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The Bonneville Estates Rockshelter rodent fauna and changes in Late Pleistocene–Middle Holocene climates and biogeography in the Northern Bonneville Basin, USA

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ABSTRACT

Excavations at Bonneville Estates Rockshelter, Nevada recovered rodent remains from stratified deposits spanning the past ca. 12,500 ^{14}C yr BP (14,800 cal yr BP). Specimens from horizons dating to the late Pleistocene and early Holocene include species adapted to montane and moist and cool habitats, including yellow-bellied marmot (*Marmota flaviventris*) and bushy-tailed woodrat (*Neotoma cinerea*). Shortly after 9000 ^{14}C BP (10,200 cal yr BP) these mammals became locally extinct, or nearly so, taxonomic diversity declined, and the region became dominated by desert woodrats (*Neotoma lepida*) and other species well-adapted to xeric, low-elevation settings. The timing and nature of changes in the Bonneville Estates rodent fauna are similar to records reported from nearby Homestead and Camels Back caves and provide corroborative data on terminal Pleistocene–early Holocene environments and mammalian responses to middle Holocene desertification. Moreover, the presence of northern pocket gopher (*Thomomys talpoides*) at Bonneville Estates adds to a sparse regional record for that species and, similar to Homestead Cave, it appears that the ca. 9500 ^{14}C yr BP (10,800 cal yr BP) replacement of the northern pocket gopher by Botta's pocket gopher in the Great Salt Lake Desert vicinity was also in response to climate change.

Introduction

Analyses of small-mammal remains from archaeological and paleontological sites in western North America have provided a wealth of information on climate change and regional shifts in mammalian biogeography and overall biotic communities (e.g., Grayson, 1981; Mead, 1981; Grayson, 1983; Lyman, 1983; Lyman and Livingston, 1983; Grayson, 1985; Heaton, 1985; Grayson and Livingston, 1989; Hockett, 2000; Lyman, 2004a,b; Blois et al., 2010; Lyman, 2011). In the Great Basin, especially the Bonneville Basin of western Utah, excavations in a number of stratified caves and shelters have recovered faunal remains dating from the late Pleistocene to the present and together offer one of the largest and most detailed small-mammal records in the world (Grayson, 2006). Most significant are Grayson's (1998, 2000a,b) identifications and analyses of the tens of thousands of small-mammal remains from Homestead Cave. By examining temporal changes in the presences and abundances of small-sized mammals adapted to montane and cool and moist environments, Grayson discovered that northerly parts of the Great Basin at the onset of the early Holocene were cool and moist. The extinctions or marked declines of these mesic-adapted mammals across low-elevation contexts, coupled with an overall decline in species richness, occurred by ca. 8300 ^{14}C yr BP (9300 cal yr BP; CalPal Online Radiocarbon Calibration program) in response to the onset of warmer and drier middle Holocene climates (Grayson, 1993; Lyman and O'Brien, 2005; Grayson, 2006, 2011).

Climatic implications of the late Pleistocene–early Holocene small-mammal record at Homestead Cave are in contrast to those drawn from the National Center for Atmospheric Research (NCAR) Community Climate Model (e.g., Thompson et al., 1993; Mock and Bartlein, 1995). Both are in agreement that the early Holocene in the northern Great Basin was relatively moist, but the Homestead data suggest that it was cool, while the NCAR climate model predicts that it was as warm, indeed warmer, than the middle Holocene. Given the array of empirical paleo-environmental data collected from across the region (e.g., Grayson, 1993; Rhode and Madsen, 1995; Grayson, 1998; Madsen et al., 2001), however, it has become clear that the area was moist and saw low temperatures. As Grayson (2000b:89) notes, "the mammal histories [alone] have been replicated in so many places by so many taxa that it seems unlikely that the problem lies with them, as opposed to lying with the models themselves."

Approximately 120 km to the south of Homestead Cave, archaeological excavations in Camels Back Cave recovered animal bones

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from stratified deposits dating to the latest Pleistocene through the latest Holocene (Schmitt and Lupo, 2005). Although the sample sizes per stratum are not nearly as large as those from Homestead Cave, the Camels Back fauna contains diverse assemblages of small mammals and temporal changes in the types and frequencies of rodents and lagomorphs mirror those at Homestead Cave and strongly support Grayson's (e.g., 1998, 2000a) findings. Specifically, mesic-adapted small mammals at Camels Back Cave declined significantly shortly before 8800 ^{14}C yr BP (9900 cal yr BP) and were extirpated ca. 8300 ^{14}C yr BP (9300 cal yr BP), there was a corresponding decline in taxonomic diversity at that time, and local populations were replaced by species adapted to more open xerophytic scrub communities at the beginning of the middle Holocene (Schmitt et al., 2002, 2004).

Recent archaeological excavations at Bonneville Estates Rockshelter along the central Nevada–Utah border recovered diverse assemblages of small-mammal remains from dry deposits. The fauna were collected from stratigraphic horizons spanning the last ≥12,500 ^{14}C yr BP (14, 800 cal yr BP) and offer a well-dated faunal record that provides exceptional data to compare with the neighboring records from Homestead and Camels Back caves. In the following we present late Pleistocene through early middle Holocene data from Homestead and Camels Back caves which illustrate temporal changes in the rodent fauna, and we discuss the implications of these changes for regional paleoclimatic and biogeographic interpretations. We then present information on the timing and nature of fossil accumulations in Bonneville Estates Rockshelter focusing on the recently analyzed rodent fauna.

