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Did climatic seasonality control late Quaternary artiodactyl densities in western North America?

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ABSTRACT

We develop and test a hypothesis here that the seasonality of temperature and precipitation played a major role in determining the population densities of artiodactyls (e.g., *Ovis canadensis*, *Odocoileus hemionus*, and *Antilocapra americana*) across the terminal Pleistocene and Holocene of western North America. For much of this region, general circulation climate models and a range of paleoclimatic data suggest that seasonal extremes in temperature peaked during the terminal Pleistocene and early Holocene and that early and middle Holocene precipitation followed a winter-wet, summer-dry pattern—conditions known to depress artiodactyl densities. These trends are mirrored in a northern Bonneville Basin macrophysical climate simulation model from which we derive terminal Pleistocene and Holocene climatic values and three indices of climatic seasonality: (1) intra-annual temperature range, (2) summer precipitation intensity, and (3) winter precipitation intensity. These indices are arrayed against three detailed late Quaternary artiodactyl abundance records in the Bonneville Basin: a unique paleontological record of fecal pellet densities, and archaeological records of artiodactyl skeletal elements and large game hunting tools. Each of these artiodactyl abundance records shows significant correlations with the model-derived seasonality indices and suggests that artiodactyls occurred in low densities from the terminal Pleistocene through the middle Holocene—substantial increases occurred during equable, summer-wet periods of the late Holocene. Archaeological vertebrate records from across western North America show very similar temporal patterns in artiodactyl abundances suggesting that the trend and its climate-based causes may be a very general one. These conclusions have far-reaching implications not only for our understanding of ancient human hunting and land use patterns, but for the future management of artiodactyls under scenarios of global warming that also project dramatic increases in extreme climate.

1. Introduction

> 'Information about mean annual climatic conditions can be…irrelevant and even misleading to paleoecological investigations if the importance of seasonality, of the intra-annual climatic texture is2 not understood… it matters when the rain falls, when spring begins…changes in seasonal character greatly affect the competitive balance between species long before the gross temperature thresholds of most species are reached. (Guthrie, 1984: 288)'

There is an interesting contrast between the climatic variables that are thought to have shaped Pleistocene mammalian faunas in North America on the one hand, and Holocene ones on the other. The highly equable climates and long growing seasons of the Pleistocene are widely seen to have influenced the tight species-packing characteristic of mammalian communities at this time. And toward the end of the Pleistocene, it is the loss of equability or the shift to dramatic seasonal swings in temperature that has long been viewed as the critical variable in disrupting mammalian faunas—playing a possible role in both the extinction of some 35 genera of mostly large taxa and tremendous range changes in a host of smaller ones. Intra-annual climatic *variation* has thus been given

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primary analytical attention in this context (e.g., Hibbard et al., 1965; Axelrod, 1967; Slaughter, 1967; Graham and Lundelius, 1984; Guthrie, 1984; Kiltie, 1984; Graham, 1992). By contrast, with the transition to the Holocene, most researchers shift to a mode-driven approach and think in terms of how *mean* annual climatic conditions may have varied through time and affected vertebrate faunas (e.g., Grayson, 1988, 1998, 2000a,b; Lupo and Schmitt, 1997; Hockett, 2000; Schmitt et al., 2002; Byers and Broughton, 2004; Wolverton, 2005; but see Grayson, 2006a).

The suggestion, for example, that the early Holocene of the western United States may have been relatively "cool and moist" (e.g., Antevs, 1948), has long fostered the perception that conditions must have been favorable for mesic-adapted taxa, including most artiodactyls, and that human foragers of the time should thus have focused on the hunting of large game (Warren, 1967; O'Connell et al., 1982; Butler, 1986; Elston, 1986; Elston and Zeanah, 2002). However, the extreme seasonality that disrupted late Pleistocene mammalian communities, it appears, may have carried well into the Holocene; model simulations and paleoenvironmental data suggest, in fact, that late Quaternary climatic seasonality peaked during the terminal Pleistocene and early Holocene over much of the Northern Hemisphere (Thompson et al., 1993; Bartlein et al., 1998; Kutzbach et al., 1998).

In this paper, we build on earlier work that examined the role that moisture history played in determining Holocene trends in artiodactyl abundances (Eckerle, 1989, 1997; Broughton and Bayham, 2003; Byers and Broughton, 2004; Byers et al., 2005; Byers and Smith, 2007), but follow Guthrie's suggestion and explore the extent to which intra-annual variation in precipitation and temperature may have also affected the populations of these animals in western North America. Our analytical taxonomic focus is on the order level, Artiodactyla, rather than on particular species, because many of our key paleo-abundance indices are limited to this level of taxonomic resolution. Collectively, however, bighorn sheep (*Ovis canadensis*), pronghorn (*Antilocapra americana*), mule deer (*Odocoileus hemionus*), and bison (*Bison bison*) comprise the vast majority of specimens we analyze here (mammalian nomenclature follows Kays and Wilson, 2002).

We begin by examining theoretical and modern empirical analyses that bear on how climatic seasonality impacts artiodactyls and summarize late Quaternary climatic models and paleoenvironmental data for western North America focusing on variation in seasonality. We then test the hypothesis that changes in terminal Pleistocene and Holocene seasonality played a major role in driving variation in artiodactyl densities by arraying model simulated trends in the former against paleontological and archaeological indices of the latter. We present a refined test for the Bonneville Basin where the longest, most detailed paleo-artiodactyl records have been derived, but conduct more coarse-grained assessments from locations across western North America. The results shed light on our understanding of the Holocene history of artiodactyls and trends in prehistoric human lifeways and land use in western North America—the analysis also has implications for the future management of artiodactyls in the context of global climate change.

2. Extreme climatic seasonality and artiodactyl population dynamics

A variety of factors related to climatic seasonality are known to impact populations of large herbivores. These have not only been well-documented from modern analyses in wildlife management contexts, but also inferred to have been instrumental in shaping mammalian faunas of the past. In the latter context, the loss of equability or enhanced climatic seasonality that was initiated toward the end of the Pleistocene in the Northern Hemisphere, remains central to favored climatic arguments for late Quaternary mammalian extinctions. Factors related to climatic seasonality have also been suggested to account for the dwarfing of ungulate taxa (e.g., Purdue, 1989; Wilson, 1996; Guthrie, 2003).

In the late Pleistocene context, the primary links between climatic seasonality and faunal change lie in how seasonality caused the simplification of plant communities and ultimately increases in inter- and intra-specific competition for resources (Graham and Lundelius, 1984; Guthrie, 1984; Grayson, 1991). However, enhanced seasonality has also been linked to both Pleistocene extinctions and more recent artiodactyl population declines for reasons independent of floral species composition (e.g., Axelrod, 1967; Gilbert et al., 1970; Barrett, 1982; Kiltie, 1984; Purdue, 1989). Such factors are related to (1) reductions in the duration and forage quality of the growing season, (2) the severity of winter conditions, and (3) the miss-timing of reproduction when seasons favorable for birth are shorter and less regular. And insofar as the most dramatic late Quaternary shifts in plant community structure occurred at the Pleistocene–Holocene transition, persisting Holocene depressions of artiodactyls due to climatic seasonality would likely have been more strongly influenced by this other set of variables (points 1–3 above). As we discuss below, all of these latter factors will more strongly impact large herbivores than small ones—taxonomic composition of small mammal faunas may thus be less sensitive to enhanced seasonality.

2.1. Summer precipitation and the duration and quality of the growing season

Empirical research on artiodactyl populations from North America suggests that most taxa are sensitive to variation in both the duration of the summer growing season and the quality of forage provided within it. The primary links between artiodactyl populations and growing season conditions stem from the effects of temperature and precipitation variation on the availability of high quality forage. The highest quality forage, in terms of digestibility and overall useable energy is provided from new growth and is typically most abundant in wetter conditions early in the growing season in spring and early summer. Hot and dry climate precludes such new growth and forage plants growing in such conditions contain more lignin and cellulose that inhibit digestibility, further reducing the overall amount of useable energy (e.g., Klein, 1965; Mattson, 1980; Guthrie, 1984). The duration and quality of the growing season thus directly effects foraging efficiency, and in turn, has profound effects on adult survival, maternal condition, initial offspring survival, adult body size, birth weight, growth rate, survival through the first winter, resistance to disease, overall recruitment rates and, ultimately, herd size (Klein, 1965; Leslie and Douglas, 1979; Mackie et al., 1982, 1998; Stephenson et al., 1985; Purdue, 1989; Byers and Hogg, 1995; Fox et al., 2000; Douglas, 2001; Peek et al., 2002; Brown et al., 2006).

The duration of high quality forage availability on summer range also has a direct effect on the extent to which animals require free drinking water. When forage plants have low water content, animals require free water sources (Mackie et al., 1982; Van Dyke et al., 1983; Smith and Krausman, 1988; Bailey, 1990; McCarty and Miller, 1998). Bighorn sheep in arid settings, for instance, require free water sources within close proximity to plant forage, thermal protection, and rocky escape terrain. The availability of water sources on the landscape thus limits population densities and maintaining and restoring them is now a serious management issue for sheep (McQuivey, 1978; Leslie and Douglas, 1979; McCutchen, 1981).

Negative effects of spring and summer drought, high temperatures and attenuated growing seasons, and positive effects of high summer precipitation have been documented for wapiti (*Cervus elaphus*), pronghorn, bison, mule deer, and bighorn sheep in a variety of western North American contexts (Longhurst et al., 1979; Kitchen and O'Gara, 1982; Lawson and Johnson, 1982; Leslie and Douglas, 1986; Frank and McNaughton, 1992; Byers and Hogg, 1995; Douglas, 2001; Howell et al., 2002; Wasley, 2004; Bright and Hervert, 2005; Brown et al., 2006; McKinney et al., 2006).

2.2. Winter severity

Wildlife biologists and paleoecologists have also recognized the detrimental effects that severe winters have on artiodactyl populations and a variety of specific indices have been developed to quantify their influence (e.g., Severinghaus, 1947; Axelrod, 1967; Slaughter, 1967; Mech et al., 1987; DelGiudice et al., 2002). Winter severity is commonly measured by the duration of freezing or below freezing temperatures and the depth, duration, and penetrability of snow or ice accumulations. The primary effects of winter severity on ungulate herds occupying temperate regions are related to the proximate effect of snow cover on foraging efficiency, locomotion, and metabolism. Most important, deep or impenetrable snow packs restrict mobility, seal-off forage and reduce food intake. Winter severity thus determines the extent of annual weight loss and the ability of animals to recover during the rest of the year.

The fecundity of animals also depends on the degree of winter malnutrition and warm season recovery. For pregnant females, maternal condition is compromised in severe winters resulting in slower fetal development, lower birth weight, and lower survivability of offspring (Gilbert et al., 1970; Picton, 1984; Telfer and Kelsall, 1984; Mech et al., 1987; see also Osborn, 1993, 2003).

Nutritionally stressed animals are also more likely to be taken by predators and, moreover, deep snows constrain mobility, which further hinders escape from predators. And although ungulate taxa differ in their toleration to winter severity related in part to different feeding ecologies, morphological adaptations, and behavioral factors (see Telfer and Kelsall, 1984), a wealth of empirical data on a wide range of North American artiodactyls document the detrimental impacts of these conditions (e.g., Severinghaus, 1947, 1972; Martinka, 1967; Gilbert et al., 1970; Barrett, 1982; Goodson et al., 1991; DelGiudice et al., 2002).

2.3. Seasonality, gestation, and artiodactyl reproduction

Kiltie (1984) detailed a set of factors that impact reproduction in large mammals in highly seasonal and unpredictable climates, unrelated to the direct effects that such conditions have on forage quality and ungulate physiology as described above (see also Axelrod, 1967; Slaughter, 1967). These factors stem from the observation that larger mammals have longer and more variable gestation periods than small mammals, and can thus more easily "miss" favorable conditions for bearing young. Because gestation time is typically longer than the favorable period for reproduction, large mammals must rely on correlated cues to initiate breeding (e.g., photoperiod). Correlated cues will increasingly fail, however, as the length and predictability of the favorable period decreases—depressed reproductive rates follow.

Larger mammals not only have longer mean gestation times than small mammals but they are also associated with greater *variances*—large taxa thus have a greater likelihood of missing favorable periods when those intervals decrease in highly seasonal environments (Kiltie, 1984). While Kiltie argued that it was the shift to highly seasonal climates at the end of the Pleistocene that stressed and ultimately caused widespread megafaunal extinctions, the logic should apply in any context where such conditions existed.

2.4. Discussion

We have examined independently the detrimental effects that extreme summer and winter climate can have on large herbivores, but emphasize that years with attenuated and low quality growing seasons followed by severe winters would have compounded impacts. Indeed, some of the most notorious, historically recorded ungulate die-offs have resulted from the coupling of these extreme conditions (e.g., Frank and McNaughton, 1992; Wasley, 2004). We also stress that these impacts are more strongly magnified for large herbivores compared to smaller mammals (Axelrod, 1967; Kiltie, 1984). Small mammals can avoid spells of seasonally severe climate by escaping to protected burrows, dens, or nests—underground, in rock piles, or in tree cavities. Many taxa also hibernate, estivate, or cache food to ride-out unfavorable periods in these protected settings. Small mammals also have shorter gestation times than large mammals—shorter than the favorable period— and can wait for direct environmental cues (food availability) to initiate mating and successfully reproduce even in favorable periods that are short and unpredictable. Additionally, most herbivorous small mammals are polyestrous, and are capable of producing litter-after-litter, maintaining high birth rates, even during relatively short favorable periods in highly seasonal environments. Just as small mammals escaped extinction when seasonality began to intensify during the late Pleistocene, they should also have been less effected than large taxa to the degree that these conditions persisted into the Holocene.

3. Holocene climatic seasonality: climate model simulations and paleorecords for western North America

Climate model simulations provide a starting point to explore the effect of variation in Holocene seasonality on artiodactyls of western North America. We begin with a consideration of general circulation models and the paleoclimatic simulations derived from them. We then summarize regional paleorecords that provide evidence for Holocene changes in the seasonality of temperature and precipitation.

3.1. A general circulation model

One of the most widely used paleoclimatic model simulation is the National Center for Atmospheric Research, Community Climate Model version 1 (NCAR, CCM1; Kutzbach et al., 1998). This model simulates climate over the past 18 000 ^{14}C years BP (unless otherwise noted, all ages in this paper are in radiocarbon years) with key controls including the topography of the ice sheet, Pacific sea-surface temperatures, the seasonal cycle of insolation, and atmospheric CO_2 concentrations.

In CCM1, summer and winter solar radiations (insolation) and surface temperatures are modeled to have varied significantly over much of the Northern Hemisphere across the late Quaternary due to orbital forcing mechanisms (see Berger, 1978; Berger and Loutre, 1991). Most notably, the greatest expression of temperature seasonality over the last 18 000 years occurred between 12 000 and 8000 BP and remained high, but gradually declined, over the next 3000 years.

