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Cover

Top photograph is a view of the Siblings West Shelter (left) and Siblings East Shelter (right), eastern Nevada; note the person at the entrance of the Siblings East Shelter. See Figure 3 for more information. The lower photograph shows Ted Goebel, Kelly Graf, and Bryan Hockett at the end of the Bonneville Estates Rockshelter site stabilization project, western Bonneville basin, Nevada.

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Faunal Extirpations, Range Shifts, and Extinctions in the Western Bonneville Basin, 17,500 to 5500 Cal YR BP—Paleobiogeography of Bonneville Estates Rockshelter and Siblings East Shelter

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ABSTRACT

We analyzed faunal remains from two rockshelters in the far western Bonneville basin of eastern Nevada: Bonneville Estates Rockshelter and Siblings East Shelter. The analysis focused on paleobiogeographic changes between 17,500 and 5500 cal yr BP. Bonneville Estates Rockshelter contains faunal remains dating to the Heinrich 1 Stadial (18,000 to 14,700 cal yr BP), whereas both shelters contain faunal remains dating to the Bølling-Allerød Interstadial (14,700 to 12,900 cal yr BP), Younger Dryas Stadial (12,900 to 11,700 cal yr BP), Early Holocene (11,700 to 9300 cal yr BP), and Middle Holocene (9300 to 5500 cal yr BP). Identified faunal remains from these records indicate cool and either moist or dry climate compared to today between 17,500 and 10,200 cal yr BP, and increasingly warm temperatures impacting animal biogeographies beginning in the latter stages of the Younger Dryas and first one-half of the Early Holocene, culminating in xeric-adapted species like today by 9300 cal yr BP. Bonneville Estates Rockshelter also contains specimens of either gray wolf (*Canis lupus*) or the extinct dire wolf (*Aenocyon dirus*) and one felid phalanx of either puma/cougar (*Puma concolor*) or the extinct North American "cheetah" (*Miracinonyx trumani*), whereas Siblings East Shelter contains a rib of an extinct large horse of the genus *Equus*. Radiocarbon dated faunal remains were found directly atop Lake Bonneville beach gravels deposited inside Siblings East Shelter on the Provo terrace of Lake Bonneville, suggesting the lake dropped from this elevation prior to 14,300 cal yr BP.

INTRODUCTION

The eastern Great Basin encompasses the Lake Bonneville basin and surrounding higher terrain that drains water into that basin (Figure 1). It is the largest of the closed basins in the Basin and Range Physiographic Province (Hubbs and Miller, 1948; O'Connor, 1993) and encompasses much of the western one-half of Utah as well as smaller sections of eastern Nevada, southeastern Idaho, and southwestern Wyoming. Climatic shifts in the Bonneville basin during the Late Pleistocene and Holocene over the past 18,000 years (cal yr BP) are indicated by a variety of proxies including lake-level fluctuations (Antevs, 1948; Mifflin and Wheat, 1979; McGee et al., 2012; Oviatt, 2015, 2024; Thompson et al., 2016; Oviatt et al., 2021; Oviatt and Pedone, 2024), macrobotanical remains (Thompson, 1990; Rhode and Madsen, 1995; Rhode, 2000; Madsen et al., 2001), faunal remains

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Figure 1. General location of Bonneville Estates Rockshelter, Siblings East Shelter, and other sites mentioned in the text in relation to the Bonneville basin and the high stand of Pleistocene Lake Bonneville.

(Grayson, 1998, 2000, 2016; Broughton et al., 2000; Hockett, 2007, 2015; Schmitt and Lupo, 2012, 2016, 2018; Milligan and McDonald, 2017), and pollen (Madsen and Currey, 1979; Spencer et al., 1984; Louderback and Rhode, 2009; Thompson et al., 2016).

These proxies result in a robust picture of inferred changes in temperature and precipitation and their impacts on biogeography and the transgressions and regressions of Lake Bonneville during the Heinrich 1 Stadial 18,000 to 14,700 cal yr BP (Naughton et al., 2023a), Bølling-Allerød Interstadial 14,700 to 12,900 cal yr BP (Naughton et al., 2023b), Younger Dryas Stadial 12,900 to 11,700 cal yr BP (Naughton et al., 2023c), Early Holocene 11,700 to 9300 cal yr BP, and subsequent Middle Holocene and later climatic episodes post-9300 cal yr BP (Rhode and Madsen, 1995; Grayson, 1998, 2000; Hockett, 2007; Louderback and Rhode, 2009; Schmitt and Lupo, 2012, 2016; Oviatt, 2015; Oviatt and Pedone, 2024).

The Bonneville basin experienced shifting cooling and warming events during the latest Pleistocene between 18,000 and 11,700 cal yr BP (Rhode and Madsen, 1995; Grayson, 1998; Louderback and Rhode, 2009; Schmitt and Lupo, 2012; Oviatt, 2015). From a regional perspective, conifers such as limber pine (*Pinus flexilis*), prostrate juniper (*Juniperus communis*), and spruce (*Picea*) inhabited areas 300 to 600 m (1000–2000 ft) below their modern distributions, with Rocky Mountain juniper (*Juniperus scopulorum*) occupying some areas now exclusively inhabited by Utah juniper (*Juniperus osteosperma*) (Rhode and Madsen, 1995; Rhode, 2000; Madsen et al., 2001). On the west side of the Snake Range in far east-central Nevada, macrobotanical remains from indurated woodrat (*Neotoma* sp.) middens demonstrate that bristlecone pine (*Pinus longaeva*) similarly occupied much lower elevations than its current range (Mead et al., 1982). Sagebrush (*Artemisia* spp.) dominated the understory now occupied by warm-adapted shrubs such as greasewood (*Sarcobatus* spp.) and shadscale (*Atriplex* spp.) (Thompson, 1990; Rhode and Madsen, 1995; Louderback and Rhode, 2009; Madsen, 2000; Madsen et al., 2001). Although Lake Bonneville submerged the modern Blue Lake marshes along the western shore of the lake during this time, pollen grains from marsh plants such as sedges (Cyperaceae) and cattail (*Typha* spp.) in relatively low frequencies indicate that shallow-water marsh habitat was present in the western Bonneville basin (Louderback and Rhode, 2009, p. 318).

Cool- and mesic-adapted extant animals also occupied much lower elevations and greater ranges than they do today. Yellow-bellied marmot (*Marmota flaviventris*), pika (*Ochotona princeps*), pygmy rabbit (*Brachylagus idahoensis*), sage vole (*Lemmiscus curtatus*), and sage-grouse (*Centrocercus urophasianus*) are among the key species that display greater geographic ranges during the Late Pleistocene (Grayson, 2000, 2006; Hockett, 2007, 2015; Schmitt and Lupo, 2012). Additionally, the western longwing katydid (*Capnobotes occidentalis*) is present in the Younger Dryas sediments of Bonneville Estates Rockshelter (BER) (Hockett, 2007, 2015) but is not present near the shelter today. Longwing katydids prefer woodlands and sagebrush habitats (Tinkham, 1944) commensurate with the presence of pygmy rabbits, sage voles, and sage-grouse. Bison (*Bison* sp.) is also present in the Younger Dryas deposits of BER (Hockett, 2015).

Shifts in patterns of abundance of extant small animals are also seen, including the dominance of bushy-tailed woodrats (*Neotoma cinerea*) in comparison to desert woodrats (*Neotoma deserti*) at lower elevations. This pattern is evident during the Bølling-Allerød at BER, dated between 14,575 and 13,255 cal yr BP, where Schmitt and Lupo (2012, p. 99) found bushy-tailed woodrats dominated in comparison to desert woodrats 94 to 6%, respectively. A similar pattern is seen during the Younger Dryas Stadial at both BER and Homestead Cave (Grayson, 2000; Schmitt and Lupo, 2012).

Several extant eastern Great Basin reptiles and amphibians are present in Heinrich 1 and Bølling-Allerød dated woodrat middens from the Snake Range including the Great Basin spadefoot (*Spea intermontana*), which belongs to the family of amphibians Scaphiopodidae and also known as spadefoots, pygmy short-horned lizard (*Phrynosoma douglasii*), and desert night snake (*Hypsiglena torquata*) (Mead et al., 1982; Holman, 1995). These species still occupy the area from which the woodrat middens were collected. Other animals that have been dated to the Late Pleistocene and likely maintained their general ranges throughout the Holocene prior to Euroamerican contact include several artiodactyls (deer [*Odocoileus*], mountain sheep [*Ovis canadensis*], and pronghorn [*Antilocapra americana*]), carnivores including wolf (*Canis lupus*) and red fox (*Vulpes vulpes*), a wide variety of aquatic birds such as grebes (Podicipedidae) and ducks (Anatidae), and raptorial birds including owls (Strigidae), falcons (Falconidae), and hawks (Accipitridae) (Livingston, 2000; Hockett, 2015; Milligan and McDonald, 2017; Duke et al., 2022).

Several extinct animals were present in the Bonneville basin or nearby during the latest Pleistocene. Heinrich 1-, Bølling-Allerød-, or Younger Dryas-dated specimens include camel (*Camelops*), short-faced bear (*Arctodus simus*), mammoth (*Mammuthus* spp.), mastodon (*Mammut*), Jefferson's ground sloth (*Megalonyx jeffersonii*), and flat-headed peccary (*Platygonus com-*

pressus) (reviewed in Schmitt and Lupo, 2016; Milligan and McDonald, 2017; Mead et al., 2023). Undated extinct animals include horse (*Equus/Harringtonhippus*) and helmeted ox (*Bootherium bombifrons*). As noted, one bison bone is present in the Younger Dryas sediments at BER (Hockett, 2007, 2015), but it is not known whether it is *Bison antiquus* or *Bison bison*.

These Pleistocene-aged plants and animals lived primarily around the margins of the dominant aquatic feature at this time—Lake Bonneville. The timing of Lake Bonneville's transgressions and regressions over the past 18,000 years is generally known although several questions remain (Oviatt, 2014, 2015, 2020, 2024; Oviatt and Pedone, 2024). Lake Bonneville reached its high-stand Bonneville shoreline no later than 18,000 cal yr BP (Oviatt, 2020, p. 309). Approximately 17,500 cal yr BP the lake began its overflow stage into the Snake River drainage system, dubbed the 'Bonneville Flood' (Oviatt, 2020, p. 310). The lake may have dropped and began carving the Provo shoreline only several years after the beginning of the overflow, and then subsequently regressed below the Provo level approximately 14,500 cal yr BP (Oviatt and Pedone, 2024, p. 34). The precise timing of the regression of the lake from the Provo terrace is still in question and is addressed again below with new data recovered from Siblings East Shelter (SES) (Figure 1). The lake then may have dropped as low as the level of Great Salt Lake before transgressing again briefly during the Younger Dryas to the "Gilbert" level, now called the "Currey cycle," before regressing once again (Oviatt, 2014, 2015; Oviatt et al., 2024).

The sites that have set the standard for understanding long-term changes in animal biogeography over the past 18,000 years in the Bonneville basin are Homestead Cave (Broughton, 2000; Grayson, 2000; Madsen, 2000) and BER (Hockett, 2007, 2015; Schmitt and Lupo, 2012). BER contains well-preserved faunal remains dating more than 14,500 cal yr BP, and Homestead Cave displays similar preservation dating to 13,000 cal yr BP. Both sites display comparable patterns of changing animal presence and abundance in response to climatic shifts throughout the latest Pleistocene and Holocene. The primary differences between these two sites are in the mode of deposition of their respective faunal remains and their microenvironmental settings within the Bonneville basin. The Homestead Cave fauna was deposited primarily by raptors, most notably owls, beginning near the onset of the Younger Dryas 12,900 cal yr BP (Madsen, 2000). Most of the BER rodent fauna was also deposited by raptors or carnivores (Schmitt and Lupo, 2012), but deposition of terrestrial sediments inside the shelter began before the onset of the Bølling-Allerød 14,700 cal yr BP (Goebel et al., 2021; this paper). Additionally, most of the Younger Dryas and Early Holocene non-rodent fauna from BER was deposited by human foragers (Hockett, 2007, 2015). BER is at 1590 m asl (5250 ft) along the high-stand Bonneville terrace. Homestead Cave, in contrast, is at 1406 m asl (4640 ft) between the Provo terrace (about 1470 m [4850 ft]) and the Younger Dryas-aged Currey cycle lake level (about 1295 m [4275 ft]). Thus, BER is approximately 175 m (574 ft) higher in elevation than Homestead Cave and was open to terrestrial sediment and biotic deposition as soon as the lake catastrophically dropped from the Bonneville terrace about 17,500 cal yr BP. Nevertheless, both sites display nearly identical biogeographic patterning in their mammalian faunal remains during the Younger Dryas and first one-half of the Early Holocene with mesic-adapted species dominating the identification lists (Grayson, 2000; Hockett, 2007, 2015; Schmitt and Lupo, 2012). In addition, both sites, as well as Camels Back Cave (Figure 1), indicate that shifts to xeric-adapted animals closely matching today's faunal communities near these sites, including the extirpation of marmots, pika, sage voles, sage-grouse, and pygmy rabbits, as well as the increased dominance of desert woodrats over bushy-tailed woodrats, occurred by 9300 cal yr BP (8300 ^{14}C yr BP) (Grayson, 2000; Hockett, 2007; Schmitt and Lupo, 2012; OxCal, v4.4; Reimer et al., 2020), marking the beginning of the Middle Holocene in this region. However, this marked shift from mesic- to xeric-adapted fauna, as well as the near abandonment of BER by human foragers, began during the Early Holocene (Grayson, 2000; Schmitt and Lupo, 2012; Goebel et al., 2021). As Schmitt and Lupo (2012, p. 98) stated when comparing the Homestead Cave and Camels Back Cave rodent faunas: "Although this combined rodent-only data represents a modification of previously reported analyses and comparisons… the results are the same; there is a sharp decline in the abundance of MA [mesic-adapted] species by approximately 9000 ^{14}C yr BP (10,200 cal yr BP)…"

Here we report on another remarkable record from SES that contains well-dated evidence of Late Pleistocene and Early Holocene biogeography in the western Bonneville basin, as well as the Heinrich 1- and Bølling-Allerød-aged fauna from BER not reported previously. SES (Bureau of Land Management Nevada site designator CRNV-11-7736) is one of a group of four rockshelters dubbed "The Four Siblings" that contains a similar record of nonculturally deposited fauna to that reported from Homestead Cave (Grayson, 2000) and BER (Schmitt and Lupo, 2012). Like Homestead Cave, owls deposited most of the bones inside SES (Hockett, 1995). However, SES is at an elevation of 1485 m (4872 ft) along a Provo-aged terrace of Pleistocene Lake Bonneville in between the elevational settings of Homestead Cave and BER. Further, faunal remains began accumulating in SES shortly after Lake Bonneville dropped from the Provo terrace and thus provides a record that potentially reaches 1300 years earlier than Homestead Cave. Also, SES provides new evidence for a minimum date for the occurrence of the drop in Lake Bonneville from the Provo terrace.