Study sites

Homestead Cave (Fig. 1) is a stratified site on Homestead Knoll in the lower reaches of the Lakeside Mountains of northwestern Utah at an elevation of 1406 m (Madsen, 2000; Madsen et al., 2001). Excavation of a 1 × 1-m column passed through 3.1-mm (1/8-in.) mesh retrieved a remarkably large and diverse assemblage of rodent remains containing over 130,000 identifiable bones and teeth (Grayson, 2000a). A total of 18 stratigraphic horizons was identified and are controlled by 33 radiocarbon age estimates spanning the late Pleistocene (11,270 ± 135 ^{14}C yr BP [13,004–13,330 cal yr BP]) to the late Holocene (1020 ± 40 ^{14}C yr BP [907–969 cal yr BP]) (Madsen and Quade, 2000; Broughton et al., 2008).

Camels Back Cave is a small, north-facing portal in a xerophytic scrub community on Camels Back Ridge (elevation 1380 m) near the southeastern edge of the Great Salt Lake Desert (Fig. 1) (Schmitt et al., 2002; Schmitt, 2004; Schmitt et al., 2004; Schmitt and Madsen, 2005). More than 6600 identified rodent remains were retrieved from 6.3-mm (1/4-in.) mesh collections in a 2 × 4-m excavation block, and an additional 3921 identified specimens were collected from two 50 × 50-cm sample columns passed through 3.1-mm mesh (Schmitt and Lupo, 2005). The stratigraphic sequence of the Camels Back Cave deposits consists of 31 horizons controlled by 28 radiocarbon dates, with the deposits spanning from an undated layer resting atop Pleistocene Lake Bonneville beach gravels (ca. 12,500 ^{14}C yr BP [14, 800 cal yr BP]) to the present (Schmitt and Shaver, 2005).

Bonneville Estates Rockshelter (Fig. 1) is a massive south-facing cavern at an elevation of 1580 m along the western margin of the

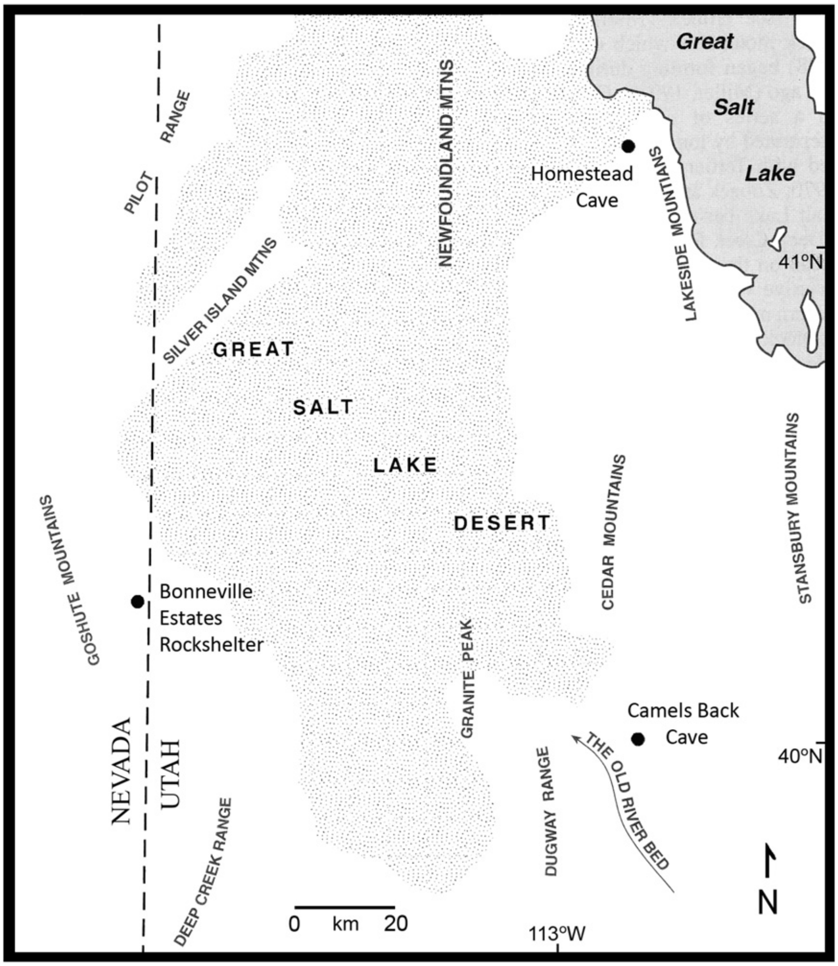

Figure 1. Map of the northern Bonneville Basin showing the location of the study sites.

Bonneville Basin (Goebel et al., 2003; Rhode et al., 2005; Goebel, 2007; Goebel et al., 2007; Graf, 2007; Hockett, 2007; Rhode and Louderback, 2007; Goebel et al., 2011). Its ceiling is approximately 10 m in height and the surface area of deposits inside the drip-line encompasses more than 250 m^2. Unlike Homestead and Camels Back caves which directly overlook deflated mudflats in valley bottoms, the shelter is in a more upland setting in the Lead Mine Hills of eastern Nevada; it is approximately 200 m higher in elevation than the two cave sites and is 7 km west of a spring-fed wetland (Blue Lake; Louderback and Rhode, 2009) which has been active since ca. 10,000 ^{14}C yr BP (11,500 cal yr BP). Modern vegetation in the shelter vicinity consists of a sparse desert shrub community containing saltbush (*Atriplex*), bitterbrush (*Purshia*), and patches of Indian ricegrass (*Achnatherum hymenoides*) and desert needlegrass (*A. speciosum*).