As modeled, a direct effect of increased summer insolation during the terminal Pleistocene (12 000–10 000 BP) and early Holocene (10 000–7500 BP) is an increase in summer temperature and decreased effective moisture during this season. However, indirect effects resulted from differential summer warming of the continent and ocean, and related shifts in atmospheric circulation. For example, model simulations for the early Holocene suggest that the Northeast Pacific subtropical high was intensified, driving hotter, drier summers for regions that are characterized by dry summers today: California, the Pacific Northwest, and the northern Great Basin. Cooler, wetter summers are simulated for the late Holocene (4500 BP–latest prehistoric) of these regions. However, for regions that currently experience a summer-wet pattern, such as the Southwest, Rocky Mountains, Great Plains, and southern Great

Basin, the model suggests that increased summer insolation during the early Holocene enhanced the onshore pull of moisture from the Gulfs of California and Mexico and intensified summer monsoons (Bartlein et al., 1998; Kutzbach et al., 1998; Brunelle et al., 2005).

As for winter climate, simulations for the western United States suggest that by 9000 BP and throughout the remainder of the Holocene, the winter location of the jet stream, and absolute winter precipitation differed little from the present. However, the late Pleistocene–early Holocene insolation anomaly implies colder winter temperatures, and greater mountain snowpack. Modeled winter temperatures increased steadily through the middle and late Holocene (Bartlein et al., 1998; Kutzbach et al., 1998; Brunelle et al., 2005).

In sum, CCM1 suggests that temperature seasonality was high from the terminal Pleistocene to the middle Holocene over the entire west, with more equable climates emerging during the late Holocene. Precipitation patterns were, however, geographically variable, but for much of the region (i.e., the current "summer-dry" area) an extreme summer-dry, winter-wet period prevailed during the early and middle Holocene with a shift to cooler, wetter summers and milder winters emerging during the late Holocene (Whitlock and Bartlein, 1993; Bartlein et al., 1998; Kutzbach et al., 1998). General agreement exists between the broad-scale features of the climate simulations and paleoecological data sets in western North America, although regional anomalies have also been documented (e.g., Bartlein et al., 1998). We focus below on paleoclimatic records bearing specifically on climatic seasonality.

3.2. *Paleoclimatic records of Holocene seasonality*

A relatively small body of paleoclimatic fieldwork has provided data bearing on season-specific variation in Holocene temperature and precipitation across western North America, with most analyses focused on summer climate. This work has provided evidence for a summer thermal maxima in the early to middle Holocene, with substantial cooling during the late Holocene. Despite this general pattern, these records also attest to considerable geographic variability—regional variation in the timing of the Holocene thermal maxima is especially noteworthy.

Much of the evidence for Holocene variation in summer temperature is derived from pollen- and macrofossil-based vegetation records, often coupled with high-resolution charcoal sequences; collectively, they suggest expansion of xerophytic plant communities and maximum fire frequencies during the early to middle Holocene. These patterns are consistent with high summer temperatures, intensified summer drought, low fuel moisture, and frequent dry convective thunderstorms (e.g., Davis et al., 1985; Heusser et al., 1985; Davis and Moratto, 1988; Anderson, 1990; Smith and Anderson, 1992; Whitlock and Bartlein, 1993; Anderson and Smith, 1994; Long et al., 1998; Millspaugh et al., 2000; Mohr et al., 2000; Doerner and Carrara, 2001; Barron et al., 2003; Brunelle and Anderson, 2003; Hallett et al., 2003; Gavin et al., 2003; Strong and Hills, 2003; West, 2004; Minckley et al., 2007).

A variety of other paleoclimatic proxies relating especially to elevated early and middle Holocene summer temperatures or cooler/wetter late Holocene summers are consistent with the studies above. These include analyses involving subalpine treeline position (Ritchie et al., 1983; Spear, 1993; Pellatt et al., 2000; Pisaric et al., 2003), grain-size and stable oxygen and carbon isotopes from soil carbonates (Davis et al., 2002), archaeological and paleontological mammalian faunas (e.g., Lupo and Schmitt, 1997; Hockett, 2000; Grayson, 2000a, 2005, 2006a; Lyman and O'Brien, 2005), wood rat (*Neotoma*) size variation (Smith et al., 1995; Smith and Betancourt, 1998), and chironomid midge-based temperature reconstructions from high elevation lakes (Pellatt et al., 2000; Palmer et al., 2002; Porinchu et al., 2003; Walker and Pellat, 2003; Rosenberg et al., 2004; Potito et al., 2006).

Other proxies, however, have been suggested to contest certain aspects of the model's predictions. In the Bonneville Basin for instance, early Holocene small mammal faunas and plant vegetation records have been suggested to indicate cool, but steadily warming, summers during the early Holocene (see especially Grayson, 1993, 2002; Rhode, 2000; Madsen et al., 2001). Such records, as we elucidate further below, may be reflecting an early Holocene that was on average relatively cool but that nonetheless was also characterized by amplified seasonal extremes.

As noted above, fewer Holocene records for the region directly address winter climate (but see Walker and Pellat, 2003: 541; Minckley et al., 2007), but several bearing on the early Holocene for the Great Basin are especially noteworthy. Pollen analysis from Mono Lake, in the western Great Basin, for instance, shows evidence for synchronous expansion of xerophytic vegetation and higher lake levels during the early Holocene (Davis, 1999). This apparent contradiction is interpreted to reflect insolation-driven seasonality. During the early Holocene, higher summer solar radiation caused summer drought—as numerous Sierra Nevada paleobotanical records attest— but lower winter insolation produced deeper snowpack, greater spring runoff, and higher lake levels (Davis, 1999).

Similar conclusions were reached from syntheses of packrat and pollen records from the Bonneville Basin (Wigand and Rhode, 2002). Within this area, paleovegetation records derived from more montane settings or those from more southerly locations tend to indicate cooler, moister early Holocene climate. By contrast, those records emphasizing early Holocene aridification tend to be derived from lowland basin floors, and non-perennial stream valley settings and are more northerly in distribution. As Wigand and Rhode (2002: 349) observe, "Enhanced seasonality resulting from orbital forcing during the early Holocene…may have affected montane woodlands in a different way than lowland shrub communities". Specifically, the persistence of mesic taxa in montane settings would appear consistent with greater winter effective precipitation and deeper snow packs. Low elevation plant communities—apart from wetlands fed by spring runoff from deep snow packs—would receive less of this benefit and thus respond more rapidly to the increasingly hot and dry summer conditions.

The latitudinal gradient in the Bonneville Basin, with more mesic indications from southern records, is also consistent with the model predicted summer incursion of monsoons, a feature evident in a wide variety of paleorecords from the southern Great Basin (Spaulding and Graumlich, 1986; Quade et al., 1998; Hockett, 2000; Jahren et al., 2001). The presence of early Holocene shallow lakes and wetlands in the Bonneville Basin (e.g., Oviatt et al., 2003) may also result from greater winter effective precipitation, deeper snowpack, and greater spring runoff.

In sum, there is a general congruence between trends in Holocene climatic seasonality derived from general circulation models (CCM1) and paleoclimatic indices that track aspects of this variable from across western North America. These trends suggest a widespread pattern of a moist cold season and a dry warm season during the early and middle Holocene with an amelioration of this condition during the late Holocene. Importantly, both model simulations and empirical data suggest that climatic seasonality varied dramatically across the last 12 000 years with its greatest expression occurring during the terminal Pleistocene and early Holocene; those sources, however, also indicate that considerable temporal and spatial variability characterized this trend.

4. Holocene seasonality and artiodactyl abundances in the Bonneville Basin, Utah

The summaries above lead us to expect a geographically widespread trend of low artiodactyl abundances during periods of high climatic seasonality during the late Quaternary, such as the terminal Pleistocene and early Holocene. However, given the apparent temporal-geographic variability in late Quaternary climatic seasonality, we also anticipate that the influence of long-term trends in this variable on artiodactyl abundances would be most readily detected through analyses involving region-specific data sets. We turn now to just such an analysis involving the Holocene history of artiodactyl populations of the northern Bonneville Basin (Fig. 1). This region has provided among the longest, most detailed, paleorecords not only for artiodactyls, but also for other biota sensitive to climatic seasonality. In order to quantitatively assess how these records relate to trends in climatic seasonality, we first introduce a paleoclimatic model specific to the northern Bonneville Basin.

4.1. A macrophysical paleoclimate model for the northern Bonneville Basin: Lakeside, Utah

Macrophysical Climate Modeling (MCM) was developed as an alternative to iterative general circulation models to produce monthly temperature, precipitation, and effective precipitation values at 100- to 500-year time intervals for specific locations over the past 40 000 years. The models are based on the same general principles and incorporate many of the same boundary conditions and initial inputs as GCMs but utilize historic weather-station data to calibrate them to specific locations (see Bryson and Bryson, 1998; Bryson, 2005; Bryson and DeWall, 2007; for details on model construction and comprehensive overviews). The foundation of an MCM is calculated temporal variations in the latitude of boundary conditions or centers of action (e.g., the North Pacific High at 135°W, the North Atlantic High at 0°W, the Intertropical Convergence at 90°W, the jet stream at 120°W, and the Northern Hemisphere temperature gradient) that influence the climate for particular regions. Other key initial inputs include cyclic variations in the amount of solar radiation reaching the Earth (i.e., Milankovitch periodicities), as modulated by volcanically determined transparencies of the atmosphere. These factors are then calibrated to local climate using non-linear regressions with climate data derived from modern weather stations. Modern relationships between the local climate and the various forcing mechanisms are then incorporated into the MCM to retrodict estimates of monthly temperature and precipitation into the past.[4]

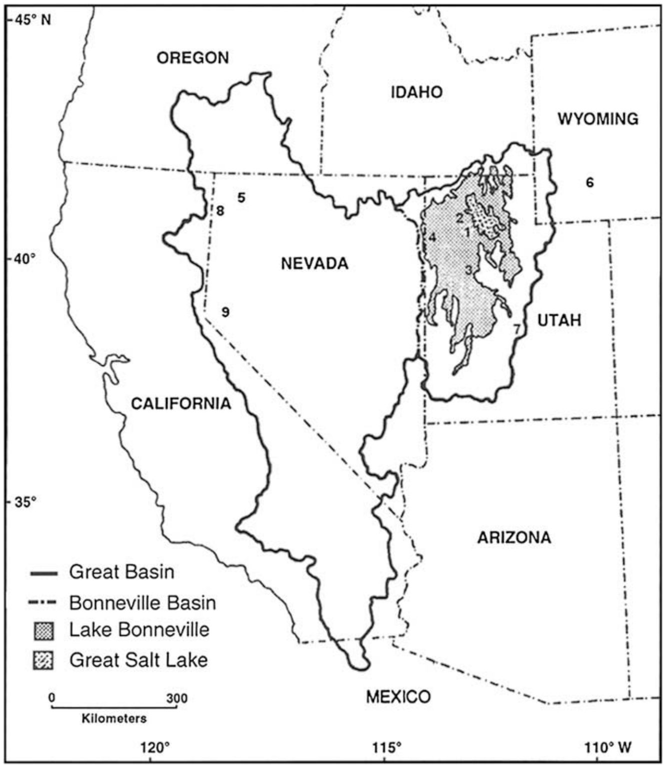

Fig. 1. A map of western North America and the Great Basin showing locations of sites discussed in the text (from Madsen et al., 2001). (1) Homestead Cave, Lakeside, (2) Hogup Cave, (3) Dugway, Camels Back Cave, (4) Danger Cave, (5) Last Supper Cave, (6) Wyoming Basin, (7) Sudden Shelter, (8) Surprise Valley, (9) Carson Desert.

The accuracy of MCM models has been demonstrated through comparisons with diverse paleoclimatic proxies across the globe. Comparative analyses of paleoclimatic data and modeled climate of several GCMs and the MCM have also demonstrated that the MCM had comparable, if not more accurate, results (Ruter et al., 2004; Bryson and DeWall, 2007). However, before applying an MCM to any particular region, model results should ideally be validated with paleoenvironmental field data, an approach we follow here. The unique virtue of an MCM is that model simulations can provide complete late Quaternary climate reconstructions in the form of point values that can be directly correlated with archaeological and paleontological indices of artiodactyl abundances (see Byers et al., 2005 for further discussion of this approach).

For this analysis, we constructed a 14 000-year MCM that provides monthly climatic values (at 200-year intervals) for Lakeside, Utah (Fig. 1)—a location very near the sites that have produced our detailed paleo-artiodactyl records. To provide an intra-regional comparison, we also utilized results from a previously constructed model for Dugway, Utah, located approximately 115 km to the south (Bryson and Coe, 2004; see Appendix A (Supplementary data) Tables 1 and 2 for the output from these models). The modeled results are provided at 200-year increments in radiocarbon years before present.

To first provide a synthesis of temperature and precipitation variation for the late Quaternary Bonneville Basin, we calculated Thornthwaite's "moisture index" (MI) (Thornthwaite, 1948; Thornthwaite and Mather, 1957) values from the simulated data provided by our MCMs. The moisture index represents an overall annual measure of precipitation effectiveness for plant growth that considers the weighted influence of water surplus and water deficiency as related to water need; in essence, it gauges the potential primary productivity of a given year.[5]

As Fig. 2 shows, the early Holocene of the northern Bonneville Basin was on average cool and moist and characterized by high primary productivity, although substantial variation within this period is also evident. The middle Holocene, by contrast, was consistently hot and dry, compared to both early and late Holocene times. In general, the late Holocene was characterized by high effective moisture and productivity, with two prominent moisture pulses— one occurring after 4000 BP and the other near 2000 BP. These trends in average annual moisture history and primary productivity are in good accord with a wide range of regional paleoclimatic data. On a finer scale, however, there are some

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[4] No error terms are provided with the modeled point values, since true values are unknown. Error is typically expressed through analyses of explained variance with paleoclimatic proxy data.

[5] For a given station, the moisture index is calculated by the formula, I_m = humidity index − 0.6(aridity index), which becomes, $I_m = \frac{100s-60d}{n}$, where I_m is the moisture index, s the water surplus, d the water deficiency, and n the water need. The calculation of s and d is made on a normal month-to-month basis, with s being the total surplus from all months having a water surplus, and d the total of all monthly deficiencies; each is represented by the difference between monthly precipitation and monthly potential evapotranspiration (in cm), or the amount of water evaporated (both as transpiration and evaporation) from the soil. Here n is the annual potential evapotranspiration (see Thornthwaite, 1948; Eckerle et al., 2002).