SETTING

Bonneville Estates Rockshelter and Siblings East Shelter rest upon relic Bonneville-era and Provo-era shorelines, respectively, of Pleistocene Lake Bonneville in the far western Bonneville basin of eastern Nevada (Figure 1). Today the floor of BER is at an elevation of about 1590 m (5250 ft) whereas SES is at about 1485 m (4900 ft). SES is approximately 4.5 km (3 mi) east of BER (Goebel et al., 2021), 4 km (2.5 mi) southwest of the Blue Lake marsh (Louderback and Rhode, 2009), 100 km (62 mi) southwest of Homestead Cave (Madsen, 2000), and 30 km (19 mi) south of Danger Cave (Jennings, 1957) (Figure 1).

Both BER and SES face southeastward (Figures 2 and 3). BER is on the foothill slopes between the Bonneville Salt Flats to the east and the Goshute Mountains to the west. The mouth of SES overlooks the Bonneville Salt Flats and the Blue Lake marsh (Figure 4) in the distance. BER is the largest known rockshelter in the area, measuring 25 m (82 ft) wide and 15 m (49 ft) deep at its center with a 10-m-high (33 ft) ceiling (Graf, 2007). SES is much smaller, measuring 9 m (30 ft) wide and 7 m (23 ft) deep with a ceiling reaching about 2.5 m high (8.2 ft). Because of their relatively low elevations, local vegetation today is sparse and desertic. However, the lower-elevation SES is characterized by shadscale, greasewood, and some cacti (e.g., *Opuntia* sp.); whereas surrounding BER, these same xerophytic plants are present with the addition of sparse sagebrush, rabbitbrush (*Chrysothamnus* sp.), ephedra (*Ephedra* sp.), and several kinds of grass including Great Basin wild rye (*Leymus cinereus*), Indian ricegrass (*Oryzopsis hymenoides*), and needle-and-thread grass (*Hesperostipa comata*) requiring somewhat cooler temperatures and more moisture. Small fauna in the area is characteristic of xeric-adapted species inhabiting the Great Basin desert including desert woodrat, various species of kangaroo rats (*Dipodomys* spp.), black-tailed jackrabbit (*Lepus californicus*), and cottontail (*Sylvilagus*). The only artiodactyl spotted near the shelters today is pronghorn. The nearest water source is the freshwater springs that create the perennial marshes along the edge of the Bonneville playa at Blue Lake about 4 km (2.5 mi) northeast of SES and 7 km (5.5 mi) east of BER. These marshes harbor a variety of waterfowl, particularly ducks.

The Bonneville and Provo shorelines are prominent features in this part of eastern Nevada, and the lake carved several east-facing caves and rockshelters in the region. The Bonneville terrace formed some 18,000 cal yr BP due to increasing moisture and decreasing evaporation. The Provo terrace formed between approximately 17,500 and 14,500 cal yr BP when the level of Lake Bonneville catastrophically fell from its high stand and then stabilized at this level for about 3000 years (Oviatt, 2015). BER has been dry and open to terrestrial sediment deposition for the past 18,000 to 17,000 years, while SES has been dry and open for at least the past 14,000 years. We found faunal remains deposited by owls sitting directly atop Provo beach gravels at SES. Stratum 20 (Heinrich 1) and Stratum 19 (Bølling-Al-

Figure 2. Bonneville Estates Rockshelter and surrounding terrain and vegetation, looking westward.

lerød) at BER produced paleontological faunal remains although the lowest of these sediments near the Bonneville high-stand beach gravels (Stratum 21) were devoid of organics in the units excavated due to poor preservation conditions (Figure 5).

MATERIALS AND METHODS

In this paper, we report the findings of the paleontological remains recovered from BER during annual field schools held between 2000 and 2009 and from test excavations at SES in 2006. At BER the two lowest terrestrial strata above the Lake Bonneville gravels, designated 20 and 19 (Figure 5), are paleontological. A description of the excavation strategy, plan view map of the area excavated within the shelter, and a representative stratigraphic profile can be found in Graf (2007) and Goebel et al. (2021). Schmitt and Lupo (2012, 2016) reported on the small rodent bones recovered from strata 20 and 19. Hockett (2007, 2015) previously reported on the Number of Identified Specimens (NISP) and Minimum Number of Individuals (MNI) of artiodactyls, carnivores, leporids (hare and cottontail), sage-grouse, and katydids throughout the Younger Dryas and Holocene-aged strata (18-1). Below we provide a final update to the values reported in Hockett (2007, 2015), with an emphasis on the non-rodent Heinrich 1 and Bølling-Allerød strata 20 and 19 fauna.

As the ten-year field study of BER was in full swing, the Elko Field Office of the U.S. Department of Interior, Bureau of Land Management discovered that SES had been looted. The goals of the SES project were twofold: first, to determine the extent of damage done by earlier looting; and second, to evaluate the site's significance for addressing important questions related to the early biogeographic history of the region. It was known to

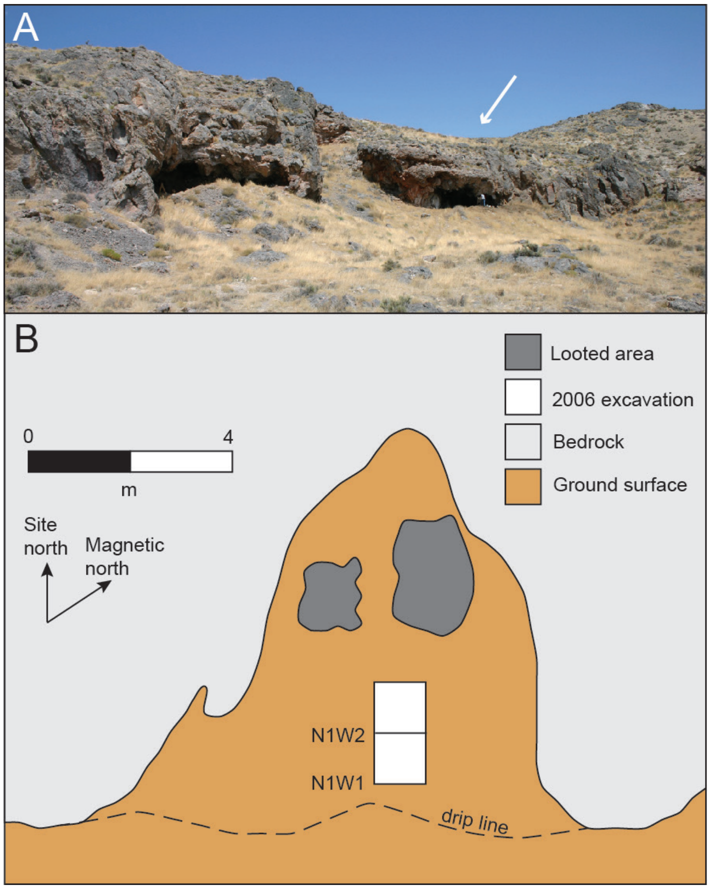

Figure 3. (A) Siblings West Shelter (left) and Siblings East Shelter (right, white arrow and person present at the entrance), eastern Nevada; (B) plan view map and location of test units excavated inside Siblings East Shelter.

us that sites like SES might contain a wealth of biogeographic information. In the early 1990s a large collection of great horned owl (*Bubo virginianus*) pellets from the surface of Dondero Shelter, near BER and SES (Figure 1), served as an important set of proxy data to assist in distinguishing leporid bones modified and deposited on the landscape by owls versus humans (Hockett, 1995).

Similarly, the surface of SES contained abundant raptor pellets, small bones exposed by degraded pellets, carnivore scats (visual inspection pointed to coyote [*Canis latrans*]), and larger bones likely carried to the site by woodrats. We excavated two contiguous 1-m^2 (3-ft^2) units in 5-cm (2-in) levels and screened all materials through 1/8” mesh. The units were designated N1W1 and N2W1 (Figure 3). We excavated N1W1 to a depth of 160 cm (63 in) below datum (bd) where we encountered a large chunk of rockfall that prevented further excavation (Figure 6). N2W1 was largely unencumbered by rockfall, and we were able to excavate it to a depth of 255 cm (100 in) bd where we encountered Provo-aged Lake Bonneville beach gravels (Stratum 9) devoid of organic remains (Figure 6). The fauna reported here are from the paleontological levels of N2W1 between 138 and 255 cm (54–100 in) bd.

We noted stratigraphic breaks during excavations at SES, and levels were ceased between identified strata. It was evidently clear during excavations that most bones were deposited via raptor pellets and carnivore scats. Depending on the level excavated, most 5-cm (2-in) levels were dominated by small rodent, leporid, waterfowl, and fish bones that were stained and polished by gastric fluids, with raptor or carnivore puncture marks evident on some bones (Andrews, 1990; Schmitt and Juell, 1994; Hockett, 1995).

The faunal analysis from both shelters focuses on those animals most sensitive to climatic change during the Late Pleistocene and Early Holocene. Ironically, waterfowl bones were abundantly present at almost every level excavated in SES, so they were not good climatic indicators. Most of the waterfowl bones were small ducks, particularly teal-sized ducks. Great horned owls occasionally hunt these ducks and other larger waterfowl (Voous, 1988, p. 85), and they are the likely depositor of their bones in pellets inside SES just as they were at Homestead Cave (Broughton, 2000). We tallied waterfowl bones and they are reported below but are not discussed in detail. Other species that we identified in low numbers that provided limited biogeographic information include the northern and southern pocket gophers (*Thomomys talpoides* and *Thomomys bottae*), pocket mice of the genus *Perognathus*, several small carnivores including long-tailed weasel (*Mustela frenata*) and badger (*Taxidea taxus*), and the pallid bat (*Antrozous pallidus*). These, along with notations of the presence of snake and raptor bones, are reported in footnotes and discussed as appropriate in the Summary and Discussion section below.

We identified bones using known specimens housed at the Natural History Museum of the University of Ne-

Figure 4. The lush Blue Lake marshes along the western edge of the Bonneville Salt Flats, looking northward. The Leppy Hills are in the background. The marsh was submerged by Pleistocene Lake Bonneville until sometime after ca. 12,500 cal yr BP.

vada, Reno (UNR), Nevada State Museum, Carson City (NSM), the San Bernardino County Museum (SBCM), Denver Museum of Nature and Science (DMNS), Museum of the North, Fairbanks, Alaska (MON), University of Kansas Natural History Museum (KUNHM), and the author's personal comparative collection (PCC). Quantification per taxon was by NISP and MNI for BER and NISP for SES. Primary methods of species identifications were as follows: the *Equus* sp. rib from SES was identified by direct comparison to a complete Pleistocene *Equus* specimen housed at NSM; sage-grouse bones were identified at the SBCM; sage vole mandibles were identified by the location of the mandibular foramen as described by Grayson (1983) and by direct comparison to specimens housed at UNR; kangaroo rat (*Dipodomys* spp.) mandibles with teeth were identified by direct comparison to specimens housed at UNR; the alveolar lengths of bushy-tailed woodrat (greater than 9.3 mm) and desert woodrat (less than 8.7 mm) mandibles were used to distinguish between these two species (Grayson, 1985, p. 150; Grayson, 1988, p. 21); the large canid bones from BER were measured and compared to gray wolf (*Canis lupus*) and dire wolf (*Aenocyon dirus*; Perri et al., 2021) housed at the DMNS, MON, and KUNHM; we identified the artiodactyls and pygmy rabbit using the author's PCC; spadefoot was identified using the author's PCC and by consulting Pugener (2010), Jorgensen (2011), Broughton and Miller (2016), and Gomez and Turazzini (2016); we identified katydids via personal communication with NSM staff. Finally, fish vertebrae were common in the lower levels of SES, but they were not identified beyond the general category "Osteichthyes." It is presumed that the fish were scavenged from the shoreline of the post-Provo regressive phase of Lake Bonneville as owls such as *Bubo virginianus* are not known to hunt fish directly from lake waters, so the presence of fish vertebrae in SES indicates fish die-offs east of the shelter along the receding shoreline. Their disappearance in the shelter likely indicates the time at which lake levels could no longer support

Figure 5. Lower sediment profile in the East Block excavation area of Bonneville Estates Rockshelter. The Bonneville high-stand beach gravel and sand (Stratum 21) are visible at the base of the profile. The two reddish-orange features near the top of the photograph are Late Pleistocene-aged hearths (Stratum 18b). Between Stratum 21 and Stratum 18b lie Strata 20 and 19, the strictly paleontological sediments inside the shelter.

fish that inhabited deeper, colder, and less saline Lake Bonneville waters (Broughton, 2000, p. 121; Broughton et al., 2000).

STRATIGRAPHY AND DATING

We mapped 21 stratigraphic units at BER (Graf, 2007; Goebel et al., 2021). Table 1 presents the beginning and ending dates of each stratigraphic unit based on the Bayesian analysis in Goebel et al. (2021). Stratum 19 is most pronounced in the western part of the shelter and contains abundant sticks and other macrobotanical remains along with some bones (Graf, 2007). It lies directly below the initial human occupation of BER designated as Stratum 18. Stratum 20, below Stratum 19, primarily consists of silt, sand, and gravel with few organic remains save bones (Figure 5). Strata 19 and 20 are strictly paleontological. Stratum 19 dates to the Bølling-Allerød Interstadial, between 14,575 and 13,255 cal yr BP. The age of the Stratum 20 sediments is bracketed by the timing of Lake Bonneville dropping below its high-stand and Stratum 19. Thus, Stratum 20 was deposited between 17,500 and 14,575 cal yr BP.

Stratum 18 at BER represents repeated short-term occupations by human foragers and was deposited during the Younger Dryas Stadial between 12,950 and 11,600 cal yr BP (Table 1; Figure 7). Stratum 17b' above Stratum 18 is similar in character and dates to the first half of the Early Holocene between 11,600 and 10,500 cal yr BP. Stratum 17 primarily consists of sterile silt and gravel and dates to the second half of the Early Holocene between 10,200 and 8475 cal yr BP. During this period of increasing warming in the Western United States (Palmer et al., 2023), BER was largely abandoned by human foragers. In contrast, the Old River Bed Delta (Figure 1) southeast of BER appears to have been intensively occupied between about 12,300 and 9500 cal yr BP due to favorable groundwater conditions that created productive marshland habitat (Madsen et al., 2015; Bradbury et al., 2020; Palacios-Fest et al., 2021; Duke et al., 2022, 2024) following the transgression of the Currey cycle between 12,700 and 12,400 cal yr BP (Oviatt et al., 2024). Nearby Danger Cave was also occupied during the Early Holocene abandonment period at BER, probably due to a reliable springhead in front of the site (Rhode et al., 2006). Strata 16-13 date between 8300 and 4900 cal yr BP and are a combination of natural sediment accumulations interspersed with short-term human occupations during the generally warm and dry Middle Holocene.

