tailed jackrabbit *Lepus townsendii* and the heather vole *Phenacomys intermedius*. Heather voles, in fact, are not known to occur anywhere in the Great Basin today.

Gatecliff provided two specimens identified as *Lepus* cf. *townsendii*, from late Holocene deposits, but this identification was based on bivariate measurements and was not considered secure (Grayson, 1983, p. 120). The identification of *Phenacomys intermedius* at Gatecliff is, on the other hand, quite secure. Indeed, Gatecliff provides the only evidence that heather voles once existed in the Great

Basin during the Holocene. While other Great Basin sites have provided these animals (e.g., Smith Creek Cave, Mad Chipmunk Cave, and the Silver Lake site: see Supplemental Table 1 for references), they are undated or late Wisconsinan in age. The Gatecliff heather vole material dates to the middle Holocene (ca 5300 yr BP), but the timing of the extirpation of this species on the Toquima Range is unknown.

The changing relative abundances of pikas through time at Gatecliff may be telling us something about the reactions of these animals to mid-Holocene warming. Here, 95% of all pika specimens were deposited between 7100 and 5100 yr BP, compared to 27% of all small mammal specimens, a decline that may reflect the upslope movement of these animals in the Toquima Range (Grayson, 1983, pp. 122–123). Pikas, however, still exist in this range, so the Gatecliff record does not directly address the degree to which middle Holocene heat and aridity may have removed montane mammals from Great Basin mountains.

Rather than coming from high elevation settings, the detailed record that is available for Great Basin montane mammals during the early and middle Holocene comes from mountain flanks and valleys at elevations below 2135 m. This lower elevation record demonstrates that a variety of now-montane mammals, including pikas, marmots, and bushy-tailed woodrats, were extirpated from low elevation settings during the middle Holocene (see, for instance, the discussion of marmots and bushy-tailed woodrats at Homestead Cave in Sections 4.3 and 4.4). At the same time, these histories show that montane mammals on Great Basin mountains became increasingly isolated during the same period. However, it does not necessarily follow from this that extinction rates for these mammals on those mountains climbed during that time, although it certainly raises the likelihood that such extinction occurred.

Given concerns over the impact of global warming on Great Basin montane mammals (e.g., McDonald and Brown, 1992; Murphy and Weiss, 1992; Beever et al., 2003; Grayson, 2005), a high priority should be given to retrieving early and middle Holocene faunal records from the upper elevations of Great Basin mountains. Only such records have the potential of clarifying the magnitude of middle Holocene extinctions on Great Basin mountains and thus of providing the data needed to assess the likelihood that future warming will lead to widespread extinctions on these mountains.

As mentioned earlier, Great Basin mammal histories may only be relevant to predicting impacts of future environmental change if such change can be expected to approximate past conditions. However, it is not clear that global warming will produce climates similar to those that marked the Great Basin during the middle Holocene (Grayson, 2000a). There is full agreement that temperatures in this region will rise substantially by the year 2100, with recent estimates predicting maximum increases of ca. 7 °C in summer and ca 10 °C in winter (Hayhoe et al., 2004; see also Mearns, 2003). On the other hand, there is little

agreement concerning precipitation, with predictions ranging from little change of any sort to substantial increases in either summer or winter rainfall (but not both: see Hayhoe et al., 2004; Mearns, 2003). The middle Holocene, however, provides an analogue only for a future that is both hot and dry. As a result, all predictions concerning the future of Great Basin mammals based on the middle Holocene may be suspect. That possibility suggests that, from a Great Basin perspective, one of our most urgent conservation biological needs is for more secure climatic predictions for the coming century.

This is not to suggest that what we have learned about Great Basin mammal history merely tells us we need to know more. The species-level mammal histories that are now available from this region provide textbook examples of the individualistic responses of those species to changes in the nature of the landscapes on which they lived (see Section 4.8). As I have noted, scientists have long recognized that such individualistic species responses mark the paleontological record, and that any hope we might have of predicting the responses of biological communities to future change requires that those predictions be built a species at a time (e.g., Davis, 1976; Graham, 1988, 1992). This view now has substantial agreement from ecologists as well (e.g., Brown, 2004), although this is a task that is far easier to suggest than to accomplish (e.g., Brown et al., 1997).

We also know with certainty that declines in sagebrush-grass habitat in the prehistoric Great Basin have caused declines in the abundance of pygmy rabbits. It does not take deep insight to suggest that future declines in this habitat will necessarily cause declines in the abundances of these animals.

We know that the Holocene history of pikas in the Great Basin has been characterized by ever-increasing lower altitudinal limits and thus of ever-decreasing population numbers, trends undoubtedly caused by climate change. Given that this trend has continued in recent decades, it is very possible that these animals—the global warming canaries of western North America—are facing extinction unless strong action is taken to reduce anthropogenic impacts on them.

Finally, we know that in at least some parts of the Great Basin, middle Holocene increases in heat and aridity caused significant declines in the abundances of both yellow-bellied marmots and bushy-tailed woodrats. Even though we do not have sufficient knowledge to predict whether future global warming will cause montane populations of these, and other, Great Basin mammals to become extinct, we can predict with certainty that similar climate change would at least cause significant decreases in the distributions and abundances of such species in the Great Basin.

Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.quascirev. 2006.03.004.

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