Table 1
Radiocarbon dates from Homestead Cave[a]

Stratum	^{14}C Age (yr BP)	Calibrated age[b]	Lab no.	Material
XVII	1020 ± 40	898–1006	Beta 101877	30 g artiodactyl pellets
XVI	1200 ± 50	1050–1263	Beta 66940	Charcoal
XV	980 ± 40	794–958	CAMS 70099	1 artiodactyl pellet
XV	1790 ± 40	1605–1823	CAMS 70100	1 artiodactyl pellet
XIV	2850 ± 50	2846–3083	Beta 103692	30 g artiodactyl pellets
XIII	3480 ± 40	3640–3847	Beta 101878	30 g artiodactyl pellets
XII	3400 ± 60	3551–3780	Beta 63179	Wood/charcoal
XI	4450 ± 40	4957–5092	CAMS 70101	1 artiodactyl pellet
XI	4750 ± 40	5447–5588	CAMS 70102	1 artiodactyl pellet
X	5330 ± 65	5987–6224	AA 14822	1 artiodactyl pellet
IX	5400 ± 40	6174–6292	CAMS 70103	1 artiodactyl pellet
IX	6270 ± 50	7150–7305	CAMS 70104	1 artiodactyl pellet
VIII	6190 ± 50	6956–7180	CAMS 70105	1 artiodactyl pellet
VIII	6200 ± 40	6994–7182	CAMS 70106	1 artiodactyl pellet
VII	6160 ± 85	6848–7258	AA 14824	1 artiodactyl pellet
VII	6185 ± 105	6826–7311	AA 14825	1 artiodactyl pellet
VI	7120 ± 70	7790–8056	AA 14826	1 artiodactyl pellet
V	8230 ± 70	9021–9334	AA 16810	1 artiodactyl pellet
IV	6600 ± 40	7433–7524	CAMS 70108	1 artiodactyl pellet
IV	8040 ± 50	8718–9034	CAMS 70107	1 artiodactyl pellet
IV	8195 ± 85	8995–9425	AA 14823	1 artiodactyl pellet
III	8450 ± 40	9422–9532	CAMS 71147	1 artiodactyl pellet
III	9650 ± 40	11 064–11 795	CAMS 71148	1 artiodactyl pellet
II	8520 ± 80	9399–9681	AA 14821	1 hackberry[c] endocarp
II	8790 ± 90	9558–9968	AA 14820	1 hackberry endocarp
II	8830 ± 240	9404–10 521	Beta 63438	Hackberry endocarps
Ib (upper 5 cm)	10 160 ± 85	11 396–12 117	AA 14819	1 *Neotoma* fecal pellet
Ib (upper 5 cm)	10 350 ± 80	11 959–12 411	AA14818	1 *Neotoma* fecal pellet
I (general)	10 910 ± 60	12 816–12 950	Beta 72205	Bone collagen
Ia (lower 5 cm)	11 065 ± 105	12 852–13 168	AA 14817	2 *Neotoma* fecal pellets
Ia (lower 5 cm)	11 181 ± 85	12 924–13 228	AA 16808	1 *Neotoma* fecal pellet
Ia (lower 5 cm)	11 263 ± 85	12 969–13 288	AA 16809	1 *Neotoma* fecal pellet
Ia (lower 5 cm)	11 270 ± 135	12 916–13 374	AA 14816	1 *Neotoma* fecal pellet

[a] From Madsen (2000) but with the 12 CAMS dates reported first here. The original dates were run primarily on individual fecal pellets or hackberry endocarps picked directly from the center of each stratum on the face of the stratigraphic column. The CAMS dates, however, were run on fecal pellets which had been sorted from the bulk sediment samples. As a result, it is unclear where they came from within each stratum and they may have come from the interfaces between strata.

[b] Two sigma ranges; calculated using CALIB 5.1.0.

[c] *Celtis reticulata*.

unexplained discrepancies, such as the model predicted high moisture index extending to about 7800 BP—several paleoclimatic data sets have been read to suggest that the eastern Great Basin climate had already become very dry by this time (e.g., Broughton, 2000a; Broughton et al., 2000; Grayson, 2000a,b; Madsen et al., 2001; Wigand and Rhode, 2002). These differences may relate to the finer-grained temporal scale provided by the MCM and further more systematic comparisons between model predictions and

Table 2
Homestead Cave ^{14}C dates, abundance indices and corresponding Lakeside MCM climate values[a]

Stratum	Date[b]	% NISP harvest mice[c]	%NISP fish	Artiodactyl pellets/liter	% NISP Sciuridae[c]	Lakeside[d] moisture index	Winter precipitation (% annual total)	Summer precipitation (% annual total)	Intra-annual temperature range (°C)
XVIII	–	0.09	0.08	2.40	0.04	–	–	–	–
XVII	1020	0.61	0.08	14.80	0.05	−40.03	22.18	9.28	28.92
XVI	1200	0.52	0.05	16.40	0.05	−40.00	22.50	9.28	28.90
XV	1385	–	–	8.70	–	−39.70	22.14	9.52	28.84
XIV	2850	–	–	3.20	–	−39.64	23.36	9.56	29.46
XIII	3400	–	–	23.90	–	−39.63	23.60	7.76	29.81
XII	3500	0.11	1.42	13.60	0.04	−39.06	24.40	7.41	29.73
XI	4600	0.03	0.06	1.20	0.04	−40.22	25.64	4.96	29.96
X	5330	–	0.04	14.90	–	−40.45	25.90	4.45	30.74
IX	5740	0.07	0.02	3.80	0.02	−40.82	26.04	3.85	31.20
VIII	6196	0.07	0.03	1.00	0.02	−40.77	25.84	3.40	31.50
VII	6171	0.05	0.03	8.70	0.01	−40.77	25.84	3.40	31.50
VI	7120	0.16	0.02	3.40	0.01	−40.36	25.67	2.83	32.52
V	8230	0.23	0.02	3.90	0.01	−38.08	24.68	3.79	32.46
IV	7285	0.50	0.04	0.60	0.01	−40.36	25.67	2.83	32.52
III	9050	0.76	1.73	0.20	0.00	−39.10	24.98	3.21	33.61
II	8650	1.16	3.17	0.30	0.00	−38.76	24.63	3.87	33.14
Ib	10261	–	–	0.90	–	−38.52	24.80	3.79	34.69
Ia	11195	–	–	1.20	–	−36.14	24.83	6.43	34.98
I	10839	0.56	26.48	–	0.01	−38.28	24.82	3.62	34.85

[a] The small mammal, fish, and pellet data are from Grayson (2000b), Broughton (2000a) and Hunt et al. (2000), respectively.

[b] The dates provided here for strata with multiple radiocarbon determinations (Table 1) were averaged using the Calib 5.1.0 software (Stuiver and Reimer, 2005).

[c] Missing values reflect strata that were not analyzed (see Grayson, 2000a).

[d] No dates are available for stratum XVIII.

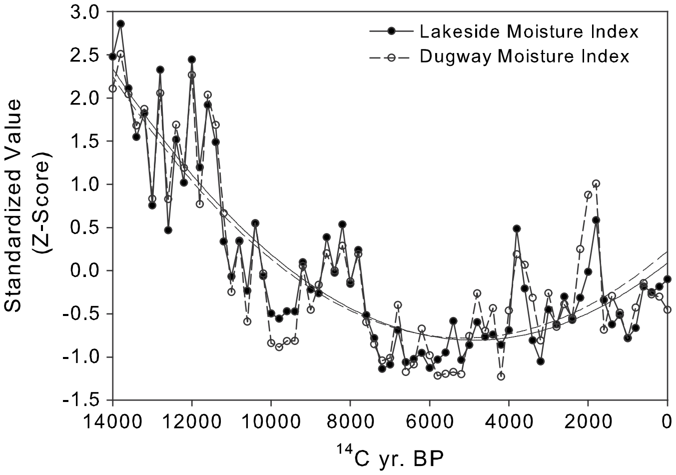

Fig. 2. Late Quaternary model simulated moisture index values (standardized, 200-year average) for Lakeside and Dugway of the Bonneville Basin, Utah.

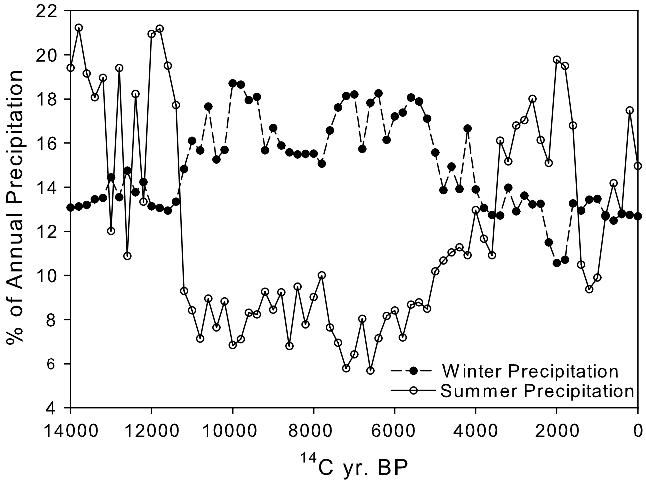

Fig. 4. Late Quaternary model simulated variation in the intensity of summer (July, August) and Winter (January, February) precipitation for Lakeside, Utah.

paleoclimatic data sets are warranted. The analysis that follows represents a detailed example this kind of comparison.

Turning to the climatic variables most relevant here, both the intra-annual temperature range and seasonal precipitation regime are modeled to have varied significantly through the Holocene. Specifically, temperature range—the difference between the extreme winter low and summer high temperatures—was at its highest during the terminal Pleistocene and early Holocene and steadily declined thereafter (Fig. 3). With respect to the seasonality of precipitation, the early and middle Holocene was characterized by a winter-wet pattern, with a high proportion of the total annual precipitation falling in the winter (January and February). A dramatic reversal to a summer-wet pattern occurred in several marked pulses during the late Holocene (Fig. 4).

In broad outline, these trends mirror those generated from the general circulation model (CCM1) discussed above. But with the point-data provided by the Lakeside MCM and our Bonneville Basin paleorecords on artiodactyl abundances that we present below, we can statistically evaluate the relationships between these region-specific climatic values and local artiodactyl populations.

Insofar as climatic seasonality affected broad-scale Holocene trends in artiodactyl population densities, we predict negative correlations between artiodactyl abundances and winter precipitation intensity, and positive relationships between the former and summer precipitation. These predictions derive from our general discussion above of the role that seasonality plays in affecting artiodactyls of western North America but we emphasize that modern analyses have documented that such factors strongly influence Bonneville Basin artiodactyl populations more specifically (e.g., Doman and Rasmussen, 1944; Robinette et al., 1952; Beale and Smith, 1970; Danvir, 2000; Aoude and Danvir, 2004). To isolate the influence of climatic extremes, we define summer as the two hottest-driest months of the year, July and August, and winter as the coldest-wettest months, January and February. Our summer precipitation index is thus the percentage of the total annual precipitation that falls in July and August and winter precipitation we define as that percentage that falls in January and February.

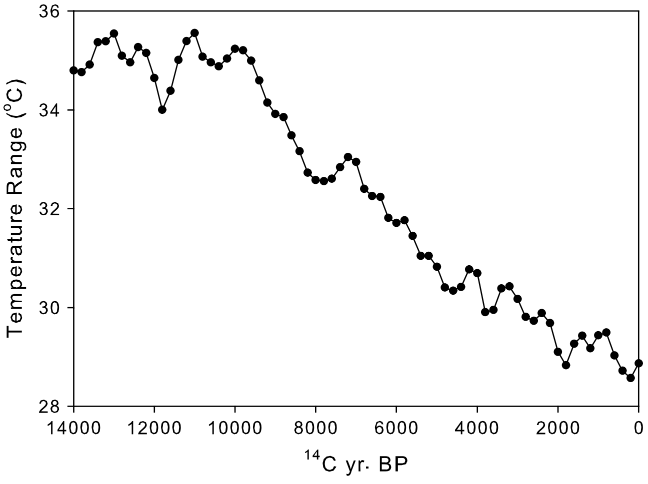

Fig. 3. Late Quaternary model simulated intra-annual temperature range values for Lakeside, Utah.

Since extreme summer heat should increase evaporation and diminish the abundance of high quality forage and extreme winter cold should maintain deeper snowpack and stress artiodactyls, as described above, we also predict negative relationships between intra-annual temperature amplitude or range and artiodactyl abundances. The latter can thus be viewed as integrator of climatic extremes that affect artiodactyl recruitment and survivorship.

We anticipate positive relationships between primary productivity as measured by the moisture index and artiodactyl abundances, other things being equal. However, the moisture index is an annual composite measure, and thus does not effectively capture the critical seasonal amplitudes in climatic stress that we hypothesize were influential to long-term artiodactyl reproduction and demography. We expect artiodactyl populations to fluctuate with variation in primary productivity, but only insofar as the effect of climatic seasonality is held constant.

4.2. Homestead Cave

The stratified deposits of Homestead Cave (Fig. 1) provided a rich array of biological materials that inform on Holocene changes in Bonneville Basin climate and biotas. As we discuss in detail below, it also represents the only detailed, Holocene paleontological sequence of artiodactyl abundances in the Great Basin; it thus provides an ideal context in which to examine the effects of regional change in climatic seasonality on artiodactyl population densities.

Homestead Cave is a wave-constructed cavern located in the Lakeside Mountains just west of Great Salt Lake, 10 km SW of Lakeside, Utah, in the northern Bonneville Basin. In 1993 and 1994, a 1-m^2 sample column was excavated to a depth of 3 m in the rear cave-floor sediments. The well-defined deposits contained 18 separate, excavatable strata. Materials removed from the column were passed through a series of 1/4 in (6.4 mm), and 1/8 in (3.2 mm), screens in the lab. The deposits consisted primarily of degrading owl pellets, rich in small vertebrate remains, with little evidence of contamination by human foragers. Originally, 21 ^{14}C assays were derived from the deposits (Madsen, 2000; Madsen et al., 2001); we add 12 new dates to the sequence here (Table 1). Overall, the chrono-stratigraphic coherency of the ^{14}C results suggests that the deposits were laid down sequentially between ~11 300 and ~1000 yr BP.

Analyses of the massive vertebrate faunal data set from Homestead Cave have substantially increased our understanding of late Quaternary paleoecology in the Great Basin (e.g., Grayson, 1998, 2000a,b, 2006b; Broughton, 2000a,b; Broughton et al., 2000, 2006; Livingston, 2000; Madsen, 2000; Madsen et al., 2001; Lyman and O'Brien, 2005). The small mammals from the site have played the most important role in those analyses as the site provided the largest well-stratified late Pleistocene and Holocene small mammal sequence from the entire Great Basin (e.g., Grayson, 1998, 2000a, 2000b, 2006b). Based on over 184 000 identified mammalian specimens, Grayson (2000a,b) has revealed a series of pronounced changes in the Holocene distributions and abundances of small mammal species that appear sensitive to broad-scale patterns in average annual Holocene temperature and precipitation regimes. Specifically, mesic small mammal species decline in abundance across the early Holocene section of deposits and are virtually absent by the beginning of the middle Holocene. While some species responded only to the apparent onset of increasing aridity of the early and middle Holocene times, other species reacted to both the onset and termination of the xeric episode. Western harvest mice (*Reithrodontomys megalotis*), for instance, are most abundant today in moister settings in the Great Basin and are known to decline during periods of drought (Whitford, 1976). These mice decline in abundance across the early Holocene strata of Homestead Cave, become scarce in the middle Holocene deposits, and return to abundance in the late Holocene layers (Grayson, 2000a). Other small mammal species from Homestead Cave display similar patterns, as do such taxa from other Holocene records in the Great Basin (Grayson, 1983, 1985, 1987, 1988; Hockett, 2000; Schmitt et al., 2002).

Values from the Lakeside climate model allow us to examine the relationships between specific climatic variables and diachronic trends in environmentally sensitive vertebrates, an approach we introduce here with the harvest mice record described just above. For correlation analyses, here and throughout the paper, we use non-parametric rank order approaches in keeping with the generally coarse-grained nature of our faunal abundance indices (see Grayson, 1984).

Our methods are also constrained by the existing chronological controls for the Homestead deposit. While 33 radiocarbon assays have been provided for Homestead Cave, these are nonetheless insufficient for establishing precise spans of time over which each stratum was deposited. We thus used the pooled mean dates for each stratum to chronologically link them to the model-derived climatic values that were provided at 200-year intervals. To account for the multi-century depositional spans for the Homestead strata, we used the average of the three climatic values that fell closest to the pooled mean date for each stratum.

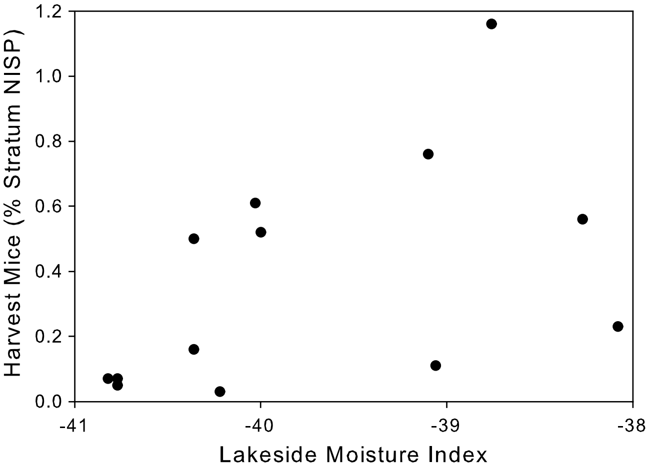

Fig. 5. The relationship between the relative abundance of harvest mice at Homestead Cave and the Lakeside moisture index. NISP = number of identified specimens.

As Fig. 5 shows, the abundance of harvest mice at Homestead Cave is positively correlated with the moisture index as derived from the Lakeside MCM ($r_s = 0.61$, $P < 0.05$; Table 2). Again, polyestrous small mammals such as harvest mice should be less sensitive to seasonal extremes in temperature and the intra-annual timing of precipitation since they are capable of producing litter-after-litter and can maintain high birth rates even during relatively short favorable periods in highly seasonal environments. We thus do not expect a consistent pattern of correlations between their abundance at Homestead Cave and the indices of climatic seasonality that we defined above. This is, in fact, the case as two of three seasonality indices are uncorrelated with harvest mice abundance (harvest mice-summer precipitation, $r_s = 0.08$, $P > 0.75$; harvest mice-temperature range, $r_s = 0.40$, $P > 0.15$; harvest mice-winter precipitation, $r_s = -0.62$, $P < 0.05$).

Similar results should be found for other mesic-oriented taxa that are sensitive to annual effective precipitation, but less so to aspects of intra-annual climatic variability, such as, for instance, most local fishes (Broughton, 2000a,b; Broughton et al., 2000). Here too, the proportionate abundance of fish, relative to all other vertebrates in the Homestead sequence is significantly correlated with the moisture index ($r_s = 0.58$, $P < 0.05$), but not consistently so for the indices of climatic seasonality (fish-summer precipitation, $r_s = 0.32$, $P > 0.25$; fish-temperature range, $r_s = 0.17$, $P > 0.55$; fish-winter precipitation, $r_s = -0.58$, $P < 0.05$). These results provide strong support for previous analyses of the Homestead Cave vertebrate fauna that suggested the abundance histories of these and other taxa reflect long-term trends in Bonneville Basin moisture history (Grayson, 1998, 2000a,b, 2006a; Broughton et al., 2000, 2006; Livingston, 2000). At the same time, they also provide a strong field validation of the Lakeside MCM for the northern Bonneville Basin.

We turn now to the artiodactyl record from Homestead and note initially that given the raptor-based origin of this fauna, it is not surprising that artiodactyl skeletal elements are virtually non-existent in the deposit (Grayson, 2000b). However, over 21 000 individual artiodactyl fecal pellets were identified from the site. The size and morphology of the pellets are consistent with pronghorn, mule deer, and bighorn sheep, but species level identifications were not attempted. Each of these taxa is known to have occupied the Lakeside Mountains in either recent or prehistoric times, and bighorn sheep and pronghorn are well-known to use caves to escape summer heat or the cold of winter (Geist, 1971; Krausman, 1979; Hunt et al., 2000). Hunt et al. (2000) describe pronghorn using Bonneville Basin caves. These animals defecate after resting and routinely leave bedding scrapes littered with pellets (Linsdale and Tomich, 1953; Geist, 1971).

Since the number of artiodactyl pellets deposited in a cave at any point in time should reflect the frequency of cave visits by these animals, the density of pellets (pellets/liter) in sediments can also serve as a proxy measure of their abundance in the surrounding landscape. We emphasize that the original identifications of the Homestead pellets were made at the order level (e.g., Artiodactyla), given the difficulty in securely distinguishing the pellets of bighorn sheep, mule deer, and pronghorn (Hunt et al., 2000). Our analysis is thus constrained to this level of taxonomic resolution.

Finally, using the number of pellets per liter of sediment as an index of change in artiodactyl abundances assumes that substantial variation in the accumulation of other sediments (owl pellets, spall, etc.) did not occur across the Homestead sequence. This appears to be the case as sediment analyses of the Homestead deposits suggests a remarkably consistent deposition rate, with the exception of three instances with little or no deposition (Madsen and Quade, 2000: Fig 34).

The density of artiodactyl pellets varies markedly across the deposits at Homestead Cave with consistently low densities during the terminal Pleistocene and early and middle Holocene, and with several marked spikes (especially at stratum XIII and XVI–XVII) during late Holocene times (Table 2; Fig. 6; see also Byers and Broughton, 2004; Byers et al., 2005). There is, however, no correlation between pellet abundances at Homestead and the composite annual moisture index derived from the Lakeside MCM ($r_s = -0.18$, $P > 0.45$). Instead, artiodactyl pellet densities at Homestead are correlated in the predicted directions with both summer precipitation ($r_s = 0.55$, $P = 0.02$), and temperature range ($r_s = -0.73$, $P < 0.01$; Fig. 11); and although the relationship between winter precipitation and artiodactyl pellet densities is not significant, it is in the expected direction ($r_s = -0.31$, $P = 0.21$; Fig. 7).

Insofar as these trends reflect the influence of long-term variation in climatic seasonality on artiodactyl reproduction and demography, similar ones should be found in mammalian taxa that share their sensitivity to climatic extremes. And while most small mammals are far less affected by climatic seasonality than larger ones, as we discussed above, certain taxa have reproductive ecologies that inhibit the facultative adjustment to climatic extremes. Most notable in this context are the monestrous rodent species represented in the Homestead fauna—those that produce a single litter a year and are thus more reproductively constrained by extreme breeding-season climate.

In the Homestead Cave small mammal fauna, only the sciurids (Sciuridae) exhibit this form of reproduction. And although four species of sciurid are present in the fauna (*Ammospermophilus leucurus*, *Tamias minimus*, *Marmota flaviventris*, *Spermophilus mollis*), the two ground squirrels—*A. leucurus* and *S. mollis*—comprise over 97% of the assemblage. This record, consisting of 3,856 identified skeletal specimens, represents the largest, highest-resolution Holocene sequence of ground squirrels in western North America (Grayson, 2000a). And, as Grayson (2000a) has documented, the changing abundance of Townsend's ground squirrel (*S. mollis*)

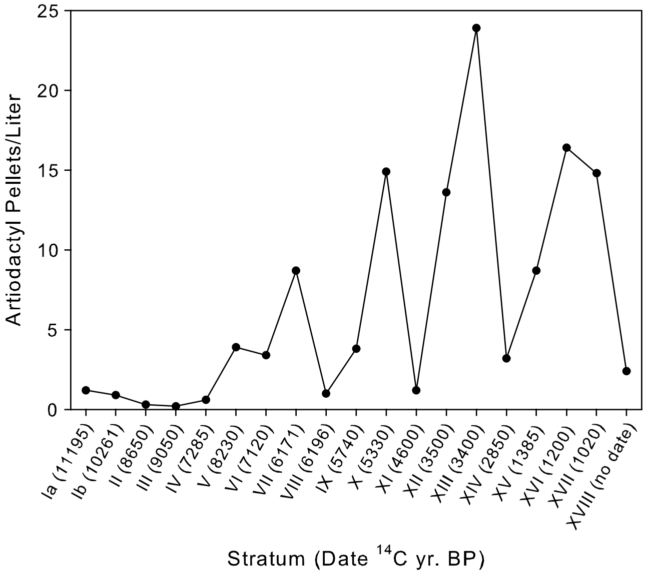

Fig. 6. The distribution of artiodactyl fecal pellet densities across the Homestead Cave strata.

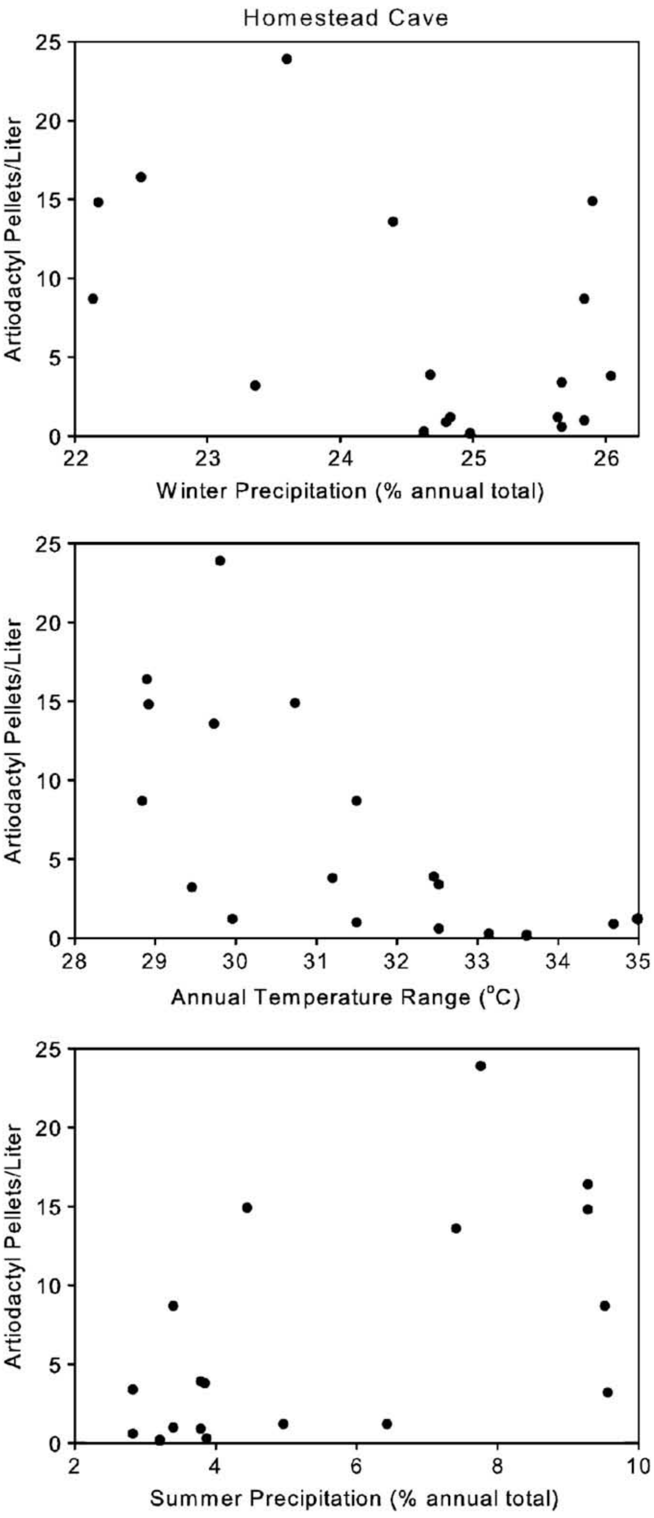

Fig. 7. The relationships between artiodactyl fecal pellet densities at Homestead Cave and modeled winter precipitation (top), intra-annual temperature range (middle), and summer precipitation (bottom).

accounts for most of the variation in the overall abundance of ground squirrels in this collection.

Townsend's ground squirrel inhabits arid high desert vegetation communities dominated by sagebrush (*Artemisia*), shadscale (*Atriplex*), or greasewood (*Sarcobatus*). Although Townsend's ground squirrel occurs in arid environments, it is most abundant in microhabitats with desert springs or near irrigated fields (Rickart, 1987). These squirrels are active for only 3–4 months of the year, typically from February through May. In these months they breed, and fatten quickly to sustain an 8–9 month period of subterranean dormancy lasting through the summer, fall and winter. Unlike all other local rodents, their reproductive success is thus highly dependent on favorable climate during their brief active period in the late winter and early spring. Indeed, in modern populations of Townsend's ground squirrel, reproduction is significantly depressed by late, cold and wet winters, or early, hot and dry springs (Rickart, 1987; Smith and Johnson, 1985; Van Horne et al., 1997). This unusual reproductive strategy should thus make them much more sensitive to extreme climatic seasonality than other rodents.

The temporal trend in the abundance of squirrels at Homestead Cave is similar in many respects to the one for artiodactyl pellets—squirrels occur in low frequencies in the terminal Pleistocene and early and middle Holocene strata but increase during the late Holocene (Fig. 8; Table 2). Indeed, the abundance of squirrels in a given stratum is significantly correlated with the density of artiodactyl fecal pellets recovered therein (Fig. 9; $r_s = 0.71$, $P = 0.01$). Further, there is no correlation between squirrel abundances at Homestead and the Lakeside moisture index ($r_s = -0.18$ $P > 0.40$), as is the case with the artiodactyl pellets, but two of the three measures of climatic seasonality are correlated in the predicted directions with ground squirrel frequencies at the site (Fig. 10; squirrels-summer precipitation, $r_s = 0.70$, $P = 0.02$; squirrels-temperature range, $r_s = -0.92$, $P < 0.01$; squirrels-winter precipitation, $r_s = -0.30$, $P = 0.31$). Finally, we observe that similar late Holocene increases in ground squirrel abundances have been detected in several other northern Great Basin deposits, most notably at Camels Back Cave (Schmitt and Lupo, 2005) and James Creek Shelter (Grayson, 1990), suggesting the Homestead pattern is not a function of a site-specific taphonomic process.

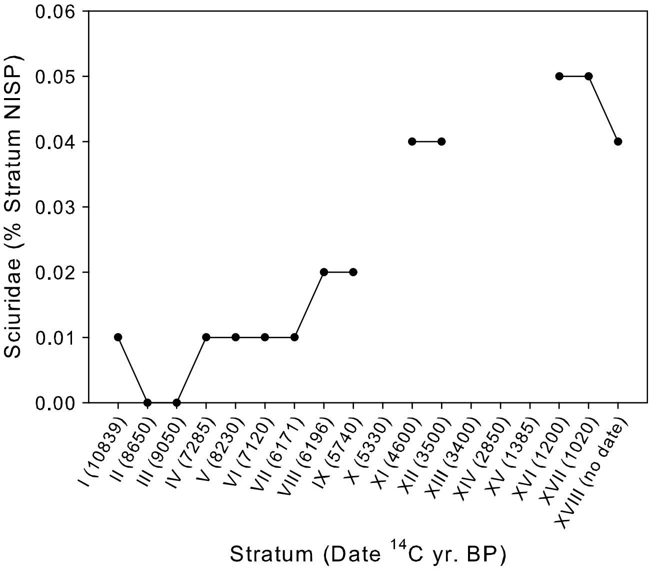

Fig. 8. The changing relative abundances of sciurid specimens through time at Homestead Cave. NISP = number of identified specimens. Missing values reflect strata that were not analyzed (see Grayson, 2000a).

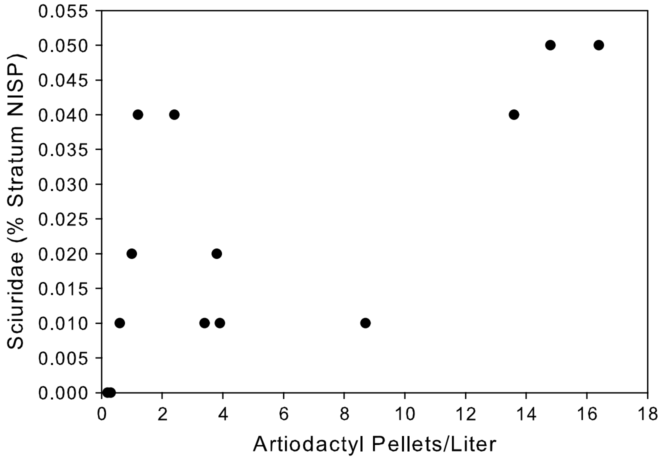

Fig. 9. The relationship between sciurid abundances and artiodactyl fecal pellet densities across the Homestead Cave strata. NISP = number of identified specimens.

In sum, correlations between the Homestead Cave pellet-based artiodactyl abundances and climatic indices derived from the Lakeside MCM are generally consistent with the hypothesis that variation in climatic seasonality affected long-term trends in artiodactyl population densities across the late Quaternary in the Bonneville Basin. An identical set of correlations was documented with ground squirrels—the other monestrous mammalian group in the deposit that should be similarly sensitive to climatic seasonality.

4.3. Hogup Cave

Hogup Cave is a limestone cavern located along the southern end of the Hogup Mountains, only 39 km northwest of Homestead Cave, and 37 km northwest of Lakeside (Fig. 1). With a relatively continuous, trans-Holocene record of human deposits, including an abundance of artiodactyl skeletal elements, materials from this site provide excellent, independent tests of our hypothesis. This is so not only because the site is located so close to Homestead and Lakeside in an identical environmental context, but since the artiodactyl specimens were accumulated by different agents—we thus use an entirely distinct set of indices to measure their abundances.

Sixteen stratigraphic units were encountered during the excavation of the Hogup Cave sediments that reached over 4 m in depth (Aikens, 1970). One-quarter-inch screens were used to collect not only an enormous sample of artiodactyl bones and other faunal remains, but an extensive record of perishable artifacts, including, textiles, nets, and moccasins (Aikens, 1970; Durrant, 1970). Thirty-two ^{14}C dates place the human occupation of the cave between about 8800 and 480 years BP (Table 3). Although several of these dates are out of stratigraphic order, as others have noted (e.g., Madsen and Berry, 1975; Grayson, 1993; Mullen, 1997), we observe here that, overall, stratigraphic position and time based on these dates are highly correlated ($r_s = 0.77$, $P < 0.0001$). Because ancient human foragers played the dominant role in depositing the Hogup Cave artiodactyl remains, we consider how such collections can inform on the densities of artiodactyls on ancient landscapes.

For a variety of reasons, artiodactyls are highly valued by human consumers. Such taxa not only yield absolutely more food energy, protein, and other nutrients per animal, compared to smaller-sized prey, but they provide larger amounts of raw materials for tools and clothing. Differences in pursuit and processing costs between large and small game typically do not offset this great disparity in economic value, and indeed experimental and ethnographic data

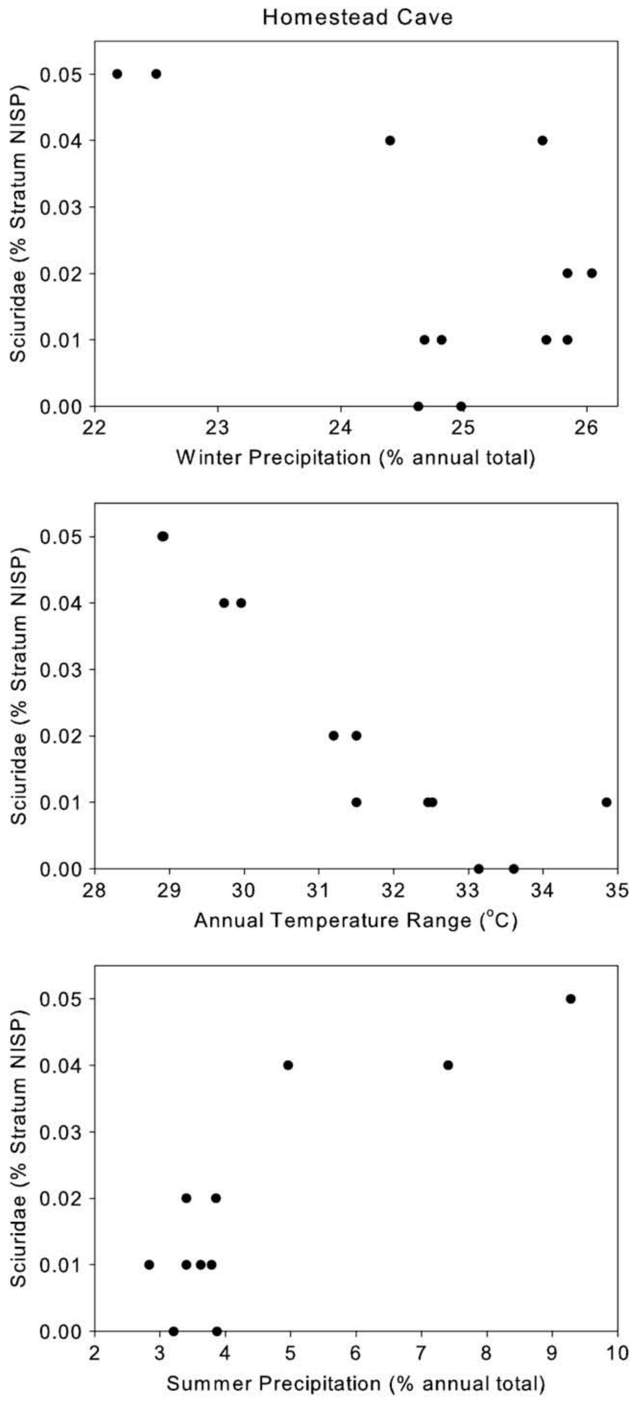

Fig. 10. The relationships between sciurid abundances at Homestead Cave and modeled winter precipitation (top), intra-annual temperature range (middle), and summer precipitation (bottom).

have demonstrated strong positive correlations between prey body size and caloric rates of return for human hunters using traditional methods (see Ugan, 2005, for a systematic analysis of these data). Moreover, many have argued that large-sized prey also rank high on other currencies, such as those associated with prestige hunting, and status and signaling rivalry (e.g., Hawkes, 1991; Hildebrandt and McGuire, 2002; Broughton and Bayham, 2003). Finally, recent ethnographic research on men's hunting goals (e.g., Hawkes, 1991, 1993; Wiessner, 2002), clearly underlines the overriding significance that hunters attach to prey body size: if large game are present on the landscape, male hunters persistently seek them out.

Table 3
Radiocarbon dates from Hogup Cave[a]

Stratum	C14 date	Calibrated age[b]	Lab no.	Material
16	480 ± 80	422–572	GaK1566	Plant stems, bark, dung
16	1810 ± 80	1545–1898	GaK1565	Grass
16	2200 ± 70	2040–2344	GaK2077	Plant stems, bark, dung
14	620 ± 70	522–677	GaK2080	Plant stems, bark, dung
14	1210 ± 100	952–1296	GaK2078	Plant stems, bark, dung
14	1951 ± 70	1718–2060	AA20857	*Lepus* bone collagen
12	1530 ± 80	1293–1569	GaK1561	Grass, reeds
12	2550 ± 70	2433–2767	GaK2079	Plant stems, bark, dung
12	2920 ± 80	2864–3269	GaK1560	Grass, plant stems, bark
10	2430 ± 245	1880–3075	SI-2338	*Phragmites*
10	2600 ± 100	2360–2877	GaK2081	Plant stems, bark
10	4490 ± 100	4857–5326	GaK2076	Feces
9	1260 ± 120	934–1369	RL-413	*Phragmites*
8	3200 ± 140	3061–3729	GaK1564	Reeds
8	4586 ± 94	4971–5484	AA20339	*Lepus* bone collagen
8	4610 ± 100	5035–5492	GaK1568	Plant stems
8	6370 ± 111	7138–7483	AA20340	*Lepus* bone collagen
8	6484 ± 117	7171–7578	AA20341	*Lepus* bone collagen
7	6190 ± 110	6790–7323	GaK2084	Feces
6	5960 ± 100	6532–7026	GaK1567	Charcoal
6	6400 ± 100	7155–7508	GaK1563	Charcoal
5	5795 ± 160	6286–6992	GX1288	*Artemisia* bark
5	7250 ± 100	7927–8315	GaK2082	Plant stems, bark
4	7815 ± 350	7980–9480	GX1287	*Artemisia* bark
3	6020 ± 380	6168–7592	GX1286	Charcoal
3	8800 ± 200	9442–10 300	GaK2083	Plant stems, dung
2	3970 ± 100	4148–4709	GaK1570	Rabbit bone
1	2274 ± 71	2106–2471	AA20856	*Lepus* bone collagen
1	4638 ± 94	5211–5586	AA20338	*Marmota* bone collagen
1	7860 ± 160	8376–9094	GaK2086	Feces, fur
1	7961 ± 102	8546–9034	AA20858	*Marmota* bone collagen
1	8350 ± 160	8976–9680	GaK1569	Charcoal

[a] Dates with lab numbers beginning with GaK and GX are from Aikens (1970); those beginning with AA are from Mullen (1997); RL, Madsen and Berry, 1975; SI, Berry, 1976.

[b] Two sigma ranges; calculated from CALIB 5.1.0 (Stuiver and Reimer, 2005).

Insofar as higher densities of artiodactyls elevated overall returns from hunting in past landscapes using any of these currencies, smaller, lower-return animals—especially lagomorphs, in the Great Basin context—are predicted to less frequently enter the targeted set of prey (e.g., Bayham, 1982; Stephens and Krebs, 1986; Broughton, 1994; Byers and Broughton, 2004). It thus follows that increasing abundances of large game in past environments should result in proportionate increases in the hunting of large game, relative to small game, other things equal. The relative frequencies of artiodactyl skeletal elements in archaeological faunas, as measured by the artiodactyl index ($\sum$ artiodactyls/$\sum$ artiodactyls + $\sum$ lagomorphs), should thus track trends in their abundance on the landscape.

Four artiodactyl species are represented by skeletal elements at Hogup Cave, including, by decreasing order of abundance, pronghorn (minimum number of individuals [MNI] = 104), mule deer (MNI = 32), bison (MNI = 22), and bighorn sheep (MNI = 15; Durrant, 1970). Lagomorphs, including both hares (*Lepus*) and cottontails (*Sylvilagus*), are also well represented in the collection with a minimum of 2022 individuals (Durrant, 1970; see also Hockett, 1993).

Variation in the representation of artiodactyl specimens across the Hogup Cave strata is presented in Fig. 11 (Table 4). Artiodactyl index values are consistently low during the early and middle Holocene but increase, with two marked spikes (strata 10–11; stratum 14), during the late Holocene. This pattern is similar to the one documented for artiodactyl pellet densities at Homestead Cave, although the Hogup sequence does not extend into the terminal Pleistocene. Not only are artiodactyl bones more abundant in the collective set of late Holocene strata, their specific fluctuations within the late Holocene are well aligned with the artiodactyl pellet

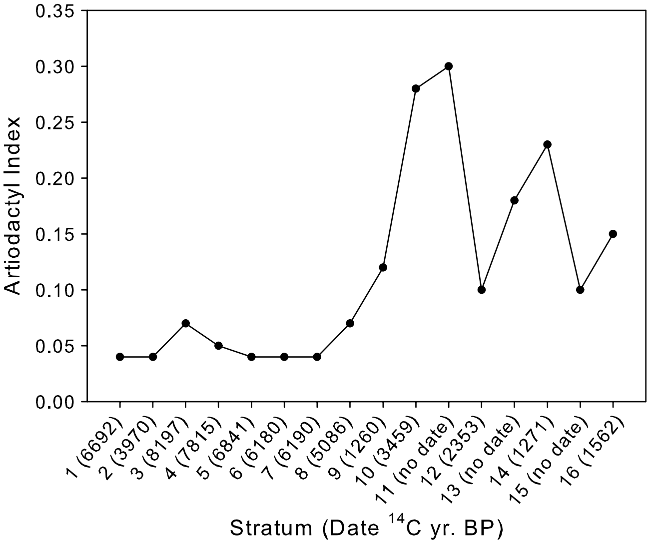

Fig. 11. The distribution of the artiodactyl index across the Hogup Cave strata.

spikes at Homestead Cave. Both data sets show dramatic peaks in artiodactyl specimens between about 4000 and 2000 yrs BP and again between 2000 and 1000 BP.

Correlations between the Hogup Cave bone-based measures of artiodactyl abundances and our climatic indices are also similar to the ones derived from the Homestead pellet analysis. Specifically, there are strong and significant correlations between the artiodactyl index and each of our indices of climatic seasonality: artiodactyl index values are negatively correlated with both winter precipitation ($r_s = -0.94$, $P < 0.01$), and temperature range ($r_s = -0.65$, $P = 0.04$), and positively correlated with summer precipitation ($r_s = 0.82$, $P < 0.01$; Fig. 12). In this case, the correlation between the artiodactyl index and the moisture index is positive, but insignificant ($r_s = 0.60$, $P > 0.05$; Table 3).

While the taphonomic history of this set of deposits is complex and people were only one of many predators that introduced bones into the cave (Hockett, 1993, 1994), several lines of evidence, presented in detail elsewhere (Byers and Broughton, 2004), suggest that the trend in the artiodactyl index is truly reflecting variation in human hunting behavior. Specifically, while it could be argued that the late Holocene rise in artiodactyl index values simply represents a proportionate increase in the human use of the cave, compared to other accumulators, analyses of trends in human, raptor, and carnivore damage on the Hogup materials provide no suggestion that this was the case (Byers and Broughton, 2004). Further, recent analysis of the demographic structure of the abundant pronghorn materials provides no evidence for change that might suggest a shift in the functional use of the cave (Hill and Byers, 2006).

We derive a final measure of Holocene variation in artiodactyl abundances in the Bonneville Basin from the relative abundance of tools that ancient hunters would have used to hunt large game. As we noted above, Hogup Cave is rich in perishable artifacts including fragments of nets and snares, items that were typically used to capture small game, such as lagomorphs (Steward, 1938; Fowler, 1986). In addition, chipped stone projectile points were also abundant in certain strata of the deposit—although they can be associated with a wide range of hunting and defensive behaviors, they are integral components of the primary weaponry used to kill artiodactyls (e.g., Steward, 1938). Insofar as nets and snares were commonly used to capture lagomorphs, and projectile points were associated with technology designed to kill artiodactyls, then the projectile point index ($\sum$ projectile Points/[$\sum$ projectile Points $+ \sum$ cordage]) should provide another indirect measure of artiodactyl abundances on the landscape.

Fig. 13 shows both the artiodactyl and projectile point indices plotted across the Hogup Cave strata. The two variables appear well aligned and a correlation analysis confirms this impression ($r_s = 0.81$, $P < 0.01$). Further, this tool-based index of artiodactyl abundances is not correlated significantly with overall annual effective moisture derived from the Lakeside climate model ($r_s = 0.37$, $P > 0.20$), but it is negatively correlated, with both winter precipitation ($r_s = -0.84$, $P < 0.01$), and seasonal temperature range ($r_s = -0.77$, $P = 0.02$) and positively correlated with summer precipitation ($r_s = 0.79$, $P = 0.01$; Fig. 14).

4.4. Summary and synthesis

Three independent measures of late Quaternary artiodactyl abundances applied to paleorecords in the northern Bonneville Basin (fecal pellets, skeletal elements, and hunting tools), with few exceptions, show significant correlations with three measures of climatic seasonality derived from the Lakeside MCM. The nature of

Table 4
Hogup Cave ^{14}C dates, abundance indices and corresponding Lakeside MCM climate values[a]

Stratum	Date[a]	Artiodactyl index	Projectile point index	Lakesidemoisture index	Winter precipitation (% annual total)	Summer precipitation (% annual total)	Intra-annual temperature range (°C)
16	1562	0.15	0.47	−38.95	22.57	8.30	28.73
15	–	0.10	0.25	–	–	–	–
14	1271	0.23	0.63	−40.00	22.50	9.28	28.90
13	–	0.18	0.35	–	–	–	–
12	2353	0.10	0.41	−39.51	24.09	9.42	29.32
11	–	0.30	0.22	–	–	–	–
10	3459	0.28	0.46	−40.11	23.49	8.04	29.88
9	1260	0.12	0.28	–	–	–	–
8	5086	0.07	0.22	−40.39	25.69	4.66	30.32
7	6190	0.04	0.12	−40.77	25.84	3.40	31.50
6	6180	0.04	0.09	−40.77	25.84	3.40	31.50
5	6841	0.04	0.13	−40.69	25.75	3.11	32.11
4	7815	0.05	0.10	−38.27	25.05	3.25	32.20
3	8197	0.07	0.15	−38.08	24.68	3.79	32.46
2	3970	0.04	0.10	–	–	–	–
1	6692	0.04	0.20	−40.63	25.80	3.28	31.87

[a] The dates for strata with multiple radiocarbon determinations are pooled mean dates calculated using Calib 5.1.0 software (Stuiver and Reimer, 2005). For strata with more than three assays, dates in excess of one standard deviation from the mean date were omitted prior to calculating the pooled mean. Stratum 2 provided a single date of 3970 but is bracketed by strata with multiple dates yielding mean values of 6692 and 8197 (Table 3). Similarly, stratum 9 yielded a single date of 1260 but is bracketed by strata with multiple dates yielding mean values of 5086 and 3459. These data strongly suggest the single assays for stratum 2 and 9 are problematic (see Aikens, 1970 for further discusssion). As a result, we do not include them in the correlation analyses. We do observe, however, that the general pattern of correlations do not change if they are included in the analysis. Raw data for abundance indices from Aikens (1970).

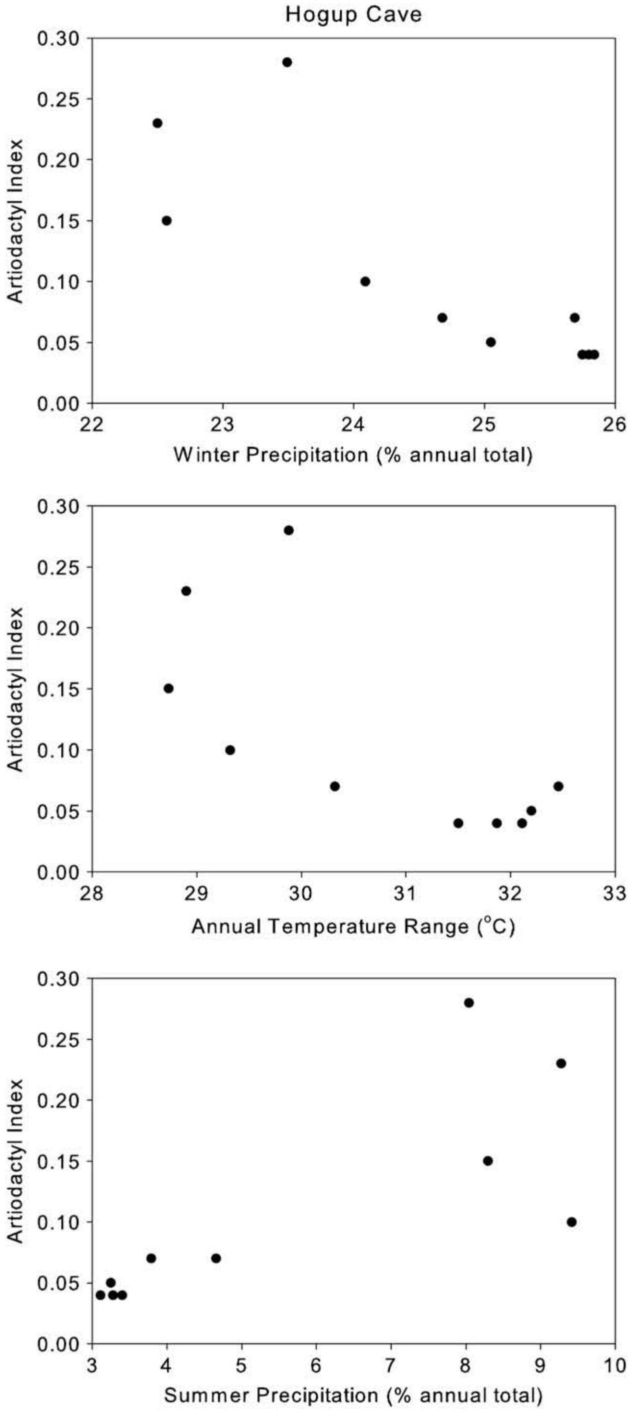

Fig. 12. The relationships between the artiodactyl index at Hogup Cave and modeled winter precipitation (top), intra-annual temperature range (middle), and summer precipitation (bottom).

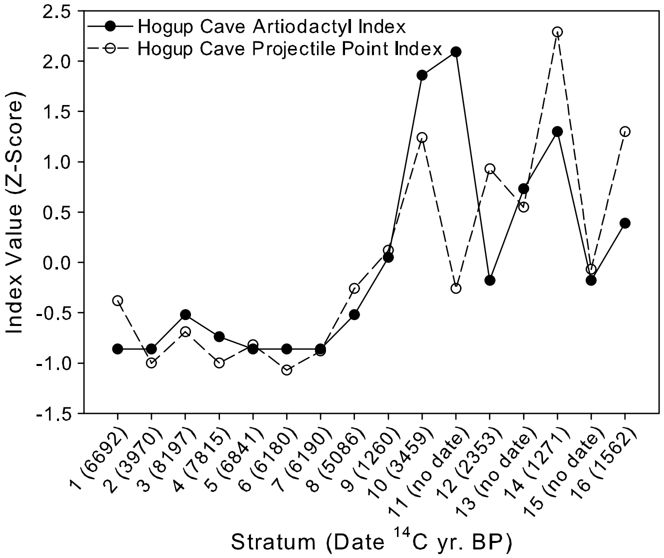

Fig. 13. The distribution of the artiodactyl and projectile point indices (standardized) across the Hogup Cave strata.

these relationships is, in fact, most apparent when the three indices of artiodactyl abundances are standardized and plotted together against our measures of climatic seasonality (Fig. 15). For each variable of climatic seasonality, there are highly significant correlations with the collective set of standardized artiodactyl abundance indices (winter precipitation–artiodactyls [Z-score], $r_s = -0.60$, $P < 0.001$; temperature range–artiodactyls [Z-score], $r_s = -0.72$, $P < 0.0001$; summer precipitation–artiodactyls [Z-score], $r_s = 0.71$, $P < 0.0001$). In addition, none of our indices of artiodactyl abundances show significant correlations with annual average effective precipitation across the late Quaternary in this region—a result that does not change when the artiodactyl Z-score values are arrayed collectively against the moisture index ($r_s = 0.18$, $P > 0.25$; Fig. 16). Moreover, while annual average effective precipitation appears to predict regional patterns in the abundances of mesic-oriented rodents in general and other taxa such as fish, this is not the case for the monestrous ground squirrels that are sensitive to extreme climate during their brief above-ground active period. Instead, ground squirrel abundances are significantly correlated with our indices of seasonality, in a pattern identical to that documented for the artiodactyls. These data support the hypothesis that climatic seasonality played a major role in driving late Quaternary variation in artiodactyl densities in the Bonneville Basin.

4.5. *Seasonality versus annual effective precipitation*

We expect artiodactyl populations to be sensitive to annual average effective precipitation and primary productivity, other things equal, and have demonstrated positive relationships between these variables elsewhere in several different contexts in the western United States—patterns especially evident in analyses comparing artiodactyl abundances across middle and late Holocene contexts (Broughton and Bayham, 2003; Byers and Broughton, 2004; Byers et al., 2005; Byers and Smith, 2007). Effective precipitation is, however, uncorrelated with our indices of artiodactyl abundances in the Bonneville Basin. We suggest the source for this may lie in the fact that the temporal coverage examined here extends into the terminal Pleistocene and early Holocene, again a period characterized by extreme climatic seasonality—the strong influence of seasonality may be swamping any affect of effective precipitation on artiodactyl populations over this extended temporal span.

This hypothesis is testable with the data sets we have presented. Specifically, we expect that correlations between the moisture index and Bonneville Basin artiodactyl abundances will strengthen insofar as the affect of climatic seasonality can be reduced. Correlations between artiodactyl abundances and annual effective precipitation should thus be stronger across middle and late Holocene contexts—that is, *after* the period of the most extreme seasonal climate.

Data from Homestead and Hogup Caves bear this out. In particular, the relationship between the moisture index and the

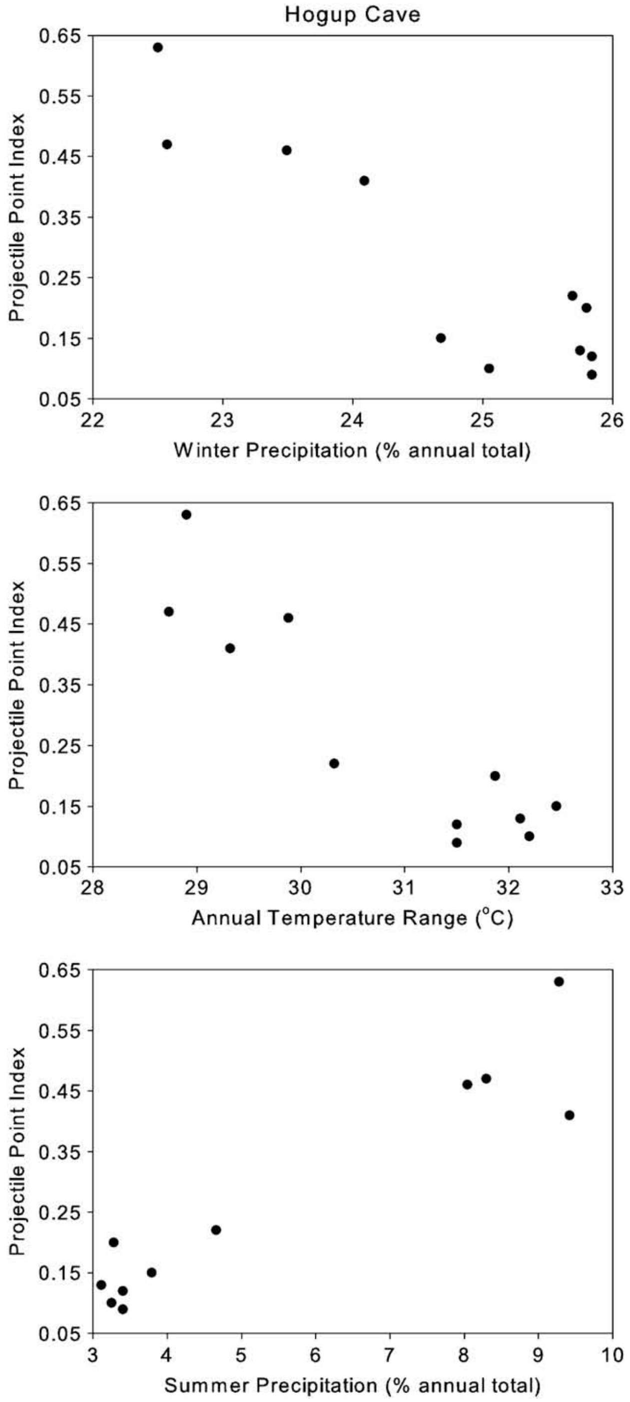

Fig. 14. The relationships between the projectile point index at Hogup Cave and modeled winter precipitation (top), intra-annual temperature range (middle), and summer precipitation (bottom).

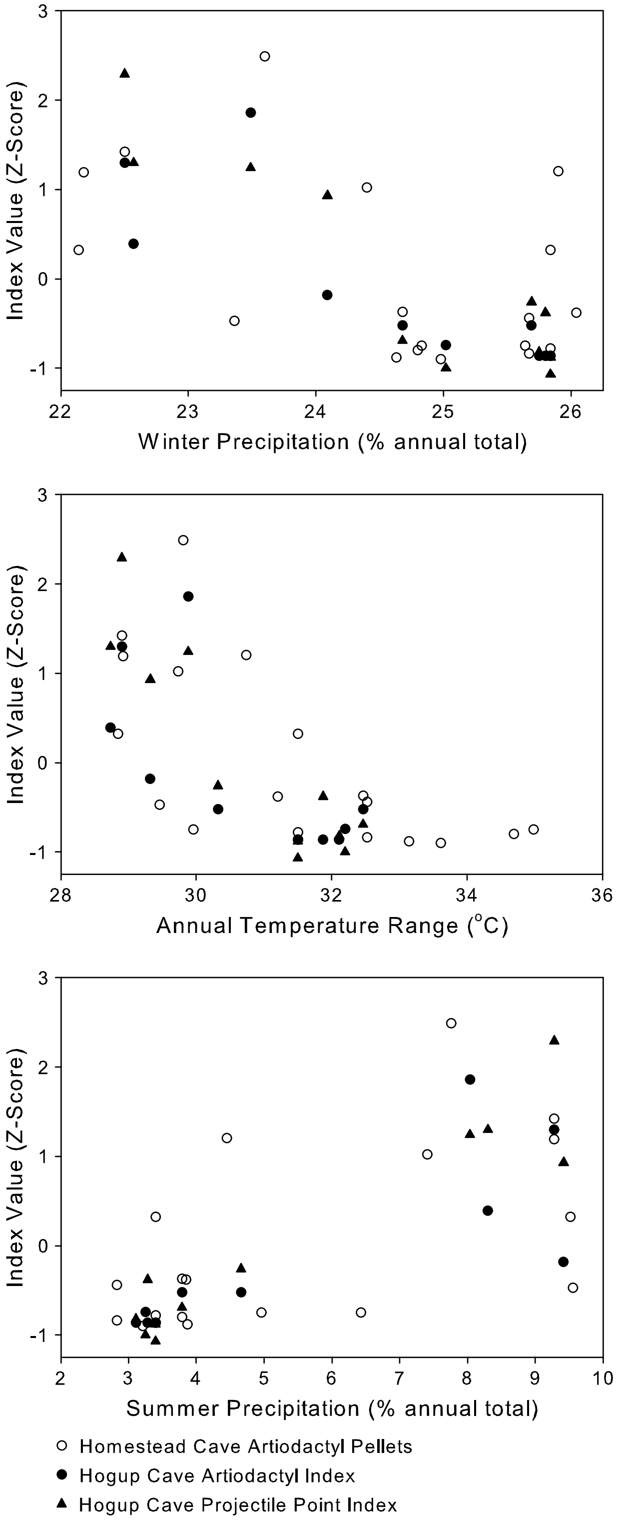

Fig. 15. The relationships between various Bonneville Basin artiodactyl abundance indices (standardized) and modeled winter precipitation (top), intra-annual temperature range (middle), and summer precipitation (bottom).

collective set of standardized artiodactyl indices (Z-scores) becomes positive and significant when the terminal Pleistocene and early Holocene samples are excluded from the analysis ($r_s = 0.67$, $P < 0.001$; Fig. 17). Notice in Fig. 17, how the terminal Pleistocene and early Holocene samples obfuscate a positive correlation between the moisture index and artiodactyl abundances—they are characterized by high moisture index values, but consistently produce low artiodactyl abundances.

Finally, it is also the case that the relationships between artiodactyl abundances and the measures of climatic seasonality remain highly significant over the samples representing only the middle and late Holocene periods (winter precipitation–artiodactyl index [Z-score], $r_s = -0.66$, $P < 0.001$; temperature range–artiodactyl index [Z-score], $r_s = -0.72$, $P < 0.001$; summer precipitation–artiodactyl index [Z-score], $r_s = 0.62$, $P < 0.01$). So, rather than replacing climatic seasonality as an influential factor affecting artiodactyl populations during the middle and late Holocene,

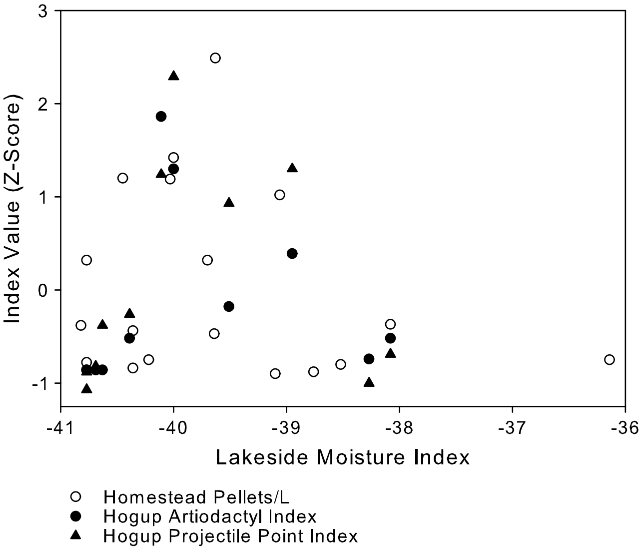

Fig. 16. The relationship between various Bonneville Basin artiodactyl abundance indices (standardized) and the Lakeside moisture index.

annual effective precipitation and primary productivity also become significant over this period.

4.6. Other Bonneville Basin records

Other Holocene Bonneville Basin archaeological vertebrate records reflect trends in artiodactyl abundances similar to those derived from Homestead and Hogup Caves. For instance, the well-documented record from Danger Cave (western Bonneville Basin) is represented by early and middle Holocene faunal records with low densities of artiodactyls with dramatic spikes in the frequencies of these animals in late Holocene sediments (Danger Cave: early and middle v. late $X^2 = 191.13$, $P < 0.000$; data from Grayson, 1988). A similar pattern exists at Camels Back Cave in the southern Bonneville Basin (Schmitt and Lupo, 2005). Although the oldest deposits reach back to 9560 years BP, the human record does not begin here until 7500 BP. Artiodactyls are virtually absent in this fauna until the early late Holocene, when these animals represent at times nearly 40% of the identified specimens (Camels Back Cave: early and middle v. late $X^2 = 1056.78$, $P < 0.000$).

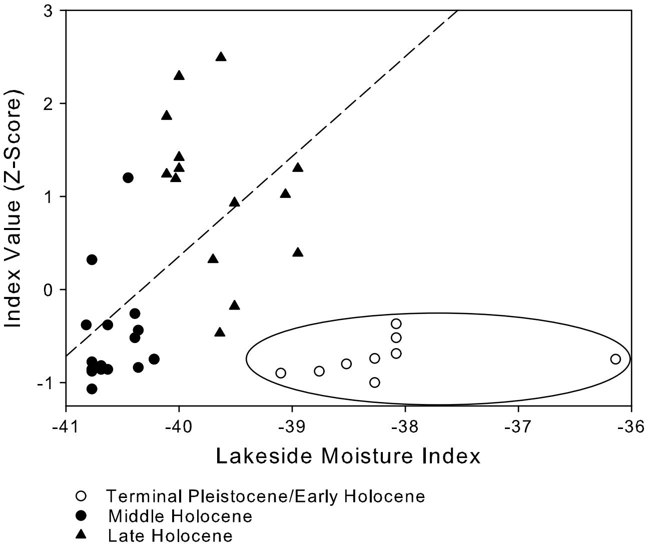

Fig. 17. The relationship between various Bonneville Basin artiodactyl abundance indices (standardized) and the Lakeside moisture index. (Data points identified by time period.)

4.7. Bonneville Basin climate change and mammalian abundances: a scenario

Collectively, these analyses suggest the following general scenario of terminal Pleistocene and Holocene climate change and mammalian abundances in the Bonneville Basin. Overall, the terminal Pleistocene and early Holocene appear to have been relatively "cool and moist" and characterized by high primary productivity. However, the seasonal swings in temperature were extreme at this time with hot, dry, summers and cold, wet, winters. Mesic small mammals and other taxa such as fishes that are less sensitive to climatic seasonality were more abundant during this time, but steadily declined across the period. Population densities of artiodactyls were, however, significantly depressed—as were other taxa, such as ground squirrels, that are also strongly influenced by climatic extremes. Intra-annual temperature range declined gradually through the middle Holocene, but precipitation continued to be characterized by a winter-wet, summer-dry pattern. Moreover, annual effective precipitation and primary productivity were consistently low during the middle Holocene, even though the seasonality of temperature had declined. Artiodactyl populations continued to struggle, as did mesic small mammals, both likely impacted here by the extremely low effective precipitation of the period. The late Holocene was characterized by the most equable temperature of the late Quaternary, and it was also marked by several periods in which the high equability occurred together with a favorable precipitation regime, namely, high overall effective precipitation coupled with a summer-wet pattern. This set of conditions allowed artiodactyl populations to expand dramatically, reaching densities higher than the region had witnessed since before the major faunal restructuring associated with late Pleistocene extinctions. Climatic conditions of the late Holocene were not uniformly favorable to artiodactyls and several periods during the last 4000 years are marked by major downturns in their abundances.

5. Other Holocene artiodactyl records in western North America

We have focused on the Bonneville Basin because it is represented not only by an exceptionally fine-grained paleoenvironmental record—including the only detailed paleontological sequence of artiodactyls in western North America—but one of the longest, and richest, trans-Holocene human-derived records of artiodactyls. Insofar as the Holocene climatic conditions and artiodactyl abundance history documented for the Bonneville Basin applies to other regions of western North America, we anticipate paleorecords of artiodactyl densities to mirror the trends documented for this location. That is, faunal records from other settings in western North America characterized by similar climatic regimes—especially within the summer-dry region of California, northern Great Basin and Pacific Northwest—should also reflect depressed populations of artiodactyls during the early and middle Holocene, with marked increases during the late Holocene. While many other archaeofaunal records have been generated from western North America, and we do not attempt a fully comprehensive review of those here, we do observe that many appear to be consistent with this hypothesis.

We turn first to other Great Basin archaeological vertebrate records and note initially that substantial late Holocene increases in artiodactyl abundances have been previously documented for many sites in the region containing both middle and late Holocene sediments (Byers and Broughton, 2004; Byers et al., 2005). We add here the observation that while other early Holocene Great Basin faunal records are few in number, they are typically associated with low densities of artiodactyls. The trans-Holocene record from Last Supper Cave (northwestern Nevada), for instance, is represented by an early and middle Holocene fauna with low frequencies of artiodactyls, but a late Holocene assemblage containing significantly higher abundances of these animals (Last Supper Cave: early and middle v. late $X^2 = 152.80$, $P < 0.000$; data from Grayson, 1988).

Pinson's (1999, 2007) systematic analysis of archaeofaunal records from 23 site components from the northwestern Great Basin is especially compelling in this context. This region is represented by more early Holocene archaeofaunal records than any other in the Great Basin and shows consistently low densities of artiodactyls during the early Holocene, with significant, but highly variable, increases after 6000 BP (artiodactyl index: early and middle v. late: Mann–Whitney $U = 27.00$, $P = .01$).

Although a systematic trans-Holocene synthesis of the California archaeological artiodactyl record has yet to be conducted, early to middle Holocene components are also typically characterized by high abundances of small vertebrate remains but with a noteworthy scarcity of artiodactyls (e.g., Basgall, 1993; Erlandson, 1994; McGuire and Hildebrandt, 1994; Erlandson et al., 1999; Wake and Simons, 2000; Jones et al., 2002). By the early late Holocene (4500–2500 BP), however, artiodactyls dominate many archaeofaunal profiles from a widely disparate set of ecological settings across the state (Broughton, 1994, 1999, 2002; Grayson, 2001; Hildebrandt and McGuire, 2002). In the Pacific Northwest Coast and Columbia Plateau, recent systematic analyses of archaeological faunas again show low frequencies of artiodactyls during the early and middle Holocene with sharp increases in late Holocene components (Lyman and Wolverton, 2002; Butler and Campbell, 2004; see also Lyman, 1992 and Chatters, 1998).

Finally, systematic analyses of over 250,000 identified specimens from 284 site components from the Wyoming Basin document dramatic late Holocene expansions of artiodactyl populations in this setting (Byers et al., 2005; Byers and Smith, 2007). Initiating the approach we have adopted here, temporal patterns in artiodactyl abundances were correlated with simulated climatic data derived from a local MCM. Those analyses documented significant correlations with artiodactyl abundances and the moisture index, a pattern especially convincing in comparisons between middle and late Holocene site components. Species-specific trends were also documented—bison numbers fluctuate more sensitively with the moisture index than do pronghorn, in a pattern consistent with their different feeding ecologies (Byers and Smith, 2007).

The impact of variation in climatic seasonality is also readily apparent with the Wyoming Basin data. In fact, when the seasonality indices we developed here are calculated from data derived from the Wyoming Basin MCM, significant correlations are revealed between them and the Holocene trends in artiodactyl abundances in that region (artiodactyl index-winter precipitation, $r_S = -0.63$, $P < 0.001$; artiodactyl index-temperature range, $r_S = -0.45$, $P = 0.001$; artiodactyl index-summer precipitation, $r_S = 0.61$, $P < 0.001$). Indeed, each of these correlations is stronger and more significant than is the one between effective precipitation (moisture index) and the artiodactyl index ($r_S = 0.39$, $P = 0.01$).

6. Geographic, site- and species-specific variability

The analyses above are consistent with the hypothesis that artiodactyl densities in western North America were depressed due to unfavorable climate during the terminal Pleistocene through the middle Holocene and that substantial increases occurred as conditions ameliorated during the late Holocene. It is important to emphasize, however, that there are reasons to anticipate considerable spatial-temporal heterogeneity within these general trends as well. Insofar as particular spatio–temporal contexts during the early and middle Holocene were characterized by more equable climate, for instance, they may also have supported higher densities of artiodactyls. Primary migration corridors may also have contained relatively high densities of game during these times. In such contexts, increases in the proportional representation of artiodactyls would not be anticipated at the middle–late Holocene transition.

Several records seem to show just this pattern. Sudden Shelter, for instance, a higher elevation (2267 m) mesic upland site located in central Utah, is situated within a major mule deer migration corridor between the Great Basin and Colorado plateau. And the record here shows consistently high artiodactyl index values (>0.87) across the sites entire occupational history, spanning from about 8000–3000 BP (Rampton, 1999). On the other side of the Great Basin in Surprise Valley, substantial natural springs apparently flowed throughout the period of middle Holocene drought. This may have provided a mesic refugium for otherwise regionally depressed artiodactyl herds. Although taphonomic issues do not permit a secure conclusion here, we note that the proportional representation of artiodactyl specimens is highest for the middle Holocene occupations of this area (O'Connell, 1975).

We stress too that artiodactyl abundances appear to have been highly variable through time *within* the late Holocene, as the Bonneville Basin paleontological and archaeological records so clearly suggest. Thus, generating predictions about variation in artiodactyl abundances at any particular spot on the landscape requires careful attention to locally derived paleoclimatic data.

Climatic conditions were, of course, not the only factors influencing the prehistoric abundances of artiodactyls in western North America. Despite generally favorable environmental conditions for artiodactyls across many stretches of the late Holocene, in certain contexts, human hunting pressure appears to have ultimately overtaken them, causing substantial population declines. Such anthropogenic depressions have now been documented in some detail in several areas of western North America, including the Great Basin (e.g., Janetski, 1997; Grayson, 2001), California (e.g., Broughton, 2002, 2004; Hildebrandt and Jones, 2002), the Southwest (Cannon, 2000, 2003), and the Pacific Northwest (Butler, 2000; but see Lyman, 2003; Butler and Campbell, 2004). In these settings, expanding densities of late Holocene human populations appear to have caused the depression of a wide range of artiodactyl taxa, including elk, mule deer, pronghorn, and bighorn sheep.

We also emphasize that variation in archaeological site function or the role that sites played in the regional settlement-mobility system can, of course, influence the energetics of prey choice and transport, and affect variation in the taxonomic composition of archaeological faunas, independent of any temporal trends in the abundances of artiodactyls on past landscapes (Bayham, 1982; Broughton, 1999, 2002; Cannon, 2003). A shift in the regional settlement pattern in which the function of a site changed from a residential base to a hunting camp, would, for instance, have obvious implications for variation in the relative abundances of large game skeletal elements or hunting tools recovered from its sediments (see Bayham, 1982; Byers and Broughton, 2004). And insofar as there is a greater likelihood that large-packaged resources will be field processed (see Metcalfe and Barlow, 1992), we anticipate kill sites to be biased towards the remains of large-sized prey, regardless of when they were deposited.

Finally, we note that our necessary focus on artiodactyls, as a unit, masks potential climate-based variation in species level abundance histories. And while conditions during the early and middle Holocene appear to have depressed the populations of all western taxa, response at the species level to the climatic amelioration of the late Holocene was undoubtedly characterized by considerable geographic complexity. In the Wyoming Basin, for instance, Byers and Smith (2007) clearly document that bison populations were more sensitive to lower amplitude Holocene fluctuations in aridity, compared to pronghorn. It is also likely that some species would be more susceptible to extremes in seasonality, while others may have a higher threshold of toleration. Predicting how a given seasonality regime would affect niche partitioning and the species balance of artiodactyl communities in different geographic contexts will require further study. Indeed, insofar as different artiodactyl species are differentially sensitive to these factors of climatic seasonality, future analyses conducted at the species level could perhaps provide further tests of our hypothesis.

7. Discussion

The data and analyses above are consistent with the hypothesis that climatic seasonality played a key role in driving late Quaternary variation in artiodactyl densities in western North America. This conclusion has far-reaching implications not only for our understanding of ancient human land use patterns, but for the future management of artiodactyls under scenarios of global warming that also project dramatic increases in extreme climatic events. We explore both issues below.

7.1. Seasonality and Holocene subsistence and land use in the Great Basin

Dramatic Holocene fluctuations in the densities of artiodactyls would have had substantial impacts on human subsistence and land use in western North America. And although we anticipate that the widespread climate-based trends in artiodactyl population histories would have significant effects on human economies wherever they occurred, we examine the issue here for the Great Basin, again the setting from which we have the most convincing support for the pattern and its underlying causes.

Ever since Antevs (1948, 1952, 1955) presented his Holocene climatic sequence, Great Basin archaeologists have sought links between climatic change and human adaptations. This tradition has, however, been one focused on Holocene trends in average annual temperature and precipitation, with far less attention devoted to intra-annual variation in temperature and precipitation. For example, soon after Antevs promoted the early Holocene as cool and moist, Great Basin archaeologists began to consider these “good times” for both large game and human populations alike (e.g., Baumhoff and Heizer, 1965; Warren, 1967; Elston, 1982). This position is still one that is held today (e.g., Grayson, 1993: 244; Beck and Jones, 1997; Elston and Zeanah, 2002; Zeanah, 2004).

In modeling resource use and settlement patterns in the Carson Desert of western Nevada, for instance, Elston and Zeanah (2002; see also Raven and Elston, 1989; Zeanah et al., 1995; Zeanah, 2004), elevate early Holocene large game densities by 75% from historic period estimates on the basis of the higher annual effective precipitation and forage quality that they suggest to have characterized the period. The result, not surprising, is the prediction of an early Holocene “hunting-oriented” subsistence system: “a residentially mobile adaptation in which men’s hunting opportunities determined residential movements” (Elston and Zeanah, 2002: 115). Our point is not to criticize the insightful analysis and modeling work of this research group, as we discuss in more detail below, but only to suggest that our analysis here predicts very different values for early Holocene game densities—very different human settlement strategies would follow, accordingly.

The early Holocene artiodactyl record emerging here also plays into—or out of, as the case appears—another widely discussed shift in aboriginal Great Basin subsistence: the shift to the intensive utilization of small seeds at or near the early–middle Holocene transition. Small seed resources have been shown to yield low caloric return-rates (Simms, 1985, 1987; see also O’Connell and Hawkes, 1981), but were a dietary staple to many native Great Basin peoples during early historic times. Early Holocene records show a paucity of seed grinding equipment (grinding stones, handstones) and other evidence of the human use of these resources, with site locations concentrated on valley bottoms near what would have been the shores of shallow lakes or marshes (Grayson, 1993; Beck and Jones, 1997; Rhode et al., 2006). As annual effective moisture decreased toward the end of the early Holocene, it is argued, so too did overall foraging returns and previously ignored, or less frequently utilized, low-return small seed resources were then added to the diet (e.g., O’Connell et al., 1982; Simms, 1987; Grayson, 1993; Rhode et al., 2006). What has not been clear, however, is the role that changes in large game abundances on the landscape may have played in this widespread subsistence shift. Some have suggested that dwindling populations of large mammals were responsible, in whole or in part, for precipitating the diet breadth expansion that marked this transition (O’Connell et al., 1982; Beck and Jones, 1997; but see Madsen, 2002, 2007 for a contrasting view). Zeanah and Simms (1999: 122) summarize this position: “seeds may have entered the diets of Great Basin foragers after 8500 B.P. in response to declining encounters with large game”. We stress again that while the early Holocene was characterized by high effective moisture and primary productivity, artiodactyl densities were nonetheless kept thin during this time due to extreme seasonality—no shift in their densities thus appears to coincide or be causally related to the shift to intensive seed use. Our analysis suggests that this shift must be accounted for by declining returns from other resources, perhaps those associated with wetlands (e.g., waterfowl, fish) and with the desiccation of shallow lakes and marshes at the end of the early Holocene (Grayson, 1993; Madsen, 2000, 2007; Rhode et al., 2006).

The trends in artiodactyl densities and their climate-based causes we have documented have perhaps the greatest implications for arguments concerning trends in late Holocene landscape use and hunting behavior (Kelly, 1985, 1995, 1997, 2001; Zeanah, 1996, 2004; Hildebrandt and McGuire, 2002; McGuire and Hildebrandt, 2005). While greater effective moisture associated with the so-called Neoglacial of the late Holocene has been suggested for some time to have favored large game populations and the consequent increase in the human hunting of such animals (e.g., Thomas, 1970; Kelly, 1985), our analysis suggests more specifically that it was a summer-wet, winter-dry pattern coupled with high overall effective precipitation and high temperature equability that drove this expansion. In any case, the documentation here of dramatic late Holocene increases in artiodactyl densities provides strong support for the models that have inferred such a pattern from paleoclimatic reconstructions alone.

Zeanah (2004), for example, has developed a model attending to the different reproductive goals and strategies that might apply to males and females and to how optimal residential site locations will vary depending on whether women’s or men’s resources are most productive. In Zeanah’s formulation, residential sites are predicted to be located in places that enable foragers to maximize the caloric delivery rate of men’s and women’s resources combined. Applying this model to the late Holocene archaeological record of the Carson Desert of western Nevada, and adjusting for climate-induced variation in the return rates of different resources, residential sites are predicted in most contexts to be located in the best habitats for women’s resources. In conjunction with this, men are predicted to have adjusted to those settlement locations and to have exhibited greater logistic mobility in their own foraging. Most relevant here, Zeanah (2004) predicted that intensified logistical hunting of artiodactyls, especially bighorn sheep, would occur as the densities of these animals increased in favorable climatic periods of the late

Holocene. Kelly (1985, 1995, 1997, 2001) derived a similar conclusion on this point from independent modeling work. Although patterns in prehistoric site distributions and other data were generally consistent with these predictions, our analysis provides strong support for the argument that artiodactyl densities increased substantially during the early late Holocene. Our analysis also undercuts the suggestion that the late Holocene increase in artiodactyl hunting occurred as a result of culturally particularistic factors unrelated to changes in the densities of these animals on the landscape (e.g., Hildebrandt and McGuire, 2002; McGuire and Hildebrandt, 2005).

7.2. Global warming and artiodactyls of western North America

As evidence for global warming continues to mount and stronger congruence emerges with model predictions for future changes, there is growing demand for forecasting changes in biodiversity, ecosystems, and the population dynamics of specific taxa (e.g., Romme and Turner, 1991; Wang et al., 2002; Epps et al., 2004; Parmesan, 2006; Saunders et al., 2006; Botkin et al., 2007). Late Quaternary biotic records can play an important role in such efforts insofar as we can reconstruct how past climatic changes impacted prehistoric faunas—especially if past climate regimes are expected to recur in the future (e.g., Graham, 1992; Grayson and Delpech, 2005). In fact, a growing literature now exists on the potential impact of global warming on extinctions and extirpations of Great Basin small mammals (McDonald and Brown, 1992; Murphy and Weiss, 1992; Lawlor, 1998; Grayson, 2002, 2005, 2006b; Beever et al., 2003), and much of this work draws, to one degree or another, on late Quaternary paleorecords of the specific taxa involved (see especially Grayson, 2006b). And while modeling work with artiodactyls has been conducted in the context of global climate change, these studies, unlike the Great Basin small mammal research, have relied almost exclusively on demographic trends in relation to limited recent time series of weather data, typically stretching less than two decades (e.g., Post and Stenseth, 1999; Wang et al., 2002; Epps et al., 2004; Weladji and Holand, 2006; but see Grayson and Delpech, 2005). Although clearly of enormous value—and we used such records to hypothesize initially how climatic seasonality would have impacted past artiodactyls—the modern records are necessarily limited by the climatic variability exhibited over the brief time series that they cover. The tight links we have documented between millennial-scale trends in Holocene artiodactyl populations and specific climatic variables could thus provide essential baseline data from which to forecast how global climate change will impact their populations.

Again, our detailed terminal Pleistocene and Holocene analyses from the Bonneville Basin documented significant negative relationships between artiodactyl abundances and both intra-annual temperature range and winter precipitation, and significant positive relationships between summer precipitation and the abundances of these animals. Moreover, patterns in these relationships also suggest critical climatic threshold values beyond which late Quaternary artiodactyl abundances were consistently depressed. These become especially apparent when our modeled climate data are arrayed against the standardized measures of artiodactyl abundances plotted together (Fig. 15). Artiodactyls reach their lowest late Quaternary abundances when either of the following occur: intra-annual temperature range values exceed about 31 °C, winter precipitation exceeds 24% of the annual total, or summer precipitation drops below 6% of the annual total.

These relationships are concerning given current model projections for future climate change. Although there is consensus that warming of about 0.2 °C is projected per decade for a range of emission scenarios (e.g., IPCC, 2007), most relevant here are projections concerning variation in the seasonal cycle of precipitation and the occurrence of extreme climatic events. In particular, projections suggest that along with increasing temperatures, it is very likely that hot extremes, heat waves, extended droughts and heavy precipitation events will continue to become more frequent (Meehl et al., 2000; IPCC, 2007). Projected patterns of seasonal precipitation for western North America in particular, predict that for much of the region, winter precipitation will increase, while summer precipitation will decrease (EPA, 1998; IPCC, 2007). Although uncertainty is greater with precipitation than temperature, and regional variation is clearly anticipated with the latter, these projections, in general, call for the return of conditions similar to those that appear to have significantly depressed artiodactyl populations during the terminal Pleistocene and early and middle Holocene. Since populations of ungulates can exert strong effects on plant communities and other ecosystem processes (e.g., McNaughton, 1985; Owen-Smith, 1989; Kay, 1995, 1997), climate-based impacts on western artiodactyls could extend to many other components of future landscapes (cf. Wang et al., 2002).

8. Conclusion

General circulation models and paleoclimatic records suggest that seasonal extremes in temperature peaked during the terminal Pleistocene and early Holocene of western North America and that early and middle Holocene precipitation followed a winter-wet, summer-dry pattern. These patterns are mirrored in a macrophysical climate model we developed for the northern Bonneville Basin and from which we derived climatic values to evaluate the response of local artiodactyls to terminal Pleistocene and Holocene variations in seasonality. Our indices of late Quaternary variation in the abundance of artiodactyls in the Bonneville Basin were derived from three independent sources, including a paleontological record of fecal pellet densities, and archaeological records of artiodactyl skeletal elements and large game hunting tools. These indices suggest that artiodactyls occurred in low densities from the terminal Pleistocene through the middle Holocene, with substantial increases occurring during certain stretches of the late Holocene. Most importantly, all three measures of artiodactyl abundances exhibit significant correlations with our measures of climatic seasonality: winter precipitation, summer precipitation, and intra-annual temperature range. Archaeofaunal records from across western North America show very similar temporal trends in the abundances of artiodactyls suggesting that the trend documented in detail for the Bonneville Basin may be a very general one.

These analyses suggest that climatic seasonality played a fundamental role in driving long-term late Quaternary variation in artiodactyl densities for much of western North America. This conclusion should perhaps come as no surprise since it has been argued for some time that the late Pleistocene of North America was a period of dramatic climatic instability and change, and that the extreme climatic seasonality that characterized the end of this period caused not only tremendous range changes in small mammals but the extinction of some 35 genera of mostly large ones. While our analysis is fully consistent with this general hypothesis, we extend it here to suggest that extreme seasonality persisted well into the Holocene and kept thin the population densities of surviving artiodactyl taxa, such as mule deer, pronghorn and bighorn sheep. For areas such as the Great Basin where megafauna taxa were either already extinct or present in very low densities when Paleoindians first entered the region (see Grayson, 2006b, 2006), this third, little explored effect of late Quaternary climate change on mammal populations, ironically, may have had the most significant impact on the subsistence economies and land use practices of early peoples. It may also be key to understanding how global climate change will impact western artiodactyls for, decades, centuries, and millennia to come.

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Appendix. Supplementary data

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