Human occupation of BER intensified after about 5300 cal yr BP and saw repeated occupations until Euroamerican contact. Strata 12 and 11 represent a transitional period between the warm and dry Middle Holocene and the cooler and wetter Late Holocene, dating between 4900 and 4150 cal yr BP. Stratum 10 was deposited during the early Late Holocene (Palmer et al., 2023) between 4150 and 4025 cal yr BP. The Neoglacial (Millar and Thomas, 2024) is represented by Stratum 9,

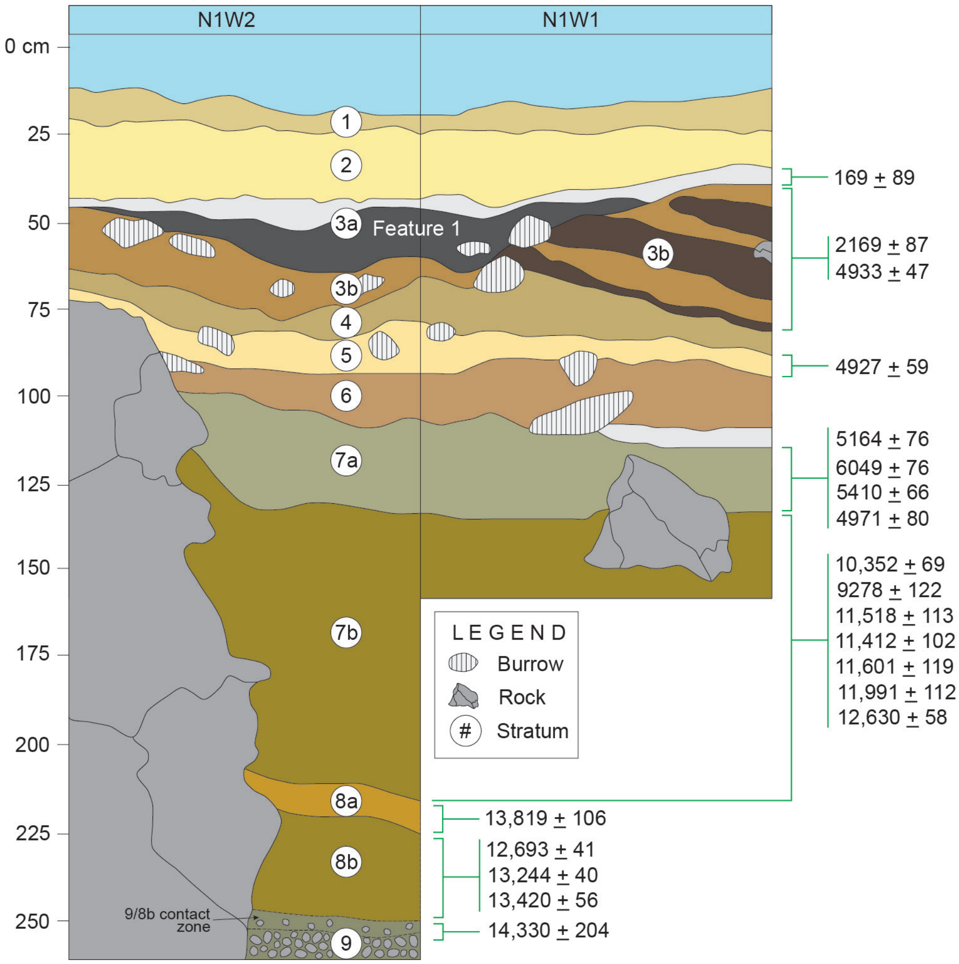

Figure 6. Log of the stratigraphic profile (north wall of 1 x 2-m [3 x 6 ft] excavation) and radiocarbon dates (cal yr BP) from Siblings East Shelter.

dating between 4025 and 2950 cal yr BP. The Late Holocene Dry Period (Mensing et al., 2013, 2023) is represented by strata 8 through 5, dating between 2950 and 1830 cal yr BP. Strata 4 and 3 were laid down during the Medieval Climate Anomaly (MCA) or Medieval Warm Period (Cook et al., 2004; Mann et al., 2009) between 1830 and 840 cal yr BP. The MCA witnessed drought conditions in the western Great Basin (Stine, 1994) but generally warm and wet conditions in the eastern Great Basin (Currey and James, 1982). Finally, strata 2 and 1 represent the Little Ice Age/modern climate (Mann et al., 2009), dating between 535 and 25 cal yr BP.

Though the SES deposits represent a consistent deposition of owl pellets and carnivore scats, we mapped nine stratigraphic units during the excavations (Figure 6; Table 2). Table 3 provides details of the stratigraphic profile from SES, including descriptive information from both N1W1 and N1W2. The upper sequence of strata in the profile, designated strata 6, 5, 4, 3b, 3a, 2, and 1, are predominantly archaeological in nature and will be described elsewhere. The paleontological strata detailed here above the Lake Bonneville beach gravels (Stratum 9), from bottom to top, are designated as Strata 8b, 8a, 7b, and 7a (basal two levels).

Owls and carnivores repeatedly occupied SES between about 14,300 and 9300 cal yr BP (Table 2). We submitted organic samples to Beta Analytic and the University of Georgia for sample preparation. Regarding the bones, only samples from terrestrial animals (e.g., hares, marmots, artiodactyls) were used for radiocarbon dating, rather than mixing terrestrial-based and water-based (e.g., waterfowl, fish) bones for consistency. Fauna appears to have been deposited shortly after Lake Bonneville's regression from the Provo shoreline standstill, generally dated between 15,000 and 14,000 cal yr BP (Oviatt, 2015). SES radiocarbon dates suggest

Table 1. Number of Identified Specimens (NISP) and Minimum Number of Individuals (MNI; parentheses) per stratum of the faunal remains and insects identified from Bonneville Estates Rockshelter[1-5].

Stratum	Age range (cal BP)	Sage Grouse	Pronghorn	Bison	Mnt. Sheep	Deer	Hare	Cottontail	Pygmy Rabbit	Katydid	Carnivora	N
1	130 – 25	0	6(1)	1(1)	2(1)	0	0	0	0	0	0	9(3)
2	535 – 130	0	7(1)	2(1)	0	0	4(1)	0	0	0	2(1)	15(4)
3a	1400 – 840	0	33(1)	13(1)	9(1)	0	9(1)	0	0	0	0	64(4)
3b/4	1830 – 1,450	0	4(1)	0	1(1)	0	54(5)	0	0	0	0	58(7)
5	1850 – 1830	0	148(3)	0	1(1)	1(1)	40(4)	0	0	0	0	190(9)
6	2000 – 1850	0	1(1)	0	1(1)	0	0	0	0	0	0	2(2)
7	2250 – 2000	0	220(4)	2(1)	6(1)	1(1)	55(5)	1(1)	0	0	0	285(13)
8	2950 – 2250	0	10(1)	0	1(1)	0	3(1)	0	0	0	0	14(3)
9	4025 – 2950	0	20(1)	5(1)	2(1)	0	2(1)	0	0	0	1(1)	30(5)
10	4150 – 4025	0	0	0	0	0	4(1)	0	0	0	0	4(1)
11	4730 – 4150	3(1)	6(1)	2(1)	1(1)	1(1)	9(1)	5(1)	0	0	0	27(7)
12	4900 – 4800	0	3(1)	0	0	0	1(1)	0	0	0	0	4(2)
13	6400 – 4900	5(1)	8(1)	0	0	0	21(2)	6(1)	0	0	0	40(5)
14	7600 – 6400	21(2)	24(1)	0	8(2)	0	117(9)	53(4)	0	0	12(1)	235(19)
15	7700 – 7600	0	1(1)	0	0	0	1(1)	0	0	0	0	2(2)
16	8300 – 7700	2(1)	0	1(1)	0	1(1)	16(2)	2(1)	0	0	0	22(6)
17a,b	10,200 – 8475	0	0	0	0	0	0	0	0	0	0	0(0)
17b'	11,600 – 10,500	90(5)	0	0	0	0	55(4)	284(19)	26(3)	0	2(1)	457(32)
18	12,950 – 11,600	516(13)	7(1)	1(1)	3(1)	1(1)	163(11)	338(24)	124(9)	21(21)	3(2)	1177(84)
19	14,575 – 13,255	17(2)	0	0	1(1)	0	33(2)	104(8)	16(2)	0	5(3)	176(18)
20	17,500 – 14,575	3(1)	1(1)	0	1(1)	0	51(4)	27(3)	4(1)	0	3(3)	90(14)
N		657(26)	499(21)	27(8)	37(14)	5(5)	638(56)	820(62)	170(15)	21(21)	28(12)	2902(240)

[1]While most of the faunal remains suggest cultural modification and deposition, the small rodent assemblage (Schmitt and Lupo 2012) indicates that raptors occasionally deposited pellets inside the shelter. In this regard, one specimen of western screech owl (*Megascops kennicottii*), one of great-horned owl (*Bubo virginianus*), and four specimens of long-eared/short-eared owl (*Asio* sp.) were recovered from Stratum 18.

[2]Raptors were likely also responsible for the deposition of the limited number of fish (Pisces), teal/pintail-sized duck (Anatidae), and long-tailed weasel (*Mustela frenata*) bones. Of the five fish bones recovered, one each was found in strata 20, 19, and 18, and two were found in Stratum 14. Of the 11 duck bones, four were found in Stratum 18 and seven in Stratum 17b'. Of the five weasel bones, three were found in Stratum 18, one in Stratum 17b', and one in Stratum 16.

[3]Eleven marmot (*Marmota flaviventris*) bones were identified from the shelter. Of these, five were found in the paleontological strata: two in Stratum 20 and three in Stratum 19. Of the remaining six marmot bones, five were found in Stratum 18 and one in Stratum 14. There is no positive evidence that any of the marmot bones represent human food waste and may have been deposited in the shelter by one of the three mammalian carnivore species noted in Footnote 4.

[4]In addition to the *Lepus, Sylvilagus*, and *Brachylagus* bones identified, a total of 707 bones were identified as Leporidae. These bones were primarily metapodials, phalanges, and skull fragments. Most of these bones (552/707, or 78%) were recovered from strata 18 and 17b'.

[5]Six species of mammalian carnivores were identified from the shelter. Collectively they only account for a total of 28 bones. Of these 24 specimens, 19 are bobcat (*Lynx rufus*), two are badger (*Taxidea taxus*), two are coyote (*Canis latrans*), two are gray wolf/dire wolf (*Canis lupus/Aenocyon dirus*), two are dire wolf, and one is cougar/North American cheetah (*Puma concolor/Miracinonyx trumani*). Of the 19 bobcat bones, one was found in Stratum 20, two each in strata 19, 18, and 17b', and 12 in Stratum 14. Some of the 16 bobcat bones recovered from strata 18, 17b', and 14 could be the result of human trapping although none of these bones were burned, and none displayed cutmarks. One badger bone was recovered from Stratum 19 and is therefore paleontological, and one was in Stratum 9. Both coyote bones were recovered from Stratum 2.

Lake Bonneville dropped below the Provo terrace by about 14,300 cal yr BP. Three radiocarbon dates indicate the lowest 25 cm (9.8 in) within Stratum 8b (255 to 230 cm [100–90 in] bd), excavated in four levels, date to the Bølling-Allerød Interstadial between 14,300 and 13,250 cal yr BP. The top of Stratum 8b/base of Stratum 7b (230 to 225 cm [91–100 in] bd) returned a radiocarbon date of about 12,700 cal yr BP near the beginning of the Younger Dryas. The transition from Bølling-Allerød to Younger Dryas is represented in the upper three levels of Stratum 8b where dates indicate five to six centuries of very slow sedimentation and owl pellet/woodrat mid-

Figure 7. Profile of an unprepared Pleistocene hearth from Stratum 18, East Block, Bonneville Estates Rockshelter. The reddish-orange layer below the charcoal layer has been stained and hardened by heat. Note two sage-grouse bones protruding from the charcoal layer to the left of the scale bar. Charcoal from the hearth returned a date of 12,635 to 12,492 cal yr BP; 10,600 ± 40 ^{14}C BP.

den accumulation. A total of 55 cm (22 in) of sediment (230 to 175 cm [91–69 in] bd) was deposited during the Younger Dryas. We excavated these upper Stratum 7b sediments in 11 levels and they are chronologically informed by four radiocarbon dates ranging between approximately 12,700 and 11,600 cal yr BP. The end of the Younger Dryas and the beginning of the Early Holocene appears to begin in the 175 to 173 cm (69–68 in) bd level. Early Holocene deposits are 27 cm (11 in) thick and were excavated in five levels, all within Stratum 7b (175 to 148 cm [91–58 in] bd). We obtained four radiocarbon ages within these levels that match near the accepted ranges of the beginning and end of the Early Holocene between 11,600 and 9300 cal yr BP. The 148 cm (58 in) bd level near the base of Stratum 7a corresponds with a 4000-year hiatus in owl pellet deposition between approximately 9300 and 5400 cal yr BP. Given there was no stratigraphic change or erosional surface observed, depositional rates appear to have exceedingly slowed resulting from prolonged drought conditions. Stratum 7a sediments are strictly paleontological between 148 to 138 cm (58–54 in) bd, and we excavated this 10 cm (4 in) block in two levels. Between 6000 and 5000 cal yr BP marks a transitional climatic phase between the warmer and drier Middle Holocene that prevailed prior to this time and the overall cooler and wetter climate that prevailed after this time, with BER witnessing a resurgence in occupation by human foragers and SES witnessing initial occupation by humans coupled with a resurgence of visiting owls. Humans began occupying SES periodically after the 138 cm (54 in) bd level within the upper part of Stratum 7a, and their presence is recorded by cultural remains from Stratum 6 to Stratum 1 (Figure 6).

RESULTS

Table 1 lists the NISP and MNI values for BER, and Table 4 lists the NISP values for SES.

Extant Species

At BER there is a clear difference in biodiversity between strata 20 and 17b' (pre-14,575 to 10,500 cal yr BP) and strata 17 through 13 (10,200 to 4900 cal yr BP). The Heinrich 1, Bølling-Allerød, Younger Dryas, and first half of the Early Holocene (strata 20 through 17b') are

Table 2. Radiocarbon dates and notable paleoecological events, Siblings East Shelter.

Stratum	Elevation (Below Datum)	Lab Number	Conventional Radiocarbon Age (^{14}C yr BP)	Calibrated Age Range (2 σ; cal yr BP)	Calibrated Age (2 σ Mean and Error; cal yr BP)	Material Dated	Notes
3a	57	Beta-221279	190 ± 40	307-present	169 ± 89	Hearth charcoal	Date first reported in Coe (2020)
3b	65-70	Beta-221280	2160 ± 40	2002-2310	2169 ± 87	Cordage fragment	Date first reported in Coe (2020)
3b	65-70	UGAMS-26684	4376 ± 25	4860-5037	4933 ± 47	Woven mat	Date first reported in Coe (2020)
5	100-105	Beta-297413	4350 ± 40	4842-5041	4927 ± 59	Point with binding	Date first reported in Smith et al. (2013)
7a	115-120	UGAMS-26683	4499 ± 25	5047-5295	5164 ± 76	Basket fragment	Date first reported in Coe (2020)
7a	132	Beta-221281	5260 ± 40	5929-6182	6049 ± 76	Artiodactyl dung	Date first reported in Coe (2020)
7a	138-143	Beta-686311	4700 ± 30	5321-5572	5410 ± 66	*Lepus* bone	
7a	143-148	Beta-689414	4400 ± 30	4862-5214	4971 ± 80	*Lepus* bone	End of Middle Holocene, beginning of Transitional Period; significant period of non-owl deposition of bones between about 10,500 and 5500 cal yr BP – essentially the entire Middle Holocene
7b	148-153	Beta-686312	9190 ± 40	10,245-10,491	10,352 ± 69	Artiodactyl bone	
7b	153-163	Beta-221282	8300 ± 90	9027-9481	9278 ± 122	Artiodactyl dung	Last appearance of marmot; date first reported in Coe (2020)
7b	163-168	Beta-689413	10,020 ± 40	11,318-11,738	11,518 ± 113	*Lepus* bone	First appearance of southern (desert) pocket gopher
7b	168-173	Beta-686313	9970 ± 30	11,264-11,613	11,412 ± 102	*Lepus* bone	First appearance of desert woodrat; bushy-tail and desert woodrats are sympatric
7b	173-175						First appearance of chisel-toothed kangaroo rat
7b	175-180	Beta-686314	10,070 ± 40	11,398-11,813	11,601 ± 119	*Lepus* bone	End of Younger Dryas, beginning of Early Holocene; end of amphibians and pygmy rabbit
7b	180-185						
7b	185-190	Beta-660161	10,270 ± 30	11,824-12,429	11,991 ± 112	*Lepus* bone	Last appearance of sage-grouse
7b	190-195						
7b	195-200						Last appearance of sage vole
7b	200-205	Beta-689412	10,600 ± 30	12,496-12,707	12,630 ± 58	*Lepus* bone	Few fish after this level
7b	205-210						
7b	210-215						First appearance of Ord's kangaroo rat
7b	215-220						
8a	220-225	Beta-660159	11,930 ± 40	13,608-14,016	13,819 ± 106	*Equus* bone	*Equus* rib*
8b	225-230	Beta-221283	10,690 ± 50	12,620-12,746	12,693 ± 41	*Lepus* bone	Beginning of Younger Dryas; date first reported in Coe (2020)
8b	230-235	Beta-660160	11,370 ± 30	13,175-13,309	13,244 ± 40	*Lepus* bone	End of Bølling-Allerød
8b	235-240						First appearance of bats
8b	240-245	Beta-221284	11,560 ± 50	13,316-13,571	13,420 ± 56	Artiodactyl dung	First appearance of the sage vole and pygmy rabbit; date first reported in Coe (2020)
8b/9 contact	245-255	Beta-660162	12,310 ± 40	14,091-14,808	14,330 ± 204	*Marmota* bone	Beginning of Bølling-Allerød; first appearance of bushy-tailed woodrat, marmot, deer/canyon mouse, little pocket mouse, amphibians, fish, sage-grouse, and waterfowl
9	> 255						Lake Bonneville gravel; Provo shoreline

*This date is out of sequence and suggests that the final presence of extinct *Equus* stratigraphically occurred more than a millennium earlier, during the time of lower Stratum 8b. Likely the bone was in a secondary context.

Table 3. Descriptions of the Siblings East Shelter stratigraphic profile.

Stratum 1: Loose, poorly sorted, surface sediment of pale-brown (10YR 6/3) silt with abundant (40-80%) rounded, medium (<1-3 cm) gravels and common (5-15%) subangular cobbles and small boulders (10-30 cm). Twigs and ungulate-sized dung are present. Unit 1 measures 5-12 cm in thickness and forms a clear, smooth boundary at its base. Archaeological materials are found in this stratum mixed with looters' overburden.
Stratum 2: Hardened light brownish-gray (10YR 6/2) silt with abundant (60-80%) dung. Stone clasts are few to common (2-10%) with both subangular (4-20 cm) and rounded (≤3 cm) gravels and cobbles. Unit 2 measures 10-22 cm in thickness and forms a clear, wavy lower boundary. Archaeological materials are found in this stratum.
Stratum 3: Unit 3a is a burn feature covering much of the northern half of the combined N1W1 and N1W2 excavation and consisting of charred, dark grayish-brown (10YR 4/2) silt in the lower <1-15 cm and light gray (10YR 7/1) ashy silt in the upper 2-10 cm. In total, 3a measures 2-20 cm in thickness and forms an abrupt, smooth boundary at its base. Unit 3b is a very loose yellowish brown (10YR 5/4) silt and rubble zone measuring 5-40 cm in thickness. Stone clasts are poorly sorted, common (5-15%) in number, mostly subangular with few (<5%) rounded gravels with most ranging from <1-5 cm. Three bands, rich in vegetation and bone organics with thicknesses of 5-7 cm, 15 cm, and 1-5 cm, respectively, are present in the easternmost 75 cm of N1W1. Boundaries between sublayers of 3b are clear and smooth. This sublayer contains several rodent burrows in the silt and rubble zone. The lower boundary of 3b is gradual and wavy. Archaeological materials are found in this stratum.
Stratum 4: Organic-rich (plant and bone debris) unit with poorly sorted brown (10YR 5/3) silt and rubble zone. Stone clasts are common (5-15%), mostly subangular, but some are rounded. All clasts are <10 cm gravels. Unit 4 measures 5-17 cm in thickness and has a gradual, wavy boundary with the underlying stratigraphic unit. Archaeological materials are found in this stratum.
Stratum 5: Unit 5 is a light yellowish-brown (10YR 6/4) silt. Subangular to rounded stone clasts are common (5-15%) and medium-coarse (<1-6 cm in diameter) gravel-sized. This unit contains very little vegetation. It ranges from 3-13 cm in thickness, and its basal boundary is mostly abrupt and smooth except in the eastern corner which had a gradual boundary due to bioturbation. Archaeological materials are found in this stratum.
Stratum 6: Loose, grayish-brown (10YR 5/2) silt with few (2-5%) organics of plant and bone debris with many (~40-50%) subangular cobbles and small boulders (5-30 cm). Rounded medium gravels (<2 cm) are very few (<2%) in the matrix. Unit 6 ranges from 7-20 cm in thickness and has a clear, wavy boundary except for in the eastern corner of the excavation where the boundary is gradual due to heavy bioturbation. Archaeological materials are found in this stratum.
Stratum 7: Unit 7a is a gray-brown (10YR 5/2) silt with heavy, packed organic lenses containing mostly twigs and rodent-sized dung, but also present were small animal (e.g., bird, rabbit) bones, raptor-pellet fragments, shredded bark, and a few archaeological materials. Subangular and rounded gravels are common (5-15%) and few (~2-5%) cobbles and small boulders (5-30 cm) are present. Toward the east, organics disappear with only silt and rubble present. Unit 7a measures 20-40 cm in thickness and generally forms a clear, smooth lower boundary. The eastern corner is bioturbated, blurring the boundary. Unit 7b is a compact, brownish-yellow (10YR 6/6) silt, rubble, and organic zone. Stone clasts size and quantity are same as 7a. Organics consist of rodent dung, twigs, few small animal bones, and several concentrations of indurated sediment and organics, especially rodent dung. This sublayer is 85 cm thick with a clear, smooth lower boundary.
Stratum 8: This unit is subdivided into 8a and 8b. Unit 8a is a dark yellowish-brown (10YR 4/6) silt, rubble and organic zone with common (5-15%) medium-coarse (<6 cm) subangular and rounded gravels. Organics were twigs, rodent dung, and occasional indurated concentrations. It measures 7-10 cm in thickness and has a diffuse boundary with underlying 8b. Unit 8b has the same characteristics of overlying unit 8a, but it is more compact, measuring 25-30 cm in thickness, and with a clear, smooth lower boundary.
Stratum 8/9 Contact Zone: Brown (10YR 5/3) silt, rubble, and light organic (including rodent dung and twigs) zone to the base of the excavation. Stone clasts are mixed subangular and rounded gravels. Thickness is 5-8 cm.
Stratum 9: Presence of well-rounded beach gravel with little fine sediment encountered below ~255 cm bd.

characterized by cool and mesic adapted animals indicating woodland habitat with an understory of mature sagebrush. These animals include sage-grouse, pygmy rabbit, and longwing katydid. While not overly abundant (MNI = 7), pronghorn and mountain sheep were present near the shelter during the Bølling-Allerød and Younger Dryas, and bison and deer were present during the Younger Dryas as well. No artiodactyl specimens

Table 4. Number of Identified Specimens (NISP) of the faunal remains recovered from the paleontological levels at Siblings East Shelter, Nevada[1-7].

Elevation (cm bd)	Calibrated Age (2σ Mean and Error; cal yr BP)	Horse	Marmot	Sage Vole	Chisel Toothed K-Rat	Ord's K-Rat	Pygmy Rabbit	Bushy-Tailed Woodrat	Desert Woodrat	Sage-Grouse	Ducks/ Geese	Fish	Spade-foot
138-143	5410 ± 66							1	3		20		
143-149	4971 ± 80							1	1		27		
148-153	10,352 ± 69							1			7		
153-163	9278 ± 122		1					2			28		
163-168	11,518 ± 113								2		7		
168-173	11,412 ± 102							2	1		42		
173-175					1			1			18		
175-180	11,601 ± 119						1				31		1
180-185								4			25		
185-190	11,991 ± 112							1		1	13	1	1
190-195								1		1	34		
195-200				1			2	2		1	31	1	3
200-205	12,630 ± 58					1	1			1	53	3	8
205-210						1		3		1	63	15	12
210-215						1		2		1	79	13	7
215-220				1							42	28	9
220-225		1					7	2		1	66	31	
225-230	12,693 ± 41			1			2	6		1	61	28	16
230-235	13,244 ± 40		1				7	6		1	58	38	13
235-240			1				7	2		1	73	28	9
240-245	13,420 ± 56		3	2			2	3		1	49	31	9
245-255	14,330 ± 204		3					1		1	43	39	17
> 255	Provo Gravels												
Total NISP		1	9	5	1	3	29	41	7	12	870	256	105

[1]One specimen of long-tailed weasel (*Mustela frenata*) was recovered from the 153-163 level. Specimen identified from the author's comparative collection.

[2]One specimen of pallid bat (*Antrozous pallidus*) was recovered from the 143-149 level. Specimen identified utilizing Hermanson and O'Shea (1983).

[3]One specimen of northern pocket gopher (*Thomomys talpoides*) was recovered from the 153-163 level, and three specimens of southern pocket gopher (*Thomomys bottae*) were recovered from the 153-173 levels, suggesting that both the warm-adapted *T. bottae* and cool-adapted *T. talpoides* were present in the vicinity of the shelter during the Early Holocene. Specimens identified utilizing Thaeler (1980).

[4]Fifteen mid-trunk vertebrae representing the snake Family Colubridae are present between levels 230-235 and 148-153. All 15 vertebrae display hemal keels, or hypapophyses, and thus constrictors such as the rubber boa (*Charina bottae*) within the Family Boidae that lack these structures (Holman, 2000, p. 34; Hollenshead 2002, p. 86) are not represented. Additionally, one mid-trunk vertebra specimen of a rattlesnake (*Crotalus* sp.) only appears in the 115-120 level dated to ca. 5100 cal yr BP.

[5]Within the artiodactyls, two specimens of mountain or bighorn sheep (*Ovis canadensis*) were identified in the 90-95 level dated to ca. 4300 cal yr BP, and one specimen of pronghorn (*Antilocapra americana*) was identified in the 110-115 level dated to ca. 5000 cal yr BP. These three specimens were found within the human occupation levels of the shelter and thus may be cultural rather than paleontological.

[6]Four specimens of little pocket mouse (*Perognathus longimembris*) were recovered between the 245-255 level (ca. 14,500 cal yr BP) and the 210-215 level (ca. 12,500 cal yr BP). Four specimens of *Peromyscus maniculates/crinitus* (deer mouse/canyon mouse) are present between the 245-255 level (ca. 14,500 cal yr BP) and the 205-210 level (ca. 12,500 cal yr BP). Two specimens of *Microtus* sp. (vole) were recovered between 153-173 levels, dating approximately 11,400 cal yr BP.

[7]Two species of raptors were identified in the deposits. Two specimens representing the prairie falcon (*Falco mexicanus*) were identified in the 240-255 levels, thus dating to the Bølling-Allerød climatic phase. In addition, one specimen of a long-eared owl (*Asio cf. otus*) was identified in the cultural zone in the 115-120 level dated to ca. 5100 cal yr BP.

were morphometrically identified from the earliest Early Holocene sediments (Stratum 17b'), but based on the "artiodactyl-size" of unidentifiable large mammal bone fragments indicate that they were present at this time. Most of the carnivore remains (MNI = 9/12 or 75%) are from these early strata. Additionally, the cottontail:jackrabbit ratio indicates cooler habitats than today surrounding the shelter. Cottontails are generally indicative of cooler and more mesic habitats than jackrabbits in the Great Basin. Of the 75 MNI representing the genera *Sylvilagus* and *Lepus*, 72% (54/75) are cottontails in the strata dating pre-14,575 to 10,500 cal yr BP.

In contrast, only four sage-grouse individuals and one carnivore are present in the sediments dating to the second half of the Early Holocene and the Middle Holocene (strata 17 through 13). The drop in sage-grouse numbers may indicate an expansion of more xeric-adapted vegetation at the expense of sagebrush habitat. Also, pygmy rabbits and longwing katydids disappear and never return in the deposits, suggesting a lack of mature stands of sagebrush and a reduction in conifers. The cottontail:jackrabbit MNI ratio drops to just 30% (6/20), again indicating a warmer climate in the region. Artiodactyls are present in low numbers, but they are as abundant as they were in the earlier sediments representing cooler climate (MNI = 6). Overall, artiodactyls do not become relatively abundant compared to earlier climatic phases until the onset of the Neoglacial, and this pattern continues through the Late Holocene Dry Period and the Medieval Climate Anomaly. This 3500-year period (strata 12 through 3a) includes a minimum of 29 individual pronghorn, bison, mountain sheep, and deer deposited in these strata, perhaps due to increased human hunting targeting these species.

Turning to the faunal record from SES, as noted above, Anseriformes (waterfowl) are present at all levels excavated. This may indicate that the lake dropped below the level of Blue Lake along the western edge of the Bonneville flats within several centuries of its regression from the Provo high-stand terrace. It could also indicate that ponds were available for waterfowl use in low-lying bowls or water catchments away from the shoreline.

The Bølling-Allerød period at SES (14,300 to 13,250 cal yr BP) contains a wealth of mesic-adapted species. Marmot, sage vole, pygmy rabbit, sage-grouse, fish, and spadefoot (Figures 8 and 9) are all relatively common. In addition, all the woodrat mandibles are from bushy-tailed woodrats, and none are from desert woodrats (Table 4). Sage vole, pygmy rabbit, and sage-grouse all indicate mature stands of sagebrush grew in the vicinity of SES at this time. Marmot and bushy-tailed woodrat indicate mesic boreal-type climate. Spadefoot are present throughout much of Nevada and the Great Basin today, but they, too, prefer sagebrush and woodland habitats, being found in higher elevations among spruce (*Picea* spp.) and fir (*Abies* spp.) forests (Stebbins, 1962). They are also known to inhabit caves and rockshelters, as one of us (Hockett) observed in July 2024, at the Connley Caves in south-central Oregon (Figure 9).

The Younger Dryas period at SES (12,700 to 11,600 cal yr BP) contains all the mesic-adapted species found at the Bølling-Allerød levels except marmot. Bushy-tailed woodrats are also the only woodrat species found in the Younger Dryas levels. However, there are indications that shifts in plant and animal biogeographies began during the later Younger Dryas. Sage vole, pygmy rabbit, sage-grouse, fish, and spadefoot are either rare or disappear by the 190 to 185 cm (77–73 in) bd level, radiocarbon dated to about 12,000 cal yr BP. In addition, *Dipodomys ordii* (Ord's kangaroo rat) enters the early Younger Dryas record by about 12,600 cal yr BP, while *Dipodomys microps* (chisel-toothed kangaroo rat) first enters during the waning centuries of the Younger Dryas. Grayson (2000) noted that chisel-toothed kangaroo rats generally become more abundant at Homestead Cave in relation to Ord's kangaroo rat post-Pleistocene as climate warmed. *D. ordii* prefers sagebrush habitat while *D. microps* prefers more xeric shadscale habitat.

Major changes in biogeography occur after 175 cm (69 in) bd during the Early Holocene at SES. One marmot bone occurred in the Early Holocene levels (175 to 148 cm [69–58 in] bd), but sage vole, pygmy rabbit, sage-grouse, fish, and spadefoot all disappear from the record during the early stages of the Early Holocene between 11,600 and 11,400 cal yr BP. The absence of fish likely means the fish die-off in the remaining remnants

Figure 8. Spadefoot (*Spea intermontana*). (A) Ilium, humerus, fused sacrum and urostyle, fused astragalus and calcaneus, radio-ulna, and tibio-fibula, Stratum 8b, Sisters East Shelter, 245 to 255 cm (96–100 in) bd, 14,300 cal yr BP. (B) Pelvis (ilium, ischium, pubis), humerus, fused sacrum and urostyle, fused astragalus and calcaneus, radio-ulna, and tibio-fibula, modern, eastern Nevada.

of Pleistocene Lake Bonneville was complete along its former western shores. The disappearance of sage vole, pygmy rabbit, Ord's kangaroo rat, and sage-grouse signals the replacement of mature stands of sagebrush with warm, xeric-adapted plants. The disappearance of spadefoot probably indicates the disappearance of former woodlands in this low elevation area. Finally, while bushy-tailed woodrats remain in lower numbers, desert woodrats appear for the first time approximately 11,400 cal yr BP.

Extinct Species

Dire wolf (*Aenocyon dirus*) (Perri et al., 2021) and the North American cheetah-like cat *Miracinonyx trumani* (Orr, 1969) may be present at BER, and a large extinct horse comparable in size to *Equus occidentalis* (Leidy, 1865; Azzaroli, 1998; Heintzman et al., 2017) is present at SES.

Our excavations at BER recovered four large canid bones, one in Stratum 20, two in Stratum 19, and one in Stratum 18. Three of these bones are from the lower foot, specifically a phalanx, calcaneus, and astragalus. The fourth bone is a patella (Figures 10 through 14). The phalanx recovered from Stratum 18 may belong to the same individual as the calcaneus and astragalus recovered in Stratum 19. The phalanx was burned (Figure 10) and Hockett (2007) previously identified it as a black bear (*Ursus americanus*). The act of burning modified the size and morphology of the bone. Further comparison to both bear and canid bones identified the bone as more likely belonging to a canid. The Stratum 19/Stratum 18 contact consisted of a concentration of

Figure 9. The Great Basin spadefoot (*Spea intermontana*) recently photographed in the Connley Hills, Oregon. Among other microhabitats, spadefoots inhabit and burrow inside caves and rockshelters.

burned sticks and twigs that we interpreted as inadvertently burned by a basal Stratum 18 hearth that was built directly above the natural accumulation of sticks in Stratum 19. The burned canid phalanx likely became charred during this process and was later retrieved in the basal Stratum 18 sediments, although, as noted, it likely was originally deposited in the Stratum 19 inadvertently burned wood feature. The canid calcaneus and astragalus from Stratum 19 are unburned. Lacking DNA analysis, we re-identify the phalanx as cf. gray wolf/dire wolf (cf. *Canis lupus/Aenocyon dirus*).

The remaining three canid bones are all too large to be coyote (*Canis latrans*), and thus they are either gray wolf or dire wolf. Although coyotes tended to be larger during the Late Pleistocene compared to their Holocene descendants, they did not reach the size of gray wolves or dire wolves (Merriam, 1912; Meachen and Samuels, 2012; Tomiya and Meachen, 2018). For example, measurements on the greatest length of a dire wolf femur from La Brea reported in Merriam (1912, p. 240) is 260 mm, whereas the mean greatest length of gray wolf femora from La Brea is approximately 225 mm (Tomiya and Meachen, 2018). In contrast, Meachen and Samuels (2012) report that the mean greatest length of coyote femora at La Brea is approximately 185 mm. Similarly, the mean greatest breadth of the distal femur where the patella is located for Pleistocene-aged gray wolves and coyotes at La Brea are approximately 42 mm and 30 mm, respectively (Meachen and Samuels, 2012; Tomiya and Meachen, 2018). The large canid patella is worn and would have been larger during the life of the animal (Figure 11). Even in its worn condition, it is significantly larger than the modern gray wolf patellae we examined, so it is very unlikely to be from a coyote. Nevertheless, dire wolves are known to vary in size between eastern and western North American specimens, and there is size overlap between dire wolves and some modern gray wolves from northern habitats (Anyonge and Roman, 2006). Like the canid phalanx, we conservatively identify the patella as gray wolf/dire wolf (*Canis lupus/Aenocyon dirus*).

The calcaneus and astragalus are exceptionally well preserved and offer greater confidence in a morphological identification. The calcaneus and astragalus are similar in size to specimens of modern gray wolf curated at the DMNS (Figures 12 and 13), and the Stratum 19 specimen is considerably less robust than a complete calcaneus of *Aenocyon dirus* from Carrol Cave, Missouri (KUNHM-72521) (Figure 14). The BER calcaneus measures 62 mm in length and 25 mm in maximum breadth, whereas the Carrol Cave dire wolf calcaneus measures 69.6 mm in length and 27.7 mm in maximum breadth. Nevertheless, two morphological features noted on the Carrol Cave *Aenocyon dirus* calcaneus are not shared by the modern gray wolf calcanei examined, and these same features are shared by the BER specimen. First, the posterior facet is round in the BER and Carrol Cave *Aenocyon dirus* calcanei but noticeably oval in the modern *Canis lupus* calcanei. Second, the distal ends of the BER and Carrol Cave dire wolf calcanei are convex whereas the modern gray wolf specimens display straight distal ends (Figures 12 and 14). No distinct features were noted between the BER and modern gray wolf astragali. The BER calcaneus and astragalus were found lying next to one another and undoubtedly be-

Figure 10. Canid phalanges. (A) *Aenocyon dirus*, Carrol Cave, Missouri (KUNHM-72521). (B) Stratum 18/19, Bonneville Estates Rockshelter. (C) *Aenocyon dirus*, Carrol Cave, Missouri (KUNHM-72521).

long to the same individual. We conclude that the large canid calcaneus and astragalus from Stratum 19 at BER probably belong to a dire wolf rather than to a gray wolf and tentatively identify them as cf. *Aenocyon dirus*. Future DNA analysis may produce a final resolution. If the identification of *Aenocyon dirus* is correct, this places the dire wolf along the western margin of the Bonneville basin in Nevada between 14,575 and 13,255 cal yr BP. Dire wolves went extinct approximately 13,000 cal yr BP (Peri et al., 2021).

The felid central phalanx from Stratum 20 at BER is too large to be either bobcat (*Lynx rufus*) or lynx (*Lynx canadensis*). It is either from the extinct North American "cheetah" (*Miracinonyx trumani*) or the cougar/mountain lion (*Puma concolor*). *Miracinonyx* and the African cheetah (*Acinonyx jubatas)* are not closely related although some of their bones are similar due to convergent evolution (Morgan and Seymour, 1997; Hockett and Dillingham, 2004). The extinct North American "cheetah" is instead more closely related to the North American cougar/mountain lion (Barnett et al., 2005).

Comparing the BER felid phalanx to several modern cougar and African cheetah specimens (the latter for illustrative purposes only) curated at DMNS (Figure

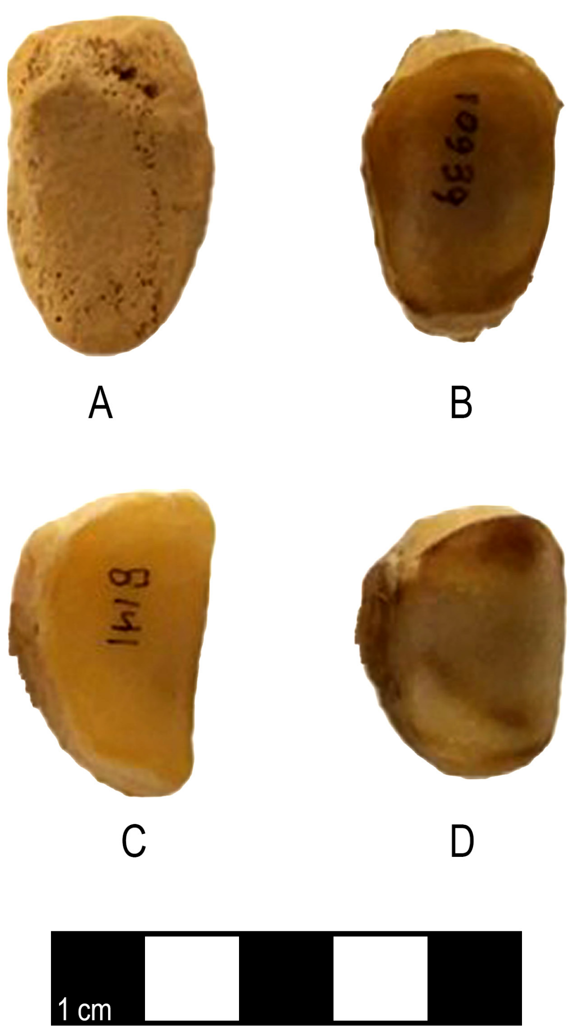

Figure 11. Canid patellae. (A) Stratum 20 (#15377), Bonneville Estates Rockshelter. (B) Modern adult female *Canis lupus* (DMNS #10939). (C) Modern adult male *Canis lupus* (DMNS #8141). (D) Modern adult female *Canis lupus* (DMNS #7731).

15) as well as a direct comparison to specimens of *Miracinonyx trumani* from Natural Trap Cave, Wyoming (Figure 16), indicates that the worn specimen from BER could identify with either *Puma* or *Miracinonyx*. If the BER specimen is *Miracinonyx*, then this places a date on the phalanx of a North American "cheetah" between 17,500 and 14,575 cal yr BP.

In 2024 the BER felid phalanx was sent to the Max Planck Institute in Germany to attempt a direct AMS date and to determine if ZooMS (Zooarchaeology by Mass Spectrometry) (Buckley et al., 2009; Antonosyan et al., 2024) could provide a definitive identification. The results of this analysis are not yet complete and will be reported at a later date.

The only extinct fauna present at SES is a horse rib from stratum 8a (Figure 17). The rib matches in size and morphology to a large Pleistocene-aged horse rib curated at the NSM, and thus we infer that it belongs to *Equus* rather than to the smaller 'stilt-legged' horse *Harringtonhippus* (formerly *Equus conversidens*) (Heintzman et al., 2017). The rib was directly dated to the Bølling-Allerød at approximately 13,800 cal yr BP.

SUMMARY AND DISCUSSION

Heinrich 1 Stadial 18,000 to 14,700 cal yr BP

Bones began accumulating in BER prior to 14,575 cal yr BP (Goebel et al., 2021); however, no bones have been dated yet from the corresponding older Stratum 20 sediments. We assume Stratum 20 began accumulating shortly after Lake Bonneville dropped below its high-stand terrace during the Bonneville flood episode estimated at 17,500 cal yr BP (Oviatt, 2020, p. 309), so bones recovered from Stratum 20 date between the onset of the Bonneville flood and the earliest date from overlying Stratum 19, or between 17,500 and 14,575 cal yr BP. Thus, with the accepted beginning of the Bølling-Allerød at 14,700 cal yr BP (Naughton et al., 2023b), most bones from Stratum 20 at BER date to the Heinrich 1 Stadial (18,000 to 14,700 cal yr BP; Naughton et al., 2023a), the beginning of which roughly correlates with the timing of the Bonneville flood.

The presence of sage-grouse and pygmy rabbit from Stratum 20 suggests an understory of mature stands of sagebrush grew near BER during Heinrich 1. Pronghorn and mountain sheep foraged in the hills surrounding the shelter. Interestingly, jackrabbits slightly outnumber cottontails. Likely the primary hare species at this time was the white-tailed jackrabbit (*Lepus townsendii*) rather than the black-tailed jackrabbit (*Lepus californicus*). While both species can be found in open grassy or sagebrush covered habitat, white-tailed jackrabbits are known to also inhabit more montane settings including coniferous forests, subalpine meadows, and even

Figure 12. Canid calcanei. (A) Stratum 19 (#21096), Bonneville Estates Rockshelter. (B) Modern adult female *Canis lupus* (DMNS #10939). (C) Modern adult male *Canis lupus* (DMNS #8141). (D) Modern adult female *Canis lupus* (DMNS #7731).

the alpine zone above tree line (Lim, 1987). Montane, mesic, or sagebrush-adapted small mammals also include marmot, sage vole, bushy-tailed woodrat, and northern pocket gopher (*Thomomys talpoides*) (Schmitt and Lupo, 2012, p. 99). One fish vertebra from Stratum 20 suggests scavenging of fish carcasses along the lake shore by raptors or carnivores. Carnivores hunting in the area included bobcat as well as a large canid (either *Aenocyon dirus* or *Canis lupus*), and a large felid (either *Miracinonyx trumani* or *Puma concolor*).

Rhode and Madsen (1995) reported on the macrobotanical contents of two Heinrich 1-aged woodrat middens in an alcove next to BER. The "BE 1a" and "BE 4b" middens date to approximately 16,550 cal yr BP (13,820 ± 90 ^{14}C BP; Beta-70607) and 15,630 cal yr BP (12,810 ± 70 ^{14}C BP; Beta-76179), respectively (Rhode and Madsen, 1995, p. 248). The vegetation surrounding the shelter at this time conforms to the faunal species present. Montane shrub vegetation dominated the midden sample. Big sagebrush (*Artemisia tridentata*), snowberry (*Symphoricarpos* sp.), prostrate juniper (*Juniperus communis*), cinquefoil (*Potentilla* sp.), currant (*Ribes* sp.), and the thistle *Cirsium* cf. *eatonii* all indicate open montane shrubby vegetation dominated the hills surrounding BER, although minor amounts of limber pine needles indicate some woodland habitat. Within this montane environment, however, two plants typically found in xeric-adapted settings today are present, rabbitbrush (*Chrysothamnus viscidiflorus*) and horsebrush (*Tetradymia* sp.).

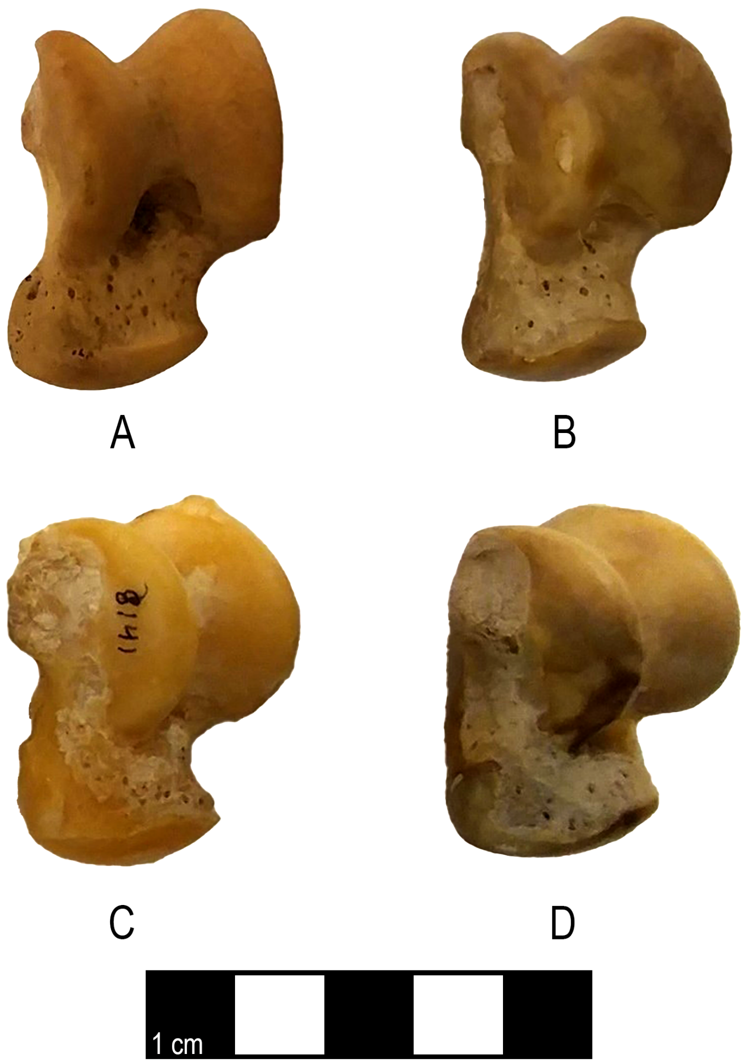

Figure 13. Canid astragali. (A) Stratum 19 (#20703), Bonneville Estates Rockshelter. (B) Modern adult female *Canis lupus* (DMNS #10939). (C) Modern adult male *Canis lupus* (DMNS #8141). (D) Modern adult female *Canis lupus* (DMNS #7731).

Bølling-Allerød Interstadial 14,700 to 12,900 cal yr BP

Stratum 19 at BER dates between 14,575 and 13,255 cal yr BP (Goebel et al., 2021). For SES, a radiocarbon date is available for the initial 10 cm (4 in) of terrestrial deposit lying directly above the Provo terrace beach gravels. This date, 12,310 ± 40 ^{14}C BP, has a calibrated age of 14,330 ± 204 cal yr BP (Reimer et al., 2020; OxCal, 2024). If Lake Bonneville fell from the Provo terrace approximately 14,500 cal yr BP (Oviatt and Pedone, 2024, p. 34), then owls began occupying SES within just a few centuries of it being dry. In any case, the estimated 14,300 cal yr BP date demonstrates the regression of Lake Bonneville from the Provo terrace in the western Bonneville basin had occurred by that time.

Fauna present in the Bølling-Allerød sediments at BER and SES are like the preceding Heinrich 1 period with montane and mesic-adapted animals dominating the samples. Sage-grouse, pygmy rabbit, sage vole, marmot, bushy-tailed woodrat, and northern pocket gopher are all present. Mountain sheep is the only artiodactyl recovered from either shelter. In contrast to the Heinrich 1 fauna, cottontails outnumber jackrabbits 4:1 at BER. Owls hunted waterfowl near SES, perhaps along the Lake Bonneville shoreline and from inland small ponds or lakes near the shelters. Owls or perhaps the prairie falcon (*Falco mexicanus*) captured spadefoot amphibians, as a prairie falcon bone was identified at SES. Owls also scavenged fish carcasses along the shoreline of the lake. Carnivores present include bobcat, bad-

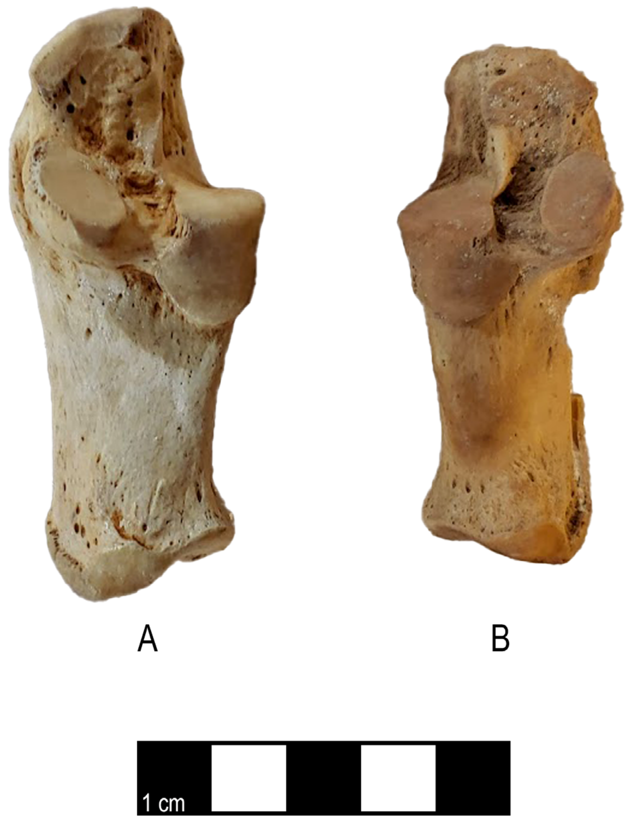

Figure 14. (A) *Aenocyon dirus* calcaneus, Carrol Cave, Missouri (KUNHM-72521). (B) Stratum 19, Bonneville Estates Rockshelter.

ger, and cf. *Aenocyon dirus*. An extinct large horse of the genus *Equus* roamed the hills near the shelters.

Vegetation growing in the area is informed by a woodrat midden collected from a shelter between BER and SES. The "PS 1" midden dates between 13,650 and 13,580 cal yr BP (11,830 ± 70 ^{14}C BP; Beta-68146) (Rhode and Madsen, 1995, p. 249). There is a shift apparent from Heinrich 1 times, with Rhode and Madsen (1995, p. 250) describing the vegetation in the region as a "limber pine woodlands and woodland/steppe mosaic." Limber pine trees are more apparent compared to the Heinrich 1 middens, while sagebrush, prostrate juniper, and snowberry continue to be present along with rabbitbrush and horsebrush. Not present in the Bølling-Allerød sample are cinquefoil, currant, and the thistle *Cirsium* cf. *eatonii*. Newcomers to the landscape include the prickly pear cactus *Opuntia*, Indian ricegrass (*Oryzopsis hymenoides*), and knotweed (*Polygonum* sp.). Overall, the fauna and flora suggest a rather cold and dry climate.

Younger Dryas Stadial 12,900 to 11,700 cal yr BP

Both shelters continued to accumulate bones throughout the Younger Dryas Stadial. Sagebrush continues to be a major shrub component in the area as sage-grouse, sage vole, and pygmy rabbit, as well as Ord's kangaroo rat are all present. Bushy-tailed woodrats and marmots continue their presence, and cottontails outnumber jackrabbits by a 2:1 margin at BER, suggesting mesic, montane conditions. New species hitherto absent from the shelters include the longwing katydid *Capnobotes occidentalis* and *Homo sapiens* at BER. The presence of human foragers explains the katydids inside BER and probably explains the expanded presence of artiodactyls including pronghorn, mountain sheep, bison, and deer at BER. It is possible that the population sizes of these smaller artiodactyls increased following the extinction of megafauna and large carnivores in the Bølling-Allerød or early Younger Dryas. Carnivores include the long-tailed weasel (*Mustela frenata*) and bobcat. Three types of owls are present at BER: the western screech owl (*Megascops kennicottii*), great horned owl (*Bubo virginianus*), and long-eared/short-eared owl (*Asio* sp). These raptors continued to hunt waterfowl and scavenge fish in the area, also depositing their bones inside SES. Extinct animals are absent in the Younger Dryas-aged sediments from both shelters. The presence of waterfowl in the SES record and their near absence in the BER record may reflect the relative proximity of SES to the marshes at Blue Lake. The absence of humans at SES during the Younger Dryas may reflect the small size and rather secluded nature of that rockshelter compared to BER.

Rhode and Madsen (1995, p. 249, Table 1) examined one fossil woodrat midden labeled "BE 3a" from the Younger Dryas and dated to approximately 12,900 cal yr BP (11,020 ± 60 ^{14}C BP; Beta-76178). The midden was in an alcove next to BER. Rhode and Madsen (1995, p. 251) describe the vegetation patterning in this midden as "sagebrush-shadscale scrub," suggesting a cooler

Figure 15. Felid central phalanges. (A) Stratum 20 (#15355), Bonneville Estates Rockshelter. (B) Modern adult male *Puma concolor* (DMNS #11070). (C) Modern adult male *Puma concolor* (DMNS #11070). (D) Modern African cheetah *Acinonyx jubatas* (DMNS #1689).

and more mesic environment than today but one that is becoming increasingly xeric. Sagebrush is present but limber pine and prostrate juniper needles are rarer than in the Bølling-Allerød-aged midden. Overall, the midden is dominated by sagebrush, shadscale (*Atriplex confertifolia*), horsebrush, rabbitbrush, and snakeweed (*Guiterrezia* sp.).

Early Holocene 11,700 to 9300 cal yr BP

Both shelters witnessed bone deposition during the Early Holocene between 11,700 and 9300 cal yr BP, but this was not an even process across the entire period. At BER, the first one-half of the Early Holocene was geologically discernible through the deposition of Stratum 17b' radiocarbon dated between 11,700 and 10,500 cal yr BP. Human foragers deposited most of this faunal debris inside the shelter. Sage-grouse and pygmy rabbit are present suggesting the continued existence of sagebrush in the area, but their bone numbers dwindle compared to the number deposited during the Younger Dryas, and both species disappear between 10,200 and 8475 cal yr BP, during the deposition of Stratum 7 at SES. No sage voles are present. Cottontails far outnumber jackrabbits (5:1) prior to 10,500 cal yr BP then disappear entirely between 10,200 and 8475 cal yr BP at BER. Cottontails similarly disappear from the Camels Back Cave record approximately 9000 cal yr BP (Schmitt et al., 2002, p. 89). No identifiable artiodactyls or katydids are found at BER between 11,600 and 8475 cal yr BP. Humans, too, are for the most part absent from BER by 10,500 cal yr BP (Goebel et al., 2021). Instead, the entire Early Holocene sediments at BER become dominated by desert woodrats (Schmitt and Lupo, 2012), and the desert woodrat enters the SES record for the first time about 11,400 cal yr BP, not surprising given SES's lower eleva-

Figure 16. Felid central phalanges. (A) Stratum 20, Bonneville Estates Rockshelter. (B) *Miracinonyx trumani* from Natural Trap Cave, Wyoming (KUNHM unnumbered).

tion. Bobcat and long-tailed weasel were present prior to 10,500 cal yr BP at BER. Owls continued to deposit bones inside SES during the Early Holocene; however, it is a depauperate fauna including single bones of marmot and the xeric-adapted kangaroo rat *Dipodomys microps*.

There is, therefore, a clear indication of a deteriorating and exceedingly xeric environment in the region during the Early Holocene. At BER, a combination of mesic- and xeric-adapted fauna persisted between 11,600 and 10,500 cal yr BP, although it was diminished compared to the Heinrich 1, Bølling-Allerød, and Younger Dryas faunas. Between 10,500 and 8475 cal yr BP humans and nonhuman animals alike largely abandoned the shelter. This pattern is starkly evident at SES where the sediments display a nearly 4000-year gap in time and very slow deposition between about 9300 and 5000 cal yr BP. The shelter appears to have been abandoned by raptors and other animals and sedimentation rates support hot and dry conditions limiting the deposition of sediment and bones during this period.

CONCLUSION AND IMPLICATIONS FOR EARLY HUMAN SETTLEMENT IN THE BONNEVILLE BASIN

Among the earliest evidence for human settlement in the Bonneville basin is found at BER during the boundary of the Bølling-Allerød Interstadial and the Younger Dryas Stadial (Goebel et al., 2021). Humans entering the basin during the early Heinrich 1 Stadial (18,000 cal yr BP) would have encountered a nearly 300-m-deep (900-ft) Lake Bonneville that stretched west-to-east from the foothills of the Goshute Mountains in Nevada to the Wasatch Range in Utah. Along the western fringes of the lake, near BER and SES, a diverse suite of cool-adapted, now-extirpated or extinct plants and animals, along with many extant species, were available to these as-yet-to-be-identified human foragers. This lake would have been relatively short-lived, as humans living in the basin 17,500 years ago likely would have witnessed the catastrophic drop in Lake Bonneville to the Provo terrace. Nevertheless, a

Figure 17. *Equus* rib from Siblings East Shelter. The bone was directly dated to 13,819 ± 106 cal yr BP.

still-formidable 200-m-deep (700-ft) lake stabilized for 3000 years, continuing to span from the foothills of the Goshute Mountains to the Wasatch Range.

Human foragers in the western Bonneville basin during the early Bølling-Allerød Interstadial (14,700 cal yr BP) would have witnessed even greater changes to the lake and its surrounding environs. Lake Bonneville's regression from the Provo terrace began by 14,300 cal yr BP and perhaps as early as 14,500 cal yr BP, with the lake dropping in elevation to near-modern Great Salt Lake levels relatively quickly thereafter (Oviatt, 2015). Only minor shifts in plant biogeography are documented in the western Bonneville basin compared to Heinrich 1 (Rhode and Madsen, 1995), and the animals inhabiting the landscape near BER and SES also did not undergo major changes in kind or distribution indicating relatively cool conditions prevailed despite the drop in lake levels.

The earliest well-dated context for human occupation of the western Bonneville basin is at BER beginning at the transition to the Younger Dryas (12,900 cal yr BP) (Goebel, 2007; Graf, 2007; Hockett, 2007, 2015; Goebel et al. 2011, 2021), and soon thereafter humans appear at nearby Danger Cave and the Old River Bed Delta (Rhode et al., 2005; Duke et al., 2022, 2024). Humans likely witnessed the resurgence of a relatively shallow 15-m-deep (50-ft) lake that once again spanned from the Nevada-Utah border to present-day Salt Lake City (Oviatt et al., 2024). During this early Younger Dryas-aged transgression, the Blue Lake marshes near SES and BER, as well as the Old River Bed Delta to the southeast became submerged underwater and devoid of marshes and the diverse plants and animals that they harbor (Louderback and Rhode, 2019; Palacios-Fest et al., 2021; Oviatt et al., 2024). BER and SES, in contrast, remained high and dry and open for habitation. Ironically, however, human foragers chose to repeatedly occupy BER throughout the Younger Dryas while no such occupation is similarly documented at SES. This is probably due to BER being a much bigger shelter situated along a major wash draining a large area of the Goshute Mountains and foothills, in contrast to SES, which is in a locally draining, lower-elevation wash. Human foragers hunted a diverse suite of large and small mammals, terrestrial birds (sage-grouse), and insects around BER in the foothill slopes above the Currey cycle lake (Hockett, 2007, 2015). Around 12,300 cal yr BP, when the lake dropped in elevation again, reaching below the Old River Bed Delta and Blue Lake, re-establishing their marshes, human foragers probably made forays between BER and the Delta allowing them to add a diverse suite of waterfowl (Duke et al., 2022) to their already diverse diet of terrestrial animal resources being consumed at BER for the previous six centuries. Ironically, SES is between BER and the Old River Bed Delta, not to mention about half the distance to the Blue Lake marsh, yet humans eschewed using the site as a domestic camp. We found no evidence for humans processing waterfowl carcasses inside SES or BER. If they were hunting these birds at Blue Lake, such processing sites are more likely buried there in open-air contexts and remain undiscovered.

The Younger Dryas pattern of hunting terrestrial and aquatic animal resources continued during the first half of the Early Holocene between 11,700 and 10,500 cal yr BP. Due to deteriorating conditions caused by increasingly warmer, and perhaps drier climate, humans largely abandoned BER by 10,500 cal yr BP, and their 2500-year history of consuming a diverse suite of terrestrial resources in the foothills of the Goshute Mountains came to a halt. Nonetheless, human foragers were able to continue to exploit marsh resources at the Old River Bed Delta for the next millennium, until approximately 9500 cal yr BP (Madsen, et al., 2015; Duke et al., 2022).

The overall warm and dry Middle Holocene that commenced by 9300 cal yr BP in the eastern Great Basin saw human foragers largely abandon both BER and the Old River Bed Delta in favor of places on the landscape that still provided reliable sources of water such as Danger Cave to the north and Hogup Cave to the northeast. SES does not contain a viable biogeographic record during most of the Middle Holocene, specifically between 9300 and about 5000 cal yr BP. The SES stratigraphic record documents a 4000-year hiatus of owl pellet and sediment deposition with no clear evidence of an erosional event. During this time, however, BER was periodically occupied by human foragers (Hockett, 2007, 2015; Goebel et al., 2021), including a brief occupation that corresponds to the 8200 cal yr BP (8.2 ka) global cooling event in the North Atlantic (Alley and Agústsdóttir, 2005; Schmidt and LeGrande, 2005) and another longer-term series of occupations between 6400 and 4900 cal yr BP (Goebel et al., 2021), the latter being associated with a late Middle Holocene transitional period of increased moisture (Hockett, 2007). SES, too, began seeing humans visiting the shelter for the first time at about 5500 cal yr BP. Humans repeatedly occupied both BER and SES thereafter until Euroamerican contact with relatively brief periods of non-occupation, such as the 550-year span of non-occupation at BER associated with the Late Holocene Dry Period (Goebel et al., 2021).

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REFERENCES

Alley, R., and Agústsdóttir, A., 2005, The 8k event—cause and consequences of a major Holocene abrupt climate change: Quaternary Science Reviews, v. 24, p. 1123–1149.

Andrews, P., 1990, Owls, caves and fossils: Chicago, University of Chicago Press, 231p.

Antevs, E. 1948, The Great Basin with emphasis on glacial and postglacial times III—climatic changes and prewhite man: Bulletin of the University of Utah, v. 38, p. 167–191.

Antonosyan, M., Hill, E., Jodry, M., Amano, N., Brown, S., Rick, T., and Boivin, N., 2024, A new legacy—potential of zooarchaeology by mass spectrometry in the analysis of North American megafaunal remains: Frontiers in Mammal Science, v. 3, p. 1–11, https://www.frontiersin.org/journals/mammal-science/articles/10.3389/fmamm.2024.1399358/full.

Anyonge, W., and Roman, C., 2006, New body mass estimates for *Canis dirus*, the extinct Pleistocene dire wolf: Journal of Paleontology, v. 26, p. 209–212.

Azzaroli, A., 1998, A synopsis of the Quaternary species of *Equus* in North America: Bolletina della Societa Paleontologica Italiano, v. 34, p. 206–221.

Barnett, R., Barnes, I., Phillips, M. J., Martin, L.D., Harington, C.R., Leonard, J.A., and Cooper, A., 2005, Evolution of the extinct sabre-tooths and the American cheetah like cat: Current Biology, v. 15, p. R1–R2.

Bradbury, C.D., Jewell, P.W., Fernandez, D.P., Lerback, J.C., DeGraffenried, J.V., and Petersen, E.U., 2020, Water provenance at the Old River Bed inland delta and ground water flow from the Sevier Basin of central Utah during the Pleistocene-Holocene transition: Quaternary Research v. 99, p. 114–127.

Broughton, J.M., 2000, The Homestead Cave ichthyofauna, *in* Madsen, D.B., editor, Late Quaternary paleoecology in the Bonneville basin: Utah Geological Survey Bulletin 130, p. 103–121.

Broughton, J.M., Madsen, D.B., and Quade, J., 2000, Fish remains from Homestead Cave and lake levels of the past 13,000 years in the Bonneville basin: Quaternary Research, v. 53, p. 392–401.

Broughton, J.M., and Miller, S.D., 2016, Zooarchaeology and field ecology—a photographic atlas: Salt Lake City, University of Utah Press, 201 p.

Buckley, M., Collins, M., Thomas-Oates, J., and Wilson, J.C., 2009, Species identification by analysis of bone collagen using matrix-assisted laser desorption/ionisation time-of-flight mass spectrometry: Rapid Communications in Mass Spectrometry, v. 23, p. 3843–3854.

Coe, M.M., 2020, Reconstructing identity in the Bonneville basin—Holocene-aged cordage and coiled basketry from the eastern Great Basin: College Station, Texas A&M University, Ph.D. dissertation, 405 p.

Cook, E.R., Woodhouse, C.A., Eakin, C.M., Meko, D.M., and Stahle, D.W., 2004, Long-term aridity changes in the Western United States: Science, v. 306, p. 1015–1018.

Currey, D.R., and James, S.R., 1982, Paleoenvironments of the northeastern Great Basin and northeastern basin rim region—a review of geological and biological evidence, *in* Madsen, D.B., and O'Connell, J.F., editors, Man and environment in the Great Basin: Society for American Archaeology Papers No. 2, p. 27–52.

Duke, D., Wohlgemuth, E., Adams, K.R., Armstrong-Ingram, A., Rice, S.K., and Young, D.C., 2022, Earliest evidence for human use of tobacco in the Pleistocene Americas: Nature Human Behavior, v. 6, p. 183–192.

Duke, D., Urban, T.M., Freund, K., Kitterman, A., and Young, D.C., 2024, The Trackway Site—human footprints from the Pleistocene-Holocene transition in western Utah's Great Salt Lake Desert [abs.]: Society for American Archaeology, 89th Annual Meeting Abstracts with Programs, p. 265.

Goebel, T., 2007, Pre-Archaic and early Archaic technological activities at Bonneville Estates Rockshelter—a first look at the artifact record, *in* Graf, K.E., and Schmitt, D.N., editors, Paleoindian or paleoarchaic?—Great Basin human ecology at the Pleistocene-Holocene transition: Salt Lake City, University of Utah Press, p. 156–184.

Goebel, T., Hockett, B., Adams, K.D., Rhode, D., and Graf, K., 2011, Climate, environment, and humans in North America's Great Basin during the Younger Dryas, 12,900-11,600 calendar years ago: Quaternary International, v. 242, p. 479–501.

Goebel, T., Hockett, B., Rhode, D., and Graf, K., 2021, Prehistoric human response to climate change in the Bonneville basin, western North America: the Bonneville Estates Rockshelter radiocarbon chronology: Quaternary Science Reviews, v. 260, unpaginated, https://www.sciencedirect.com/science/article/abs/pii/S0277379121001372.

Gomez, R.O., and Turazzini, G.F., 2016, An overview of the ilium of Anurans (Lissamphibia: Salientia) with a critical appraisal of the terminology and primary homology of main ilial features: Journal of Vertebrate Paleontology, v. 36, p. 1–12.

Graf, K.E., 2007, Stratigraphy and chronology of the Pleistocene to Holocene transition at Bonneville Estates Rockshelter, eastern Great Basin, *in* Graf, K.E., and Schmitt, D.N., editors, Paleoindian or paleoarchaic? Great Basin human ecology at the Pleistocene-Holocene transition:

Salt Lake City, University of Utah Press, p. 82–104.

Grayson, D.K., 1983, The paleontology of Gatecliff Shelter—small mammals, *in* Thomas, D.H., editor, The archaeology of Monitor Valley 2. Gatecliff Shelter: New York, Anthropological Papers American Museum of Natural History, v. 59, no. 1, p. 99–135.

Grayson, D.K., 1985, The paleontology of Hidden Cave—birds and mammals, *in* Thomas, D.H., editor, The archaeology of Hidden Cave, Nevada: New York, Anthropological Papers American Museum of Natural History, v. 61, no. 1, p. 125–161.

Grayson, D.K., 1988, Danger Cave, Last Supper Cave, and Hanging Rock Shelter—the faunas: New York, Anthropological Papers American Museum of Natural History, v. 66, no. 1, 130 p.

Grayson, D.K, 1998, Moisture history and small mammal community richness during the latest Pleistocene and Holocene, northern Bonneville Basin, Utah: Quaternary Research, v. 49, p. 330-334.

Grayson, D.K., 2000, The Homestead Cave mammals, *in* Madsen, D.B., editor, Late Quaternary paleoecology in the Bonneville basin: Utah Geological Survey Bulletin 130, p. 67–89.

Grayson, D.K., 2006, The Late Quaternary biogeographic histories of some Great Basin mammals (Western USA): Quaternary Science Reviews, v. 25, p. 2964–2991.

Grayson, D.K., 2016, Giant sloths and sabertooth cats—extinct mammals and the archaeology of the Ice Age Great Basin: Salt Lake City, University of Utah Press, 421 p.

Heintzman, P.D., Zazula, G.D., MacPhee, R.D.E., Scott, E., Cahill, J.A., McHorse, B.K., Kapp, J.D., Stiller, M., Wooller, M.J., Orlando, L., Southon, J., Froese, D.G., and Shapiro, B., 2017, A new genus of horse from Pleistocene North America: eLife v. 2017, no. 6, p. 1–43, https://doi.org/10.7554/eLife.29944.

Hermanson, J.W., and O'Shea, T., 1983, *Antrozous pallidus*: Mammalian Species, v. 213, p. 1–8.

Hockett, B., 1995, Comparison of leporid bones in raptor pellets, raptor nests, and archaeological sites in the Great Basin: North American Archaeologist, v. 16, p. 223–238.

Hockett, B., 2007, Nutritional ecology of Late Pleistocene to Middle Holocene subsistence in the Great Basin—zooarchaeological evidence from Bonneville Estates Rockshelter, *in* Graf, K.E., and Schmitt, D.N., editors, Paleoindian or paleoarchaic? Great Basin human ecology at the Pleistocene-Holocene transition: Salt Lake City, University of Utah Press, p. 204–230.

Hockett, B., 2015, The zooarchaeology of Bonneville Estates Rockshelter—13,000 years of Great Basin hunting strategies: Journal of Archaeological Science Reports, v. 2, p. 291–301.

Hockett, B., and Dillingham, E., 2004, Paleontological investigations at Mineral Hill Cave: U.S. Bureau of Land Management Technical Report 18, 177 p.

Hollenshead, M., 2002, Late Pleistocene to Holocene reptiles from Mineral Hill Cave, north-central Nevada: Flagstaff, University of Northern Arizona, M.A. thesis, 169 p.

Holman, J.A., 1995, Pleistocene amphibians and reptiles in North America: New York, Oxford University Press, 243 p.

Holman, J.A., 2000, Fossil snakes of North America: Bloomington, Indiana University Press, 357 p.

Hubbs, C.L., and Miller, R.R., 1948, The Great Basin with emphasis on glacial and postglacial times II—the zooarchaeological evidence: Bulletin of the University of Utah, v. 38, p. 18–166.

Jennings, J.D., 1957, Danger Cave: Memoirs of the Society for American Archaeology, no. 14, 328 p.

Jorgensen, M.E., 2011, The evolution of jumping in frogs: Journal of Morphology, v. 272, p. 149–168.

Leidy, J., 1865, Bones and teeth of horses from California and Oregon: Proceedings of the Academy of Natural Sciences of Philadelphia, v. 17, p. 1–94.

Lim, B.K., 1987, *Lepus townsendii*: Mammalian Species, no. 288, p. 1–6.

Livingston, S.D., 2000, The Homestead Cave avifauna, *in* Madsen, D.B., editor, Late Quaternary paleoecology in the Bonneville basin: Utah Geological Survey Bulletin 130, p. 91-102.

Louderback, L.A., and Rhode, D.E., 2009, 15,000 years of vegetation change in the Bonneville basin—the Blue Lake pollen record: Quaternary Science Reviews, v. 28, p. 308–326.

Madsen, D.B., 2000, Late Quaternary paleoecology in the Bonneville basin: Utah Geological Survey Bulletin 130, 190 p.

Madsen, D.B., and Currey, D.R., 1979, Late Quaternary glacial and vegetation changes, Little Cottonwood Canyon area, Wasatch Mountains, Utah: Quaternary Research, v. 12, p. 254–270.

Madsen, D.B., Rhode, D., Grayson, D.K., Broughton, J.M., Livingston, S.D., Hunt, J., Quade, J., Schmitt, D.N., and Shaver, M.W., III, 2001, Late Quaternary environmental change in the Bonneville basin, Western USA: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 167, p. 243–271.

Madsen, D.B., Schmitt, D.N., and Page, D., 2015, The paleoarchaic occupation of the Old River Bed delta: University of Utah Anthropological Papers 128, 280 p.

Mann, M.E., Zhang, Z., Rutherford, S., Bradley, R.S., Hughes, M.K., Shindell, D., Ammann, C., Faluvegi, G., and Ni, F., 2009, Global signatures and dynamical origins of the Little Ice Age and Medieval Climate Anomaly: Science, v. 326, p. 1256–1260.

Mead, J.I., Thompson, R.S., and Van Devender, T.R., 1982, Late Wisconsin and Holocene fauna from Smith Creek Canyon, Snake Range, Nevada: Transactions of the San Diego Society of Natural History, v. 20, p. 1–26.

Mead, J.I., Swift, S.L., McDonald, H.G., and Emslie, S.L., 2023, First Shasta ground sloth (*Nothrotheriops*; Xenarthra) from the eastern Great Basin, Nevada: Western North American Naturalist, v. 83, p. 269–276.

McGee, D., Quade, J., Edwards, R.L., Broecker, W.S., Cheng, H., Reiners, P.W., and Evenson, N., 2012, Lacustrine cave carbonates—novel archives of paleohydrologic change in the Bonneville Basin (Utah, USA): Earth and Planetary Science Letters, v. 351-352, p. 182–194.

Meachen, J.A., and Samuels, J.X., 2012, Evolution in coyotes (*Canis latrans*) in response to the megafaunal extinctions: Proceedings of the National Academy of Sciences, v. 109, p. 4191–4196.

Mensing, S.A., Sharpe, S.E., Tunno, I., Sada, D.W., Thomas, J.M., Starratt, S., and Smith, J., 2013, The Late Holocene Dry Period—multiproxy evidence for an extended drought between 2800 and 1850 cal yr BP across the central Great Basin, USA: Quaternary Science Reviews, v. 78, p. 266–282.

Mensing, S.A., Wang, W., Rhode, D., Kennett, D.J., Csank, A., Thomas, D.H., Briem, C., Harper, T.K., Culleton, B.J., George, R.J., and Southon, J., 2023, Temporal and geographic extent of the Late Holocene Dry Period in the central Great Basin, USA: Quaternary Science Reviews, v. 300, https://www.sciencedirect.com/science/article/abs/pii/S0277379122005315.

Merriam, J.C., 1912, The fauna of Rancho La Brea, Part II—Canidae: Berkeley, Memoirs of the University of California, v. 1, p. 215–272.

Mifflin, M.D., and Wheat, M.M., 1979, Pluvial lakes and estimated pluvial climates of Nevada: Reno, University of Nevada, Mackay School of Mines Bulletin 94, 57 p.

Millar, C.I., and Thomas, D.H., 2024, Reconciling Neoglacial climates during the Late Holocene Dry Period, Great Basin, USA: Quaternary Science Reviews, v. 327, https://www.sciencedirect.com/science/article/pii/S0277379124000325?via%3Dihub.

Milligan, M., and McDonald, H.G., 2017, Shorelines and vertebrate fauna of Pleistocene Lake Bonneville, Utah, Idaho, and Nevada: Geology of the Intermountain West, v. 4, p. 181–214.

Morgan, G.S., and Seymour, K.L., 1997, Fossil history of the panther (*Puma concolor*) and the cheetah-like cat (*Miracinonyx inexpectatus*) in Florida: Bulletin of the Florida Museum of Natural History, v. 40, p. 177–219.

Naughton, F., Sánchez-Goñi, M.F., Landais, A., Rodrigues, T., Riveiros, N.V., and Toucanne, S., 2023a, Heinrich Stadial 1, *in* Palacios, D., Hughes, P. D., García-Ruiz, J. M., and de Andres, N., editors, European glacial landscapes—the last deglaciation: Amsterdam, Elsevier, p. 37–44.

Naughton, F., Sánchez-Goñi, M. F., Landais, A., Rodrigues, T., Riveiros, N. V., and Toucanne, S., 2023b, The Bølling-Allerød Interstadial, *in* Palacios, D., Hughes, P.D., García-Ruiz, J.M., and de Andres, N., editors, European glacial landscapes—the last deglaciation: Amsterdam, Elsevier, p. 45–50.

Naughton, F., Sánchez-Goñi, M.F., Landais, A., Rodrigues, T., Riveiros, N.V., and Toucanne, S., 2023c, The Younger Dryas Stadial, *in* Palacios, D., Hughes, P.D., García-Ruiz, J.M., and de Andres, N., editors, European glacial landscapes—the last deglaciation: Amsterdam, Elsevier, p. 51–57.

O'Connor, J.E., 1993, Hydrology, hydraulics, and geomorphology of the Bonneville flood: Geological Society of America Special Paper 274, 83 p.

Orr, P. C., 1969, Felis trumani—a new radiocarbon dated cat skull from Crypt Cave, Nevada: Santa Barbara Natural History Museum, Department of Geology Bulletin, v. 2, p. 1–8.

Oviatt, C.G., 2014, The Gilbert episode in the Great Salt Lake basin, Utah: Utah Geological Survey Miscellaneous Publication 14-3, 20 p.

Oviatt, C.G., 2015, Chronology of Lake Bonneville, 30,000 to 10,000 yr BP: Quaternary Science Reviews, v. 110, p. 166–171.

Oviatt, C.G., 2020, G.K. Gilbert and the Bonneville shoreline: Geology of the Intermountain West, v. 7, p. 301–320.

Oviatt, C.G., 2024, Late Neogene and Quaternary lacustrine history of the Great Salt Lake—Bonneville basin, *in* Vanden Berg, M.D., Ford, R.L., Frantz, C., Hurlow, H., Gunderson, K., and Atwood, G., editors, Great Salt Lake and the Bonneville basin—geologic history and anthropocene issues: Utah Geological Association Publication 51, p. 1–16

Oviatt, C.G., Atwood, G., and Thompson, R.S., 2021, History of Great Salt Lake, Utah, USA—since the termination of Lake Bonneville, *in* Rosen, M.R., Finkelstein, D.B., Park Boush, L., and Pla-Pueyo, S., editors, Limnogeology—progress, challenges and opportunities: Switzerland, Springer Cham., p. 233–271.

Oviatt, C.G., and Pedone, V.A., 2024, Chronology of the early transgressive phase of Lake Bonneville: Quaternary Research, v. 121, p. 32–39.

Oviatt, C.G., Young, D.C., and Duke, D., 2024, The Currey cycle of Great Salt Lake—an early Younger Dryas lake in the Bonneville basin, Utah, USA: Journal of Quaternary Science, v. 39, no. 6, p. 932–945.

OxCal v.4.4, 2024, https://c14.arch.ox.ac.uk/oxcal/OxCal.html#: University of Oxford, U.K.

Palacios-Fest, M.R., Duke, D., Young, D.C., Kirk, J.D., and Oviatt, C.G., 2021, A paleo-lake and wetland paleoecology associated with human use of the distal Old River Bed Delta at the Pleistocene-Holocene transition in the Bonneville Basin, Utah, USA: Quaternary Research, v. 106, p. 75–93.

Palmer, H.M., Vriesman, V.P., Livsey, C.M., Fish, C.R., and Hill, T.M., 2023, Holocene climate and oceanography of the coastal Western United States and California current system: Climate of the Past, v. 19, p. 199–232.

Perri, A.R., Mitchell, K.J., Mouton, A., et al., 2021, Dire wolves were the last of an ancient New World canid lineage: Nature, v. 591, p. 87–91.

Pugener, A., 2010, Developmental evolution of the Anuran sacro-urostylic complex: Journal of Herpetology, v. 4, p. 193–209.

Reimer, P. J., Austin, W.E.N., Bard, E., et al., 2020, The IntCal20 northern hemisphere radiocarbon age calibration curve (0–55 cal kBP): Radiocarbon, v. 62, p. 725–757.

Rhode, D., 2000, Middle and Late Wisconsin vegetation in the Bonneville Basin, *in* Madsen, D.B., editor, Late Quaternary paleoecology in the Bonneville basin: Utah Geological Survey Bulletin 130, p. 137–147.

Rhode, D., and Madsen, D.B., 1995, Late Wisconsin/Early Holocene vegetation in the Bonneville basin: Quaternary Research, v. 44, p. 246–256.

Rhode, D., Madsen, D.B., and Jones, K.T., 2006, Antiquity of Early Holocene small-seed consumption and processing at Danger Cave: Antiquity, v. 80, p. 328–339.

Rhode, D., Goebel, T., Graf, K.E., Hockett, B., Jones, K.T., Madsen, D.B., Oviatt, C.G., and Schmitt, D.N., 2005, Latest Pleistocene-early Holocene human occupation and paleoenvironmental change in the Bonneville basin, Utah-Nevada, *in* Pederson, J., and Dehler, C., editors, Interior Western United States: Geological Society of America Field Guide 6, 10.1130/2025.fld006(10).

Schmidt, G., and LeGrande, A., 2005, The Goldilocks abrupt climate change event: Quaternary Science Reviews, v. 24, p. 1109–1110.

Schmitt, D.N., and Juell, K., 1994, Toward the identification of coyote scatological faunal accumulations in archaeological contexts: Journal of Archaeological Science, v. 21, p. 249–262.

Schmitt, D.N., and Lupo, K.D., 2012, The Bonneville Estates Rockshelter rodent fauna and changes to Late Pleistocene-Middle Holocene climates and biogeography in the northern Bonneville basin, USA: Quaternary Research, v. 78, p. 95–102.

Schmitt, D.N., and Lupo, K.D., 2016, Changes in Late Quaternary mammalian biogeography in the Bonneville basin: Developments in Earth Surface Processes, v. 20, p. 352–370.

Schmitt, D.N., and Lupo, K.D., 2018, On Early-Holocene moisture and small-mammal histories in the Bonneville basin, Western United States: The Holocene, v. 28, p. 492–498.

Schmitt, D.N., Madsen, D.B., and Lupo, K.D., 2002, The worst of times, the best of times—jackrabbit hunting by Middle Holocene human foragers in the Bonneville basin of Western North America, *in* Mondini, M., Muñoz, S., and Wickler, S., editors, Colonization, migration, and marginal areas: Durham, Proceedings of the 9th ICAZ Conference, p. 86–95.

Smith, G.A., Barker, P., Hattori, E.M., Raymond, A., and Goebel, T., 2013, Points in time—direct radiocarbon dates on Great Basin projectile points: American Antiquity, v. 78, p. 580-594.

Spencer, R.J., Baedecker, M.J., Eugster, H.P., Forester, R.M., Goldhaber, M.B., Jones, B.F., Kelts, K., McKenzie, J., Madsen, D.B., Rettig, S.L., Rubin, M., and Bowser, C.J., 1984, Great Salt Lake, and precursors, Utah—the last 30,000 years: Contributions to Mineralogy and Petrology, v. 86, p. 321–334.

Stebbins, R. C., 1962, Amphibians of Western North America: Berkeley, University of California Press, 539 p.

Stine, S., 1994, Extreme and persistent drought in California and Patagonia during Mediaeval time: Nature, v. 369, p. 546–549.

Thaeler, C.S., Jr., 1980, Chromosome numbers and systematic relations in the genus *Thomomys* (Rodentia: Geomyidae): Journal of Mammalogy, v. 61, p. 414–422.

Thompson, R.S., 1990, Late Quaternary vegetation and climate in the Great Basin, *in* Betancourt, J.L., Van Devender, T.R., and Martin, P.S., editors, Packrat middens—the last 40,000 years of biotic change: Tucson, University of Arizona Press, p. 200–239.

Thompson, R.S., Oviatt, C.G., Honke, J.S., and McGeehin, J.P., 2016, Late Quaternary changes in lakes, vegetation, and climate in the Bonneville basin reconstructed from sediment cores from Great Salt Lake, *in* Oviatt, C.G., and Shroder, J.F., Jr., editors, Lake Bonneville—a scientific update: Developments in Earth Surface Processes, v. 20, p. 221–291.

Tinkham, E.R., 1944, Biological, taxonomic and faunistic studies on the shield-back katydids of the North American deserts: The American Midland Naturalist, v. 31, p. 257–328.

Tomiya, S., and Meachen, J.A., 2018, Postcranial diversity and recent ecomorphic impoverishment of North American gray wolves: Biological Letters, v. 14, https://royalsocietypublishing.org/doi/10.1098/rsbl.2017.0613.

Voous, K.H., 1988, Owls of the northern hemisphere: Cambridge, Massachusetts Institute of Technology Press, 320 p.