Bonneville Estates was subject to a series of large-scale investigations conducted between 2000 and 2009. Excavations centered on opening contiguous blocks in the eastern (ca. 15 m^2) and western (ca. 40 m^2) portions of the shelter that were connected by a 1-m-wide trench 8 m in length (Graf, 2007: Fig. 5.3) with all deposits passed through 3.1-mm mesh. These investigations retrieved artifacts and human subsistence residues spanning the past ca. 11,000 ^{14}C yr (12,900 cal yr BP) and include materials deposited by Paleoarchaic foragers in direct association with hearth features dating to the Younger Dryas stade (e.g., Goebel, 2007; Hockett, 2007; Goebel et al., 2011). Similar to Homestead and Camels Back caves, the Bonneville Estates deposits are well-stratified and the ages of most horizons are controlled by multiple radiocarbon estimates; to date, 63 organic samples have been subject to radiocarbon assay and have provided dates spanning from 12,390 ± 40 ^{14}C yr BP (14,270–14,937 cal yr BP) to 160 ± 30 ^{14}C yr BP (30–258 cal yr BP) (Goebel et al., 2007; Graf, 2007).

Methods

Analysis of the Bonneville Estates rodent fauna involved the identification of crania and mandibles retrieved from all excavations conducted from 2000 to 2008, and we identified and tallied all rodent specimens (including identifiable postcranial remains) from a contiguous 2 × 3-m block in the western portion of the shelter. Skeletal remains were identified by direct comparison with known specimens housed at the Conner Museum, Washington State University and those in our possession. All specimens were quantified by the number of identified specimens per taxon (NISP) (e.g., Grayson, 1984). In most instances species-specific identifications relied on differences in tooth (notably occlusal surface) morphology and specimen size, including measurements of molars and tooth rows. Our identification of the shelter's woodrat fauna involved inspection of the re-entrant angle of the anterior prism of the upper first molar and measurements of alveolar and molar occlusal lengths to distinguish *Neotoma cinerea* from the more diminutive *N. lepida* (Grayson, 1983, 1988). When present, we examined the morphology of lower first molars and upper third molars to separate sage voles (*Lemmiscus curtatus*) from meadow voles (*Microtus* sp.) (Barnosky and Rasmussen, 1988), and identifications of edentulous mandibles were based on the location of mandibular foramina (e.g., Grayson, 1983). White-footed mice were largely segregated on the basis of size, including comparisons of modern *Peromyscus* mandibular alveolar lengths (Grayson, 1985:147–149) with the recovered specimens, and we identified the shelter's pocket gophers (*Thomomys talpoides* and *T. bottae*) by examining rostral and lower fourth premolar morphology discussed in Thaeler (1980).

Analyses also involved taphonomic scrutiny of the bones for damage types and patterns that might provide information on accumulative mechanisms at the shelter, and it appears that most, if not all, of the rodents were deposited by non-human agents. Hockett (2007) reports cut marks and other human damage on a number of small-sized animal specimens (notably jackrabbit [*Lepus* sp.] and sage grouse [*Centrocercus urophasianus*]) from late Pleistocene–early middle Holocene deposits. It is possible that human foragers prepared rodents for food in a manner that left no taphonomic traces, but the shelter's assemblages show no unequivocal evidence of human transport or processing. Rather, some specimens are complete and undamaged and probably represent on-site deaths, while many others are fragmentary and exhibit chemical attrition in the form of overall polish, pitting, staining, and/or rounding of fracture surfaces characteristic of bones deposited in carnivore scatological droppings and egested raptor pellets (e.g., Andrews, 1990; Schmitt and Juell, 1994).

Given the wealth of rodent remains collected from limited excavations in the two caves, especially Homestead Cave, the paucity of rodent bones from expansive excavations at Bonneville Estates reflects a very different taphonomic history. Common small-mammal predators in the region include coyotes (*Canis latrans*), foxes (e.g., red fox [*Vulpes vulpes*] and swift fox [*V. velox*]), bobcats (*Lynx rufus*), and a variety of owls (e.g., screech owl [*Otus kennicotti*], short-eared owl [*Asio flammeus*], and barn owl [*Tylo alba*]) and some of these animals doubtless deposited prey remains in each of the sites. However, conspicuous differences in skeletal abundances strongly suggest that the extent of fossil accumulations in the three sites was disparate. Homestead Cave shows evidence for long-term owl pellet-bone accumulations (see Broughton, 2000; Grayson, 2000b; Livingston, 2000), including debris cones of droppings and disaggregated pellets below active roosts (Schmitt, 2000: Fig. 14), and at Camels Back Cave there is evidence of occupations by avian predators and especially *C. latrans* throughout most of its depositional history (Schmitt and Lupo, 2005). In contrast, it appears that Bonneville Estates did not support long-term roosts or nests of predators that rely on rodents for food, specimens were largely deposited by local terrestrial and avian carnivores during brief and sporadic visits to the site, and skeletal abundances suggest that these visits were most frequent ca. 11,000–6500 ^{14}C BP (12,600–7400 cal yr BP).

Using the identified rodent faunas, we investigate the timing and nature of changes in regional climates and biotic communities during the late Pleistocene–Holocene transition by examining within-site abundances of five mesic-adapted (MA) rodent species that were identified in each of the three sites (Table 1). These animals do not occur or are uncommon residents in the immediate vicinity of the sites today (Hall, 1946; Durrant, 1952) and our rationale for selecting these taxa is based on their habitat preferences and distribution in the modern Bonneville Basin. Two of these mammals—*Marmota flaviventris* and *N. cinerea*—occupy cool and moist settings in the region and predominantly occur in boreal habitats on Great Basin mountains (Hall, 1946; Brown, 1971; cf. Lawlor, 1998; Grayson and Madsen, 2000; Grayson, 2011). *Perognathus parvus* and *Reithrodontomys megalotis* largely occur in moist habitats containing a thick grass understory (Hall, 1946; Webster and Jones, 1982), and *L. curtatus* also inhabit mesic grasslands that contain dense stands of big sagebrush (*Artemisia tridentata*), accompanied by temperate winters and cool summers (e.g., Hall, 1946; Carroll and Genoways, 1980).

Homestead Cave and Camels Back caves

Excavations in Homestead Cave recovered 136,377 rodent bones and teeth identified to at least genus. Of these, 74,483 specimens representing a total of 21 different taxa were collected from the

Table 1
Identified Mesic-adapted (MA) Rodent Species from late Pleistocene–Early middle Holocene Deposits in Homestead and Camels Back Caves and Bonneville Estates Rockshelter.

Species	Common name
Marmota flaviventris	Yellow-bellied marmot
Neotoma cinerea	Bushy-tailed woodrat
Lemmiscus curtatus	Sage vole
Perognathus parvus	Great Basin pocket mouse
Reithrodontomys megalotis	Western harvest mouse

seven earliest strata dating from the late Pleistocene into the middle Holocene (ca. 6000 ^{14}C yr BP [6850 cal yr BP]). Figure 2 illustrates the relative abundance of the five MA species (Table 1) compared with all identified rodent specimens recovered from the early deposits in the cave. Although this combined rodent-only data represents a modification of previously reported analyses and comparisons (Grayson, 2000a,b; Schmitt et al., 2002; Grayson, 2011), the results are the same; there is a sharp decline in the abundances of MA species by approximately 9000 ^{14}C yr BP (10,200 cal yr BP), and they became locally extinct, or nearly so, by 8300 ^{14}C yr BP (9300 cal yr BP). Based on their modern habitat requirements and distributions, the presences and abundances of these MA rodents during the first few hundred years of the early Holocene strongly suggest that the Homestead Knoll vicinity was cool and moist and supported grasslands and stands of *Artemisia*, and their marked decline at the end of the period reflects the rather rapid onset of desertification, including the transition to more open xeric-adapted vegetation communities containing greasewood (*Sarcobatus vermiculatus*) and shadscale (*Atriplex confertifolia*) (Grayson, 2000a,b; Rhode, 2000; Madsen et al., 2001; Schmitt et al., 2004).

To investigate regional moisture history further, Grayson (1998, 2000b) also examined changes in small-mammal taxonomic richness (the number of species present) across the well-stratified deposits at Homestead Cave, including all rodents, hares, and rabbits. It is well known that under most circumstances there is a positive correlation between precipitation, productivity, and mammal species richness in arid environments (e.g., Brown, 1973; Meserve and Glanz, 1978; Abramsky and Rosenzweig, 1984; Rosenzweig, 1995). This relationship between moisture and small-mammal richness, or positive richness-response, is clearly evident at Homestead Cave as assemblages that date before ca. 8300 ^{14}C yr BP (9300 cal yr BP) are more rich than those that accumulated after a cool and moist eastern Great Basin was supplanted by increasingly warmer and drier environments (Grayson, 1998, 2000b; see also Lyman and O'Brien, 2005).

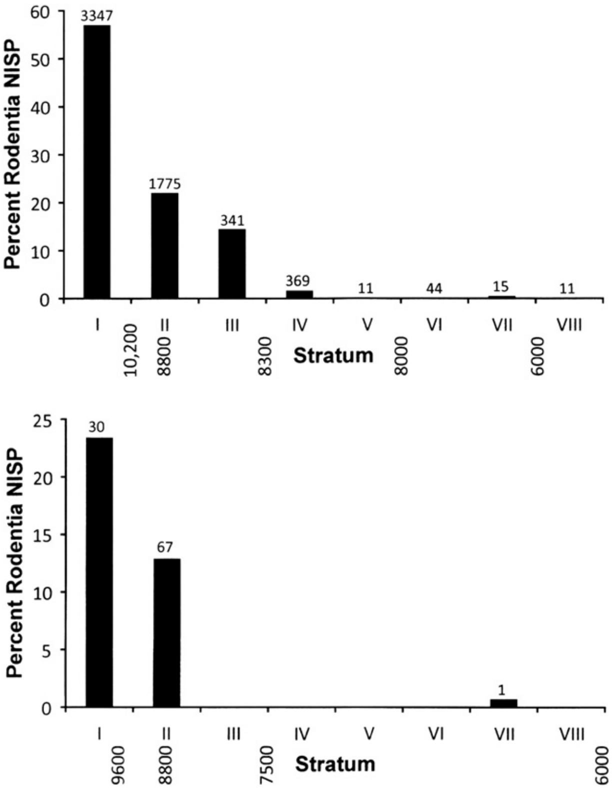

Figure 2. The relative abundance of five rodents well-adapted to cool and moist contexts (see Table 1) compared with all rodents identified to genera in the early deposits at Homestead (top) and Camels Back (bottom) caves. The numbers above the bars provide the total number of these specimens identified in each stratigraphic aggregate and the vertical numbers (bottom) provide ^{14}C yr BP ages.

Archaeological investigations at Camels Back Cave retrieved 1515 identifiable rodent specimens from the earliest deposits in strata I–VIII (Schmitt et al., 2002; Schmitt and Lupo, 2005). Although Homestead Cave has a significantly larger sample of identified specimens, the Camels Back Cave assemblage contains a similarly diverse array of species that are well-adapted to cool and moist contexts, and others that characteristically inhabit arid low-elevation settings. There are also some rather conspicuous changes in the presences and abundances of these animals through time. Figure 2 presents the relative abundance of the five MA rodents (Table 1) in the latest Pleistocene through early middle Holocene deposits at Camels Back Cave. As at Homestead Cave, these taxa were common during the early Holocene. Save for a single *P. parvus* specimen in stratum VII MA species became locally extinct by about 8300 ^{14}C yr BP (9300 cal yr BP), and there was a significant decline in small-mammal (rodent and lagomorph) taxonomic richness as cool and moist biotic communities were replaced by increasingly warmer and drier ones as the early Holocene came to an end (Schmitt et al., 2002; Schmitt and Lupo, 2005). In fact, small-mammal richness is greatest in the cave's late Pleistocene–early Holocene horizons I and II and together they contain larger numbers of species than those that accumulated throughout the remainder of the Holocene (Schmitt et al., 2002).

Bonneville Estates Rockshelter

The rodent fauna from Bonneville Estates Rockshelter consists of a small yet diverse assemblage of 1080 identified bones and teeth collected from deposits spanning the last ca. 12,500 ^{14}C yr BP (14,800 cal yr BP), with most specimens (NISP = 1008) recovered from late Pleistocene–middle Holocene horizons 20–11 (Tables 2 and 3). Like the neighboring caves, Bonneville Estates contains a diverse array of taxa well-adapted to montane and cool and moist habitats (e.g., *N. cinerea*, *M. flaviventris*, and *L. curtatus*), and species that are common residents of arid low-elevation environs (e.g., *Neotoma lepida*, *Urocitellus mollis*, and *Thomomys bottae*). Figure 3 illustrates the changing proportions of the five MA species in the late Pleistocene–middle Holocene deposits at the shelter. Similar to Homestead and Camels Back caves, there is a marked decline in these animals at approximately 9000 ^{14}C yr BP (10,200 cal yr BP), and by about 8300 ^{14}C yr BP (9300 cal yr BP) two of these species (*N. cinerea* and *R. megalotis*) became locally extinct while the others occur in low numbers extending into the middle Holocene. Given the more upland setting of Bonneville Estates Rockshelter and the proximity of Blue Lake, the somewhat inflated proportions of the MA rodents in the post-8300 ^{14}C yr BP deposits (horizons 16 and 14; Fig. 3) likely reflect the presence of patches of grasslands in the shelter vicinity for the next several hundred years. Most notable are the presences of *P. parvus* and *L. curtatus* (Table 2) who prefer moist grassland habitats, and it possible these rodents were taken by local avian/terrestrial predators foraging at Blue Lake where small ponds persisted into the early middle Holocene (Louderback and Rhode, 2009).

Regardless of this possible subtlety, changes in the Bonneville Estates rodent fauna provide corroborative data on Bonneville Basin mammalian biogeography and paleoenvironments and these shifts are particularly evident in comparisons of the shelter's abundant woodrat fauna. The remains of *N. cinerea* and *N. lepida* were collected throughout the deposits and represent the largest aggregates of specimens identified to species within a genus (Table 2). By comparing temporal changes in the ratio of *N. cinerea* (a mesic taxon) to both *N. cinerea* and *N. lepida* (a desert species), the results (Fig. 4) are again strikingly similar to those reported at the two neighboring cave sites (Grayson, 1998, 2000a,b; Schmitt et al., 2002; Schmitt and Lupo, 2005; Grayson, 2011); *N. cinerea* were most abundant during the cool and moist late Pleistocene–early Holocene, *N. lepida* populations expanded

Table 2
Numbers of identified rodent specimens by taxon in strata 20-12/11 (ca. 12,500–4500 ^{14}C yr BP) at Bonneville Estates Rockshelter.

Species	Stratum													Total
	20	19	18b	18a	18b/a	17b'	17b	17a	17[a]	16	14[b]	13	12/11	
Marmota flaviventris	2	2	3	2	–	1	–	–	–	–	1	–	–	11
Tamias sp.	–	–	–	1	–	–	–	–	–	–	–	–	–	1
Urocitellus sp. (large)	13	–	–	1	–	–	–	–	–	–	–	–	–	14
Urocitellus sp. (small)	13	2	5	1	1	1	–	–	3	2	4	3	1	36
Urocitellus cf. *mollis*	–	–	–	1	–	–	–	–	–	1	–	1	–	3
Urocitellus mollis	–	–	–	–	–	–	–	–	–	2	–	–	–	2
Thomomys sp.	23	7	18	34	7	12	–	6	18	17	18	3	5	168
Thomomys cf. *bottae*	–	–	–	–	–	–	1	–	–	–	3	–	–	4
Thomomys bottae	–	–	–	–	–	–	–	–	–	1	3	2	1	7
Thomomys cf. *talpoides*	1	1	1	–	–	–	–	–	–	–	–	–	–	3
Thomomys talpoides[c]	1	–	1	2	–	–	–	–	–	–	–	–	–	4
Perognathus sp.	–	–	–	1	2	–	–	–	–	–	–	–	–	3
Perognathus longimembris	–	–	–	–	–	–	–	–	2	–	–	–	1	3
Pergnathus cf. *parvus*	–	–	–	–	–	–	1	–	–	–	–	–	–	1
Perognathus parvus	–	2	1	2	4	1	–	–	1	2	1	–	–	14
Dipodomys sp.	1	2	4	13	4	54	14	9	73	31	–	7	6	218
Dipodomys cf. *microps*	–	–	–	–	–	–	–	–	–	–	1	–	–	1
Dipodomys microps	–	–	–	–	–	2	–	–	–	–	2	–	–	4
Peromyscus sp.	1	–	–	–	–	–	1	–	–	–	1	1	–	4
Peromyscus sp. (large)	1	–	1	–	1	–	1	–	–	–	1	–	–	5
Peromyscus cf. *maniculatus*	–	2	1	1	–	–	1	1	–	–	–	–	–	6
Peromyscus maniculatus	3	1	6	3	2	1	1	–	–	1	1	–	–	19
Neotoma sp.	–	7	–	7	–	3	1	–	5	1	3	–	–	27
Neotoma cf. *cinerea*	9	17	13	17	8	4	1	–	–	–	–	–	–	69
Neotoma cinerea	2	2	2	3	–	2	1	–	–	–	–	–	–	12
Neotoma cf. *lepida*	–	2	1	4	–	42	8	15	90	49	7	10	12	240
Neotoma lepida	–	–	–	–	–	12	3	1	2	4	20	4	3	49
Arvicoline	17	3	7	10	9	–	4	–	–	3	2	–	–	55
Microtus sp.	1	–	1	–	1	–	1	–	–	–	1	–	–	5
cf. *Lemmiscus curtatus*	1	–	1	–	1	–	–	–	–	–	–	–	–	3
Lemmiscus curtatus	3	–	1	9	2	–	–	–	–	1	–	–	–	16
Reithrodontomys megalotis	–	–	1	–	–	–	–	–	–	–	–	–	–	1
Total	92	50	68	112	42	135	39	32	194	115	69	31	29	1008

[a] Includes specimens from mixed 17c, 17b and/or 17a deposits.
[b] Includes specimens from 14b, 14a, and mixed 14b/a deposits.
[c] An additional *T. talpoides* specimen was recovered from mixed 18 and 17b' deposits.

ca. 9000 ^{14}C yr BP (10,200 cal yr BP), and *N. lepida* "replaced" *N. cinerea* as regional desertification took hold at the end of the early Holocene.

At first glance, differences in rodent species richness at Bonneville Estates (Tables 2 and 3) lend support to the timing and nature of changing environments as richness is greatest in deposits dating prior to ca. 9500 ^{14}C yr BP (10,800 cal yr BP). However, there is a moderately significant correlation between the number of species present and NISP (Table 3; $r = 0.675$, $p = 0.06$) and richness alone is not a reliable indicator of community change in this particular context. When diversity measures that incorporate evenness are employed, however, there is a marked shift in the composition of the shelter's rodent fauna during the middle of the early Holocene. Changes in evenness are examined here because declines in taxonomic abundance precede extinction and evenness measures incorporate abundance (after Blois et al., 2010).

Community change at the ca. 9000 ^{14}C yr BP (10,200 cal yr BP) onset of increasing desertification was investigated by calculating Shannon diversity indices (H') of the rodent fauna from deposits dating prior to 9000 ^{14}C yr BP (strata 20–17b′), and the combined aggregates of specimens dating after that time to the end of the middle Holocene (strata 17b–11). These analyses used the NISP of all specimens identified to species and included *Microtus* sp., *Tamias* sp., and large *Urocitellus* sp. [= *Spermophilus*]). Both NISP and richness in the pre- and post-9000 ^{14}C yr BP assemblages are similar (Table 3; NISP = 226/12 species and NISP = 265/11 species, respectively), but the composition of the early rodent fauna ($H' = 1.84$) is significantly different than the 9000–4500 ^{14}C yr BP (10,200–5200 cal yr BP) aggregate ($H' = 0.69$) ($t = 10.85$, $p < 0.001$). This difference offers further evidence for changes in local biotic communities; the early assemblage contains a more even distribution of specimens across species, including mesic-adapted *N. cinerea* and *L. curtatus*, while the post-9000 ^{14}C yr BP fauna is dominated (NISP = 228) by the desert-dwelling *N. lepida*. In addition, and of particular importance in identifying community change, there is a within-genus turnover of animals with different ecological requirements, including woodrats and, as discussed below, pocket gophers.

Ground squirrels, meadow voles and pocket gophers

Three additional rodent taxa collected from the earliest deposits at Bonneville Estates Rockshelter warrant discussion as each was extirpated, or nearly so, by or shortly after 9000 ^{14}C yr BP (10,200 cal yr BP). First, 14 specimens of large ground squirrel (*Urocitellus* sp.) were collected from horizons 20 and 18a (Table 2) and date between ≥12,500 and 9600 ^{14}C yr BP (14,800–11,000 cal yr BP). Although these specimens were not identified beneath the level of genus, they compare favorably with the Wyoming ground squirrel (*U. elegans* [= *richardsonii*]) and Belding's ground squirrel (*U. beldingi*) and it is likely that they represent one or both of these species. *U. elegans* and *U. beldingi* largely inhabit mesic meadows in more northerly parts of the Great Basin and are not present in the Bonneville Estates vicinity today (Hall, 1946:303–309). It appears that local populations became extinct at the beginning of the early Holocene, most likely in response to increasingly warmer and drier environs in the region (e.g., Louderback and Rhode, 2009).

Second, four of the five identified meadow vole bones (*Microtus* sp.; Table 2) were recovered from layers deposited before ca. 8700 ^{14}C yr BP (9650 cal yr BP) with the remaining specimen (Stratum 14b) dating

Table 3
Numbers of identified rodent specimens[a] (NISP), taxonomic richness[b] (NTaxa), and age estimates by stratigraphic horizon at Bonneville Estates Rockshelter.

Stratum	NISP	NTaxa	Age ^{14}C yr BP-cal yr BP[c]	Lab no(s).
1	2 (1)	1	160 ± 30 258–30	AA 58584
3	26 (18)	2	1710 ± 35–1380 ± 60 1682–1576–1347–1255	AA 58586–Beta 164228
5/4	6 (1)	1	1900 ± 40 1888–1794	Beta 16422
7	18 (11)	3	2250 ± 80–2090 ± 40 2332–2160–2118–2014	Beta 29543–Beta 228722
9	20 (10)	2	3670 ± 40–2830 ± 40 4074–3942–2998–2890	Unspecified–Beta 230514
12/11	29 (17)	3	4530 ± 40 5283–5091	AA 58582
13	31 (17)	3	4795 ± 40 5584–5489	AA 58583
14	69 (40)	7	6510 ± 50–6040 ± 80 7470–7357–7015–6800	Beta 228729–Beta 29542
16	115 (61)	6	7280 ± 50–7190 ± 50 8153–8041–8073–7972	CAMS 72352–Beta 164230
17	265 (128)	7	8900 ± 50[d]–7420 ± 50 10,041–9937–8317–8203	Beta 243004–CAMS 72351
17b'	135 (65)	6	9580 ± 40–9340 ± 60 11,056–10,814–10,643–10,463	Beta 207010–Beta 243001
18	222 (94)	11	11,010 ± 40–9940 ± 60 13,018–12,818–11,553–11,289	Beta 207009–Beta 243005
20/19	142 (64)	9	≥12,500–10,640 ± 60 ≥14,800–12,711–12,557	Beta 200875

[a] Total NISP (Table 2) and (parentheses) specimens identified to species and including *Tamias* sp., *Microtus* sp., and large *Urocitellus* sp.

[b] Specimens identified to species and including *Tamias* sp., *Microtus* sp., and large *Urocitellus* sp.

[c] CalPal Online Radiocarbon Calibration program.

[d] This date, and an age estimate of 8720 ± 60 ^{14}C yr BP (Beta 243003) (9830–-9606 cal yr BP) are from hearth charcoal samples near the stratum 17b-a contact.

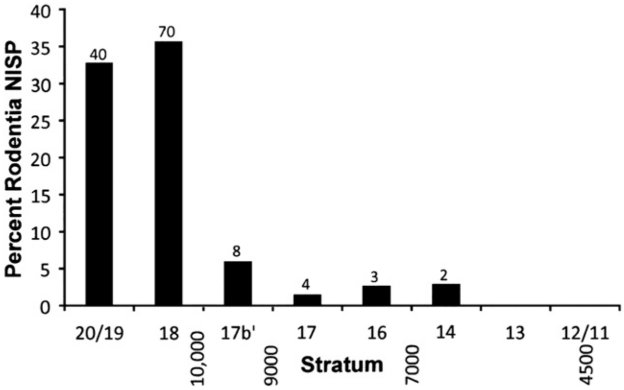

Figure 3. The relative abundance of five rodents well-adapted to cool and moist contexts (see Table 1) compared with all rodents identified to genera in the early deposits at Bonneville Estates Rockshelter. The numbers above the bars provide the total number of these specimens identified in each stratigraphic aggregate and the vertical numbers (bottom) provide ^{14}C yr BP ages.

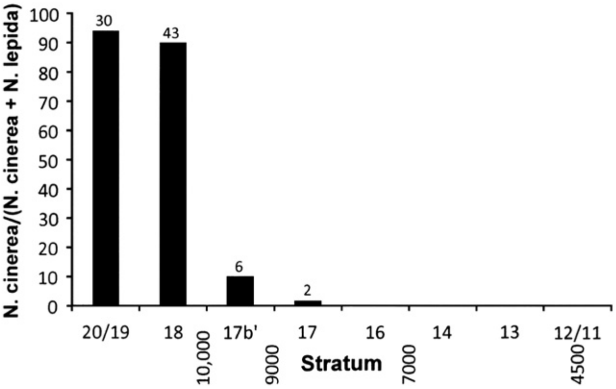

Figure 4. The ratio (× 100) of *Neotoma cinerea* (NISP = 81: Table 2) to *N. cinerea* and *N. lepida* (NISP = 289) in the late Pleistocene–middle Holocene deposits at Bonneville Estates Rockshelter. The numbers above the bars provide the total number of identified *N. cinerea* in each aggregate and the vertical numbers (bottom) represent ^{14}C yr BP age estimates.

to about 6300 ^{14}C yr BP (7200 cal yr BP). Both the montane vole (*M. montanus*) and long-tailed vole (*M. longicaudus*) can be found in nearby settings today (Hall, 1946; Durrant, 1952) and the recovered *Microtus* remains probably represent at least one of these species. While both animals are known to occur in a variety of habitats, they show poor ability to thermoregulate at high temperatures (Wunder, 1985) and prefer cool and moist grasslands, especially *M. montanus* (e.g., Hall, 1946; Getz, 1985); it appears that meadow vole populations in the Bonneville Estates vicinity also waned in response to increasing desertification. Similar declines in *Microtus* can be found in the records from Homestead and Camels Back caves. At Homestead Cave meadow voles are abundant in deposits dating 11,300–8300 ^{14}C yr BP (13,200–9300 cal yr BP), their numbers decline dramatically between 8300 and 7000 ^{14}C yr BP (9300–7850 cal yr BP), and only a few isolated specimens occur throughout the remainder of the Holocene (Grayson, 2000a). Each of the four identified *Microtus* sp. specimens in Camels Back Cave was collected from the earliest horizons (I and IIb) and date prior to ca. 8500 ^{14}C yr BP (9500 cal yr BP) (Schmitt and Lupo, 2005). Elsewhere in the region, the single identified *Microtus* sp. specimen from Danger Cave was collected from stratum DI and dates to ≥10,000 ^{14}C yr BP (11,500 cal yr BP) (Grayson, 1988; see also Goebel et al., 2007), and all of the provenienced *Microtus* bones from excavations at the Sunshine Locality in Long Valley, Nevada were collected from fluvial or overlying organic deposits that date prior to 9000 ^{14}C yr BP (10,200 cal yr BP) (Cannon et al., 2009; Holmes and Huckleberry, 2009). Again, meadow voles are known to inhabit a variety of settings, but the timing of their presences and abundances in regional low desert sites suggests that they, too, were affected by increasing aridity.

Third, and perhaps most significant, is the occurrence of the northern pocket gopher (*T. talpoides*). *T. talpoides* currently inhabit cool settings in more northerly parts of the Great Basin (Hall, 1946) and represent the only member of the genus present at Bonneville Estates prior to 9500 ^{14}C yr BP (10,800 cal yr BP) (Tables 2 and 3). After this time *T. talpoides* was replaced by *T. bottae*, a common resident of desert valleys and low-elevation foothills (Hall, 1946; Durrant, 1952), and the extirpation of *T. talpoides* and colonization by *T. bottae* at the shelter coincides with the onset of warmer and drier conditions as reflected by shifts in the nearby Blue Lakes pollen record (Louderback and Rhode, 2009). Changes in the Bonneville Estates *Thomomys* mirror those at Homestead Cave where *T. talpoides* occur only in the earliest deposits and were replaced by *T. bottae* after the Pleistocene came to an end (Grayson, 2006, 2011). In fact, Homestead Cave "provided 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" (Grayson, 2011:196), and the Bonneville Estates *Thomomys* fauna provide a corresponding record.

Finally, and although details on the Bonneville Estates Rockshelter leporid fauna are not addressed here, it is worth noting that the remains of pygmy rabbits (*Brachylagus idahoensis*) are also reported in the shelter's deposits that predate ca. 8800 ^{14}C yr BP (9900 cal yr BP) and skeletal abundances indicate that they were common residents of the Lead Mine Hills during the Younger Dryas stade (Hockett, 2007). Since *B. idahoensis* largely occur in northern Great Basin valleys and upland plains dominated by dense stands of big sagebrush (e.g., Green and Flinders, 1980; Katzner and Parker, 1997), their extirpation at the end of the early Holocene offers additional evidence for the onset of increasingly warmer and drier climates and corresponding reductions in regional *Artemisia tridentata* habitats. This pattern, however, is certainly not unique as a number of regional sites in low-elevation contexts contain markedly similar extinction records for *B. idahoensis*, including Homestead and Camels Back caves (Grayson, 1988, 1993, 2000a,b; Schmitt et al., 2002; Schmitt and Lupo, 2005; Grayson, 2011).

Discussion and conclusion

Save for a few subtle differences, some of which are doubtless the products of aforementioned differences in site contexts, the Bonneville Estates Rockshelter rodent fauna provide a new series of well-dated assemblages that match the records from Homestead and Camels Back caves. These assemblages manifest three independent taphonomic histories that reflect markedly similar mammalian responses at the Pleistocene–Holocene transition and, contrary to some climatic models (e.g., Mock and Bartlein, 1995), they offer a large body of compelling data which suggest the region remained cool and moist after the Pleistocene came to an end. In addition, the timing and nature of the faunal changes at these sites match plant macrofossil and pollen records collected from a number of nearby locations (e.g., Rhode, 2000; Madsen et al., 2001; Kiahtipes, 2009; Louderback and Rhode, 2009).

The Bonneville Estates rodents add to a growing body of information on small-mammal histories in the Great Basin and, similar to a number of other North American archaeological faunas, they may offer useful data on modern conservation biology and wildlife management issues (e.g., Livingston, 1999; Lyman and Cannon, 2004), including insights on the responses of small mammals to global warming in arid environments (e.g., Lawlor, 1998; Grayson, 2006 and references therein). Both the types and variety of late Pleistocene–early Holocene small mammals suggest that the Bonneville Estates vicinity was cool and moist and supported grasses and stands of *Artemisia*. Included are *M. flaviventris*, *N. cinerea*, *P. parvus*, and *L. curtatus*, as well as a new low-elevation record for *T. talpoides* in the prehistoric Bonneville Basin. The rodent fauna strongly suggest that early middle Holocene desertification brought forth significant changes in regional plants and animals, including a rather rapid transition to more open desert shrub communities dominated by *Atriplex*. Moreover, while overall taxonomic diversity declined across the region in response to increasingly arid conditions, there were increases in the abundances of small mammals well-adapted to xeric, low-elevation environments, most notably *N. lepida*, *T. bottae*, and *U. mollis*. Save for regional mountain tops and high-elevation foothills, these communities have dominated the Bonneville Basin for the last ca. 8000 ^{14}C yr BP (8850 cal yr BP) and are similar to native desert habits that occur today, although not quite as arid as during the heart of the middle Holocene (e.g., Wigand and Rhode, 2002; Grayson, 2011: 260–261). While the rodent accumulations at Bonneville Estates Rockshelter tell us little about prehistoric subsistence strategies and other human adaptations, they offer important and useful information on the climatic regimes and biotic communities in which these people lived. Furthermore, it is becoming increasingly clear that late Quaternary Great Basin mammalian biogeography has been and continues to be shaped by a series of complex extinction and colonization events (e.g., Grayson et al., 1996; Lawlor, 1998; Grayson and Madsen, 2000; Grayson, 2011), and the Bonneville Estates rodent fauna provide further testimony to the dynamic nature of this record.

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