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HOLOCENE ENVIRONMENTAL CHANGE, ARTIODACTYL ABUNDANCES, AND HUMAN HUNTING STRATEGIES IN THE GREAT BASIN

David A. Byers and Jack M. Broughton

Despite a deep Great Basin tradition of incorporating paleoenvironmental change within ecologically oriented analyses of past human lifeways, there has been little attention focused on Holocene variation in artiodactyl abundances and the human hunting strategies dependent upon them. Here, we draw upon recently generated paleontological evidence from Homestead Cave of the Bonneville Basin to document a late Holocene artiodactyl population increase. We then use the prey model of foraging theory to predict late Holocene increases in the hunting of artiodactyls, relative to lagomorphs. That prediction is then tested against several fine-grained archaeological records of hunting behavior in the Bonneville Basin, Hogup Cave and Camels Back Cave, and a variety of more coarse-grained faunal records from throughout the Great Basin. Close fits are found between the deductively derived prediction and the empirical records of hunting behavior: dramatic proportional increases in artiodactyl hunting occurred during the late Holocene. The results have far-reaching implications for our understanding of prehistoric human adaptations in the Great Basin.

A pesar de que en la Gran Cuenca hay una tradición enraizada de incorporar los cambios paleoambientales en los análisis de tipo ecológico acerca de los modos de vida de las poblaciones antiguas, se ha prestado muy poca atención a la variación en abundancia de artiodáctilos durante el Holoceno y su influencia en las estrategias de caza de los seres humanos. En este artículo utilizamos nuevas evidencias paleontológicas obtenidas en la cueva Homestead y la cuenca del Bonneville para documentar incrementos en la población de artiodáctilos durante el Holoceno tardío. Además, se hace uso del modelo de presa de la teoría de forrajeo para predecir incrementos en la cacería de artiodáctilos con respecto a los lagomorfos, durante el Holoceno tardío. Finalmente, se comparan estas predicciones con datos detallados arqueológicos sobre prácticas de cacería en la cuenca del Bonneville, las cuevas Hogup y Camels Back, y con un grupo de datos más generales sobre la fauna en toda la Gran Cuenca. Encontramos una fuerte correlación entre las predicciones teóricas y los datos empíricos acerca de prácticas de cacería: durante el Holoceno hubieron dramáticos incrementos en la caza de artiodáctilos. Estos resultados tienen implicaciones importantes concernientes a nuestra concepción de las adaptaciones prehistóricas humanas en la Cuenca Grande.

For over half a century, Holocene paleoclimatic records from the Great Basin (Figure 1) have suggested that the middle Holocene (8000 to 5000 B.P.) was hot and dry (see reviews in Benson et al. 2002; Grayson 1993, 2000a; Madsen 2000; Madsen et al. 2001). While some degree of regional variability in the timing and intensity of middle Holocene xericity is clearly apparent, recently derived geologically based climate records from the Pyramid and Owens Lake basins underline the severity and potential biotic impact of climatic conditions during this time (Benson et al. 2002). Those records reflect paleolake levels for the

two basins and suggest that severe droughts characterized regional climates for most of the middle Holocene. Not only did drought conditions prevail, but average temperatures appear to have been a full 3–5° C warmer than those of the late Holocene (Benson et al. 2002). These results are consistent with a variety of sedimentological, chemical, and physical records produced over the last several decades from localities distributed across the Great Basin. Antevs' (1955) characterization of the middle Holocene as a "Long Drought," it now seems, was not too far off. However, in many settings across the arid West, it also appears that warmer

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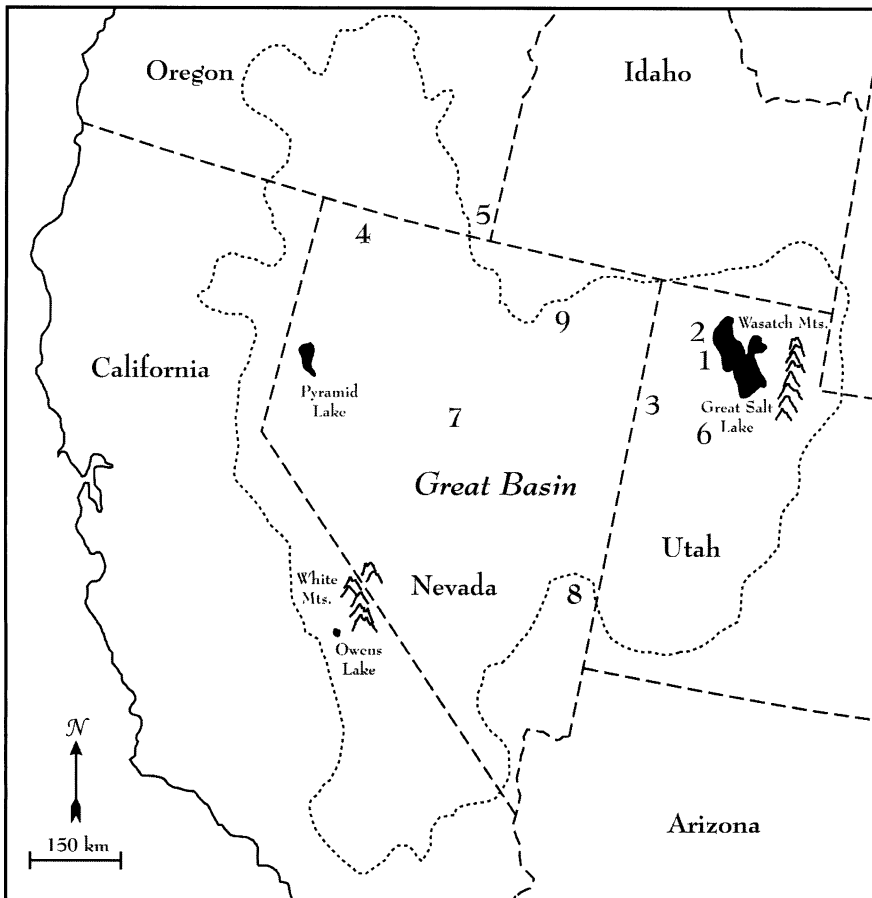


Figure 1. The Great Basin (indicated by the dotted line), with locations of places mentioned in the text. Key to numbered sites is as follows: 1, Homestead Cave; 2, Hogup Cave; 3, Danger Cave; 4, Last Supper Cave; 5, Dirty Shame Rockshelter; 6, Camels Back Cave; 7, Gatecliff Shelter; 8, O'Malley Shelter; 9, Pie Creek Shelter.

and drier conditions were initiated earlier—within the early Holocene between 10,000 to 8000 B.P. (e.g., Brunelle and Anderson 2003; Davis et al. 1985, 2002; Mensing 2001; Mohr et al. 2000; Wigand and Rhode 2002). In addition, seasonal swings in temperature and precipitation may have been more pronounced during the early Holocene than any time after (e.g., Davis 1999; Thompson et al. 1993; Zielinski and Mershon 1997).

The biotic response to Holocene climatic change has been the focus of intensive research over the last several decades as well. Holocene vegetational dynamics and small mammal biogeography have been especially well-studied (Grayson 2000a; Madsen 2000; Rhode 2000; Rhode and Madsen 1995; Spaulding 1991; Wigand and Rhode 2002), and a rough outline of human population fluctuations has been established for many areas as well (Benson

et al. 2002; Bettinger 1999; Grayson 1993, 2000a; Kelly 1997).

Early and middle Holocene changes in Great Basin floras have been documented primarily through detailed studies of packrat (*Neotoma* sp.) middens, pollen records, and treeline movements. The established trends follow predictably from early and middle Holocene increases in temperature and decreases in precipitation. In the Bonneville Basin of western Utah, the abundances of more mesic plant taxa, including conifers in the upper elevations and sagebrush (*Artemisia* spp.) in lowland settings, decline during this time (Madsen and Currey 1979; Madsen et al. 2001; Rhode 2000). In the White Mountains of southeastern California, dramatic upslope movements occurred during the middle Holocene for both pinyon-juniper woodland and bristlecone pine (*Pinus longaeva*) (Jennings

and Elliot-Fisk 1993; LaMarche 1973). In the Mojave Desert to the south, the abundance of thermophilous shrubs increased at the expense of more mesic taxa (Spaulding 1991). Similarly, in lowland settings of northern Nevada, sagebrush-dominated communities were replaced by shadscale (*Atriplex* spp.) and other more heat-tolerant plants (Mehringer 1985; Wigand and Mehninger 1985).

The response of small mammals to Holocene climatic change is in close accord with the vegetation record and is best exemplified by the well-stratified and well-dated 13,000-year faunal sequence from Homestead Cave in the Bonneville Basin. Based on over 184,000 identified mammalian bones and teeth, Grayson (2000a, 2000b) has revealed a series of pronounced changes in the Holocene distributions and abundances of small mammal species. 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 increasing aridity of 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 in number during periods of drought (mammalian nomenclature follows Kays and Wilson [2002]). These mice decline substantially across the early Holocene strata of Homestead Cave, are scarce in the middle Holocene deposits, and return to abundance in the late Holocene layers of the cave. A number of small mammal species from Homestead Cave display similar patterns as do other Holocene records, not only in the Bonneville Basin (Schmitt et al. 2002a) but also in a variety of other Great Basin contexts as well (e.g., Grayson 1983, 1987, 1988).

Early and middle Holocene aridity also appears to have negatively affected indigenous human populations in the Great Basin. In fact, the Holocene history of human populations in many locations is broadly parallel to that of the mesic small mammals summarized above. At least to judge from such proxy measures as the number of sites or radiocarbon dates per unit of time, human population densities were low through much of the early and middle Holocene but increased substantially in the late Holocene (Benson et al. 2002; Bettinger

1999; Grayson 1993, 2000a; Madsen 2002). Of course, Great Basin archaeologists have long afforded environmental change a critical role in shaping many other aspects of past human lifeways (see the review in Rhode 1999).

In spite of this intensive research effort devoted to understanding the biotic responses to climate change and the fact that human-environment relationships has been “arguably *the* problem in Basin anthropology over the last half century” (O’Connell and Elston 1999:263; emphasis in original), there has been little attention focused on Holocene variation in artiodactyl abundances and the response of human hunters to that variation (but see Grayson 1982; Pippin 1977; Thomas 1970). In this paper, we draw upon the available paleontological evidence bearing on Holocene changes in artiodactyl abundances and then use the prey model of foraging theory to predict how human hunters would have responded to the documented trends. These predictions are then tested in detail with several high-resolution archaeological sequences of hunting behavior in the Bonneville Basin and, more generally, with a wide variety of coarser-grained records distributed throughout the Great Basin. This analysis suggests that artiodactyl populations increased as climate ameliorated during the late Holocene and human foragers took full advantage of the increased abundance of high-ranked prey. The results have far-reaching implications for our understanding of prehistoric human adaptations in the Great Basin and perhaps other regions of North America characterized by similar paleoenvironmental histories.

Artiodactyl Response to Climatic Change

Empirical research on artiodactyl populations from the Great Basin and other regions of the arid West suggests that mule deer (*Odocoileus hemionus*), pronghorn (*Antilocapra americana*), bison (*Bison bison*), bighorn sheep (*Ovis canadensis*), and elk (*Cervus elaphus*) are sensitive to variation in temperature and precipitation. This information, coupled with our current understanding of Holocene climatic changes in the Great Basin, provides a basis to anticipate substantial Holocene variation in artiodactyl population densities in the region. Although the relationship between weather patterns and artiodactyl abundances are complex and species specific, and a variety of nonclimatic fac-

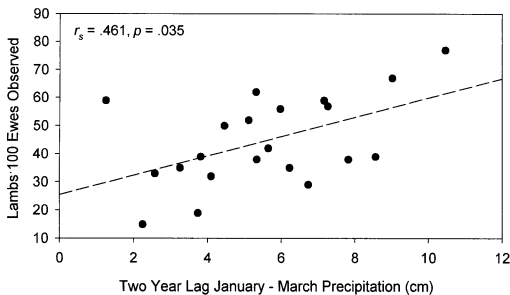


Figure 2. The relationship between a given year's winter precipitation and the number of new bighorn sheep lambs per 100 ewes two years later in Canyonlands National Park, Utah (data from Douglas 2001).

tors clearly affect herd size (e.g., predation, disease), hot and dry climates negatively impact all Great Basin artiodactyl species. The primary links between artiodactyl populations and climate patterns stem from the effects of temperature and precipitation variation on forage quality and the availability of drinking water.

Environmental productivity and forage quality are positively correlated with effective precipitation and soil moisture in the arid West (e.g., Douglas 2001; Murphy 1970). The availability of high-quality forage, in turn, has profound effects on maternal condition, initial offspring survival, birth weight, growth rate, survival through the first winter, resistance to disease, overall recruitment rates, and, ultimately, herd size (Byers and Hogg 1995; Douglas 2001; Fox et al. 2000; Leslie and Douglas 1979; Mackie et al. 1998; Peek et al. 2002; Stephenson et al. 1985). The availability of high-quality forage also has a direct effect on the extent to which animals require free drinking water. When forage plants have low water content (performed water), animals require free water sources (Bailey 1990; McCartney and Miller 1998; Smith and Krausman 1988; Van Dyke et al. 1983). Bighorn sheep in arid settings, for instance, require free water sources within close proximity to plant forage, thermal protection (caves and rockshelters), and rocky escape terrain. The availability of water sources on the landscape thus severely limits population densities, and maintaining and restoring those sources is now a serious management issue for bighorn sheep (Leslie and Douglas 1979; McCutchen 1981).

Due to these factors, positive effects of increased precipitation and cooler temperatures and strongly negative effects of drought and high temperatures

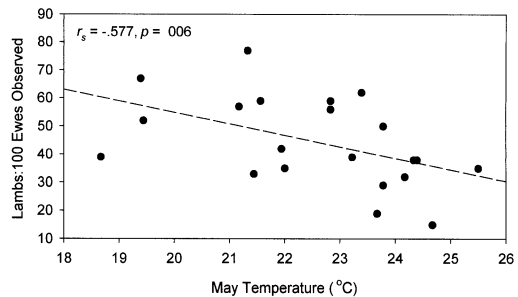


Figure 3. The relationship between a given year's average May temperature and the number of new bighorn sheep lambs per 100 ewes in Canyonlands National Park, Utah (data from Douglas 2001).

have been documented for elk, pronghorn, bison, mule deer, and bighorn sheep in a variety of contexts across the arid West (Byers and Hogg 1995; Douglas 2001; Frank and McNaughton 1992; Howell et al. 2002; Kitchen and O' Gara 1982; Longhurst et al. 1979, Van Vuren and Bray 1986). Figures 2 and 3 display the results of a 23-year study of bighorn sheep in southern Utah that clearly demonstrates the general relationships between precipitation, temperature and artiodactyl reproduction.

Although it seems clear that long-term drought conditions will negatively impact artiodactyl abundances in general, other climatic factors are important as well. Extreme seasonality in temperature and the distribution of precipitation, for instance, appear especially influential; hot, drought-stricken springs and summers, coupled with cold winters with deep snowpacks, can clearly cause substantial mortality and reduce herd sizes (e.g., Bartman and Bowden 1984; Benedict 1999; Mackie et al 1982; see also Graham and Lundelius 1984; Kiltie 1984).¹

Overall, these data suggest that artiodactyl populations would have been adversely affected by the hot and dry or highly seasonal climatic conditions of the early and middle Holocene. Great Basin paleontological records should thus reflect expansions of artiodactyl populations as climate ameliorated at the beginning of the late Holocene.

Paleontological Evidence from Homestead Cave, Bonneville Basin

Homestead Cave

The stratified deposits of Homestead Cave (Madson 2000) provided a rich array of biological mate-



Figure 4. Photograph of Homestead Cave (courtesy David B. Madsen and Monson Shaver III).

rials that inform on Holocene changes in Bonneville Basin climate. This deposