4-5-2012

Shifting prehistoric abundances of leporids at Five Finger Ridge, a central Utah archaeological site

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Prehistoric biogeographic data obtained from archaeological records may be used to identify changes in taxonomic ranges in response to shifting climate (e.g., Grayson 2000, 2002, 2005, 2006, Grayson and Madsen 2000, Butler and O'Connor 2004, Eda and Higuchi 2004, Schmitt 2004, Byers et al. 2005, Grayson and Delpech 2005, Bovy 2007). Here I report on the temporal distributions of 3 leporids, *Sylvilagus audubonii* (desert cottontail), *S. nuttallii* (mountain cottontail), and *Lepus* sp. (jackrabbit) from Five Finger Ridge, an archaeological site in the eastern Great Basin of central Utah (Fig. 1). This site was occupied by the Fremont during a time of climate fluctuations related to the Medieval Warm Period and Little Ice Age and is located in the vicinity of the modern range of the 2 cottontail species. By evaluating the relative abundances of leporids from dated contexts in light of local paleovegetation records, it is possible to obtain a greater understanding of the distribution of these leporid species and their response to changing environmental conditions.

**LEPORIDS IN CENTRAL UTAH**

According to Durrant (1952), *S. nuttallii* has a distribution through central Utah limited to the central north–south mountain ranges, including the Wasatch Range, Pahvant Range, and Tushar Mountains (Fig. 2). Although Hall (1951, 1981) and others map the distribution of *S. nuttallii* throughout the eastern Great Basin of Utah, Durrant (1952) excludes most of the Bonneville Basin and Colorado Plateau. The species occupies sagebrush-dominated areas in the northern part of its range, but it is generally limited to timbered areas of the Transition life zone at higher elevations in the southern part of its range (Hall 1951, Durrant 1952, Chapman 1975, Hall 1981). Orr (1940) lists the elevation limit between 1372 m and 3200 m in California, where the range of *S. nuttallii* covers the same general span of latitudes as in central Utah. Considering the elevation limits and the lack of records from the Bonneville Basin and Colorado Plateau reported by Hall and others, Durrant’s map of the distribution of *S. nuttallii* is probably a more accurate representation of the species’ modern range.

In contrast to *S. nuttallii*, *S. audubonii* is found in dense, brushy areas of desert scrub and plains–desert grasslands of the Lower Sonoran life zone at elevations from sea level to 1829 m (Hall 1946, Chapman and Willner 1978, Hoffmeister 1986). Due to the lower elevation threshold of *S. audubonii* compared
to *S. nuttallii*, the range of the former covers much of the territory where the latter is absent (Durrant 1952, Hall 1981; Fig. 2). However, the ranges of the 2 species overlap at times in Utah’s southern latitudes. Where both species are present, *S. nuttallii* is limited to higher altitudes of the Upper Sonoran and Transition life zones, while *S. audubonii* occupies lower desert valleys (Hall 1946, 1951, Chapman 1975, Chapman and Willner 1978, Hoffmeister 1986).

Three species of *Lepus* are present in central Utah. The distribution of *L. townsendii* (whitetailed jackrabbit) follows that of *S. nuttallii*, with similar elevation limits in the southern portion of its range (Durrant 1952). As with *S. nuttallii*, others have mapped a wider distribution of *L. townsendii*, which encompasses most of Utah (Hall 1951, 1981, Lim 1987), but Durrant states that individuals are not found below approximately 2400 m in the southern limits of its range. The black-tailed jackrabbit, *L. californicus*, is found throughout most of Utah in the Upper Sonoran and Transition life zones (Hall 1951, Durrant 1952, Best 1996). *Lepus americanus* (snowshoe hare) is limited to the Boreal life zone in central Utah, at altitudes much higher than of concern here (Hall 1951, Durrant 1952).
FIVE FINGER RIDGE

Five Finger Ridge is located in Clear Creek Canyon, Sevier County, Utah (Fig. 1). The site sits on top of an alluvial knoll with a series of 5 ridges ranging from 1814 m to 1829 m above sea level (Janetski 1998, Janetski et al. 2000, Talbot et al. 2000). This places the site at roughly the modern altitudinal limit of *S. audubonii* (Chapman and Willner 1978), and Durrant’s (1952) map shows that the present range limit is immediately to the east of Clear Creek. Chapman and Willner’s (1978) map shows that the present range limit is immediately to the east of Clear Creek. Chapman and Willner’s (1978) map shows that the present range limit is immediately to the east of Clear Creek. Five Finger Ridge is also near the southern range limits of *S. audubonii*, where the species is generally found at higher altitudes. Thus, the site is in a key location for evaluating temporal fluctuations in the relative abundances of leporid species. Climate conditions favoring the expansion of woodlands to lower altitudes should result in greater frequencies of *S. nuttallii* in the vicinity of the site.

Vegetation surrounding the site consists of scattered sagebrush (*Artemisia* sp.), saltbrush and shadscale (*Atriplex* spp.), grasses, prickly pear (*Opuntia polyacantha*), skunkbush (*Rhus trilobata*), and other forbs and shrubs. Pinyon pine (*Pinus edulis*) and juniper (*Juniperus osteosperma*) trees are scattered on portions of the site. The Clear Creek floodplain contains cottonwood (*Populus fremontii*), ash (*Fraxinus* sp.), sagewrack (*Artemisia* sp.), willow (*Salix* sp.), wildrose (*Rosa* sp.), wild grape (*Vitis* sp.), Mormon tea (*Ephedra* sp.), rabbitbrush (*Chrysothamnus* sp.), grasses, and scrub oak (*Quercus gambelii*) (Talbot et al. 2000).

Settlement of Five Finger Ridge is attributed to the Fremont, whose culture was present in the eastern Great Basin and adjacent Colorado Plateau regions between ca. AD 400 and 1300 (Madsen 1989, Talbot and Wilde 1989, Madsen and Simms 1998). Although there is considerable variation in Fremont life ways, their culture is defined largely on the archaeological presence of maize horticulture, ceramics, and distinct basketry. The Fremont occupied the region during a period of increased summer temperatures and moisture which allowed for maize, bean, and squash cultivation. They exhibited considerable behavioral plasticity between farming and foraging, with maize production dependent on favorable environmental conditions (Berry 1980, Grayson 2011) and consumption largely dependent on sex and prestige (Coltrain and Stafford 1999, Coltrain and Leavitt 2002). The Fremont was the only cultural group in the Great Basin with a ceramic tradition at that time, and they differ from adjacent, contemporary pottery-producing groups (such as the Anasazi to the south) by their thin-walled, coiled grayware that is generally undecorated (Janetski 1994). Fremont coiled basketry is likewise distinguished from neighboring groups by one-rod-and-bundle and half-rod-and-bundle construction that was present throughout the region (Adovasio et al. 2002). Other characteristics of the Fremont include distinctive rock art styles, anthropomorphic figurines, and presence of large residential sites.

Five Finger Ridge was occupied toward the end of the Fremont period, roughly from AD 1100 to 1350 (Talbot et al. 2000). Eighty-one structures and 33 activity areas have been excavated. Each was assigned a temporal period based primarily on radiocarbon dates with support from dendrochronology, archaeomagnetic dates, and obsidian hydration, as well as association with other, more securely dated site contexts. Distribution of dates indicates that the occupation can be divided into 4 temporal periods: Period 1 (prior to AD 1200), Period 2A (AD 1200 to 1250), Period 2B (AD 1251 to 1300), and Period 3 (post-AD 1300).

Talbot and Janetski (2000) evaluated the distribution of bone located on a select number of structure and activity area floors and in the superimposed fill to determine whether bone debris recovered from the floor represented activities immediately prior to abandonment of living spaces or was simply debris deposited after the location was abandoned. The distribution of bone appears to differ between floor and lower fill contexts, suggesting that the bones were deposited as separate events. Using a variety of taphonomic data, such as bone survivorship and markers indicating carnivore chewing, I found that carnivores, likely domestic dogs, may have transported large mammal remains (e.g., deer and mountain sheep) between surface contexts. However, among *Sylvilagus* remains, there was relatively high survivorship and lower frequencies of carnivore markers (Fisher 2010). This suggests that the *Sylvilagus* remains from occupational surfaces are likely temporally associated with those surfaces.

The faunal assemblage of this area had been partly analyzed by the Brigham Young
Shifting Abundances of Leporids

Table 1 lists leporid taxa identified at Five Finger Ridge that could be assigned to a temporal period. The most dominant taxon in the assemblage is Sylvilagus, with 1950 identified specimens, where a specimen is defined as a bone, tooth, or fragment thereof. The 2 species of Sylvilagus may be distinguished in skeletal materials by differences in degree of crenulation of the occlusal surface of the lower third premolar (PM3; Dalquest et al. 1989, Sharp 1992). Due to the subjectivity inherent in using the occlusal morphology of PM3, I used a 7-point ordinal scale ranging from no crenulation to strong crenulation. Figure 3 illustrates the number of specimens identified for the entire assemblage (including undated contexts) across these crenulation categories. As can be seen in Table 1, the 2 species are nearly equally represented in the site, with 26 S. audubonii and 31 S. nuttallii specimens from dated contexts.

Lepus sp. is the second most common taxon, with 391 specimens identified from dated contexts. Previously, Grayson (1977) used alveolar length to distinguish L. townsendii from L. californicus, but later retracted this method because of the possibility that clinal variation explains the differences in observed size (Purdue 1980, Grayson 1987). As such, Lepus sp. is treated here at the genus level, although it is possible that both
L. townsendii and L. californicus were present in the vicinity of Five Finger Ridge during its occupation.

To test whether there is a significant change in taxa through time, I use the Cochran–Armitage test for linear trend. This is a form of chi-square analysis that may be used to evaluate the presence of a trend in relative abundance among multiple ordinal samples (e.g., temporal periods) while taking into account the influence of sample size (Zar 1996, Cannon 2000, 2001). The test divides the total chi-square value ($\chi^2$) for a contingency table into 2 parts: a linear trend ($\chi^2_t$) and the departure from that trend ($\chi^2_d = \chi^2 - \chi^2_t$). The test for trend shows that the proportion of the 2 Sylvilagus species changes significantly through time during the occupation of Five Finger Ridge ($\chi^2_t = 3.98$, $P = 0.05$; $\chi^2_d = 0.25$, $P = 0.62$), with S. nuttallii becoming more frequent through time (Table 2). Likewise, there is a significant decrease in Lepus sp. through time compared to Sylvilagus spp. ($\chi^2_t = 10.81$, $P < 0.001$; $\chi^2_d = 1.77$, $P = 0.41$).

These data demonstrate that the composition of leporids in the vicinity of Five Finger Ridge shifted through time. The low-elevation threshold of S. nuttallii and the high-elevation threshold of S. audubonii shifted downwards from approximately AD 1100 to 1350. The reduced numbers of Lepus sp. suggest that similar processes may be driving the local abundances of both Lepus sp. and S. audubonii. Exactly what these processes are may be clarified using local paleoenvironmental records.

**Regional Paleoclimate Record**

Pollen sequences obtained from Sheep Shelter and Cave of 100 Hands, both located within 3 km of Five Finger Ridge (Fig. 1), provide local paleo-vegetation data that may be used to contextualize the shifting abundances of leporids (Newman 2000). These datasets largely corroborate climate data obtained elsewhere in the eastern Great Basin and northern Colorado Plateau during Fremont times. The Fremont as a whole occupied the eastern Great Basin during a period of warm and wet winters and increased summer temperatures and summer moisture (Rhode 2000, Wigand and Rhode 2002, Grayson 2006a).

The pollen record from the Cave of 100 Hands shows a decrease in grasses and pine relative to Artemisia shortly before AD 1100, indicating increased winter precipitation (Newman 2000). After AD 1100, grasses and pine increase, and their abundance peaks by the end of Period 2A, signifying a shift toward greater summer precipitation during a period coeval with the Medieval Warm Period (MWP). This climatic anomaly lasted from approximately AD 950 to 1250 and consisted of warm and arid conditions with prolonged droughts in interior northern America (Mann et al. 2009). In the eastern Great Basin, an increase in summer precipitation expanded the growing season of grasses and allowed for the spread of maize horticulture, which marks the presence of the Fremont culture (Wigand and Rhode 2002). The MWP was followed by the Little Ice Age (LIA) from approximately AD 1400 to 1700—a period of cooler temperatures (Mann et al. 2009). There is considerable spatial variability in climate within the Great Basin during the LIA, with some regions exhibiting increased moisture and decreased temperatures while others show evidence for some of the warmest and driest conditions of the Holocene (Wigand and Rhode 2002). At Cave of 100 Hands, the shift toward the LIA is reflected by a slight increase in the ratio of sagebrush to grass pollen and a decrease in the ratio of pine to sagebrush pollen beginning with Period 2B and continuing into Period 3, suggesting cooler spring temperatures and increased winter precipitation (Newman 2000).

The data from Sheep Shelter are of lower resolution but show similar patterns (Newman 2000). The period from approximately AD 500 to 1150 is characterized by warm and moist conditions, with pine pollen occurring in higher abundances relative to juniper. Likewise, freshwater plants, such as sedges and cattails, are more abundant than the xerophilic cheno-ams (Chenopodium or Amaranthus). An increase in sagebrush may indicate an influx of winter precipitation around AD 1000. Around AD 1150, vegetation is dominated by juniper, grass, and cheno-ams. This shift toward more open vegetation continues until AD 1550 and likely represents a climatic shift from a summer monsoonal pattern to greater winter precipitation.

Additional data are provided by botanical remains recovered from Five Finger Ridge. These demonstrate shifting use of wild and cultivated plants corresponding to varying climate conditions (Talbot et al. 2000). In particular, the relative abundance of Zea mays (maize) macrofossils fluctuates through time in
relation to other taxa. Although relatively high in Period 1 (6.99%, \(n = 186\)), \(Z. mays\) reaches its highest abundance during Period 2A (25.89%, \(n = 409\)) and declines substantially in Period 2B (1.30%, \(n = 6473\)). This result suggests that Period 2A may correspond with a period of increased summer precipitation that favored maize horticulture.

Fig. 4 illustrates selected pollen profiles from the Cave of 100 Hands alongside the relative mammalian abundances discussed above. Here I use indices (Table 2) to simplify the graphical representation of significant trends observed in leporid taxa. The use of indices has become standard in zooarchaeology to evaluate changes in resource depression and diet breadth, as such measures have previously been applied to studies in the Fremont culture region (e.g., Janetski 1997, Janetski et al. 2000, Ugan 2005, Bird and O’Connell 2006). To show the relative abundance of the mountain cottontail, a \(S. nuttallii\) index was computed by dividing the number of identified specimens (NISP) of \(S. nuttallii\) by the total NISP of \(Sylvilagus\) identified to species. The leporid index is computed by dividing the \(Sylvilagus\) NISP by the total leporid NISP.

It appears that the \(S. nuttallii\) and the leporid indices follow the same general pattern seen in the Cave of 100 Hands pollen sequence. During Periods 1–2B, \(S. audubonii\) and \(Lepus\) sp. frequencies decrease through time as grass and pine pollen increase. Newman (2000) suggests that this period may have witnessed a brief expansion of pinyon-juniper woodlands and possibly increases in both summer and winter precipitation, corresponding to the Medieval Warm Period. Figure 5 illustrates the modern distribution of pinyon-juniper woodlands and sagebrush scrublands along an elevation profile crossing the site location on a north–south axis. The expansion of woodlands to lower elevations at the

Table 2. The Sylvilagus nuttallii index and leporid index across temporal periods. The \(S. nuttallii\) index was computed by dividing \(S. nuttallii\) NISP by the sum of \(Sylvilagus audubonii\) and \(S. nuttallii\) NISP. The leporid index was computed by dividing the \(Sylvilagus\) NISP by the sum of \(Lepus\) and \(Sylvilagus\) NISP.

<table>
<thead>
<tr>
<th></th>
<th>(S. nuttallii) index</th>
<th>Leporid index</th>
</tr>
</thead>
<tbody>
<tr>
<td>Period 1</td>
<td>0.37</td>
<td>0.81</td>
</tr>
<tr>
<td>Period 2A</td>
<td>0.60</td>
<td>0.82</td>
</tr>
<tr>
<td>Period 2B</td>
<td>0.68</td>
<td>0.87</td>
</tr>
<tr>
<td>Period 3</td>
<td>—</td>
<td>0.85</td>
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expense of sagebrush habitats (Fig. 5) would have been a factor limiting the relative abundances of both *S. audubonii* and *Lepus* sp.

**DISCUSSION**

Distinct changes in the relative frequency of leporid taxa correspond largely with vegetation data recovered from pollen cores in the vicinity of Five Finger Ridge. The shift from *S. audubonii* to *S. nuttallii* occurs at the same time that *Lepus* sp. becomes less abundant. This shift in leporid frequencies is likely a reflection of the expansion of pinyon-juniper woodlands into lower elevations, resulting in a more closed landscape in and around the site—a condition that was less favorable for *S. audubonii* and *Lepus* sp.

This interpretation assumes that cottontail rabbits were captured locally. It is conceivable that such small game were not captured in the immediate vicinity of the site and that the increased number of *S. nuttallii* reflects increased hunting of rabbits in upland areas. However, this would imply that local *Sylvilagus* populations were significantly reduced by either overhunting or climate change and that hunters responded by expanding hunting to higher elevations. Considering the high reproductive rates of leporids, it is unlikely that human predators could have reduced *Sylvilagus* populations to a point that would require such a response. Instead, the most parsimonious explanation is that there was change in the kinds of leporids present in the areas immediately surrounding Five Finger Ridge.

Although local pollen records show altering climate conditions at the end of the Fremont Period (Newman 2000), faunal responses to these changes in this area have been limited to a handful of species (Grayson 2006a, 2006b, Grayson and Fisher 2009). The location of Five Finger Ridge at the modern altitudinal boundary between *S. audubonii* and *S. nuttallii* has provided a unique opportunity to compare the relative frequency of the 2 species through time with corresponding changes in local pollen profiles. Although other archaeologists have used the relative abundance of jackrabbits to cottontail rabbits to identify changes in the landscape resulting from climate and horticultural activities in western North America (e.g., Szuter and Bayham 1989, Szuter 1991, Quirt-Booth and Cruz-Uribe 1997), such a change in cottontail species has not previously been documented in the eastern Great Basin. As such, data from this study may be added to a growing database of mammalian responses to climate change in the region.

**ACKNOWLEDGMENTS**

I thank Jeff Bradley, collections manager of mammalogy at the Burke Museum of Natural History and Culture for the use of comparative skeletal collections. Kari Carlisle, curator at Fremont Indian State Park, provided access to the Five Finger Ridge faunal collections. Dr. Joel Janetski and Richard Talbot of the Office of Public Archaeology at Brigham Young University provided unpublished data on the site excavations. Analysis was completed with assistance from Dr. Donald K. Grayson, Lindsay Tibke, Dana Kubilus, and Meriah Dainard. Don Grayson and Lisbeth Louderback provided invaluable comments on earlier drafts. I also thank R. Lee Lyman and Bryan Hockett for their reviews of earlier versions. This material is based on work supported by the National Science Foundation under Grant No. 0840847.
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Received 1 February 2011
Accepted 14 November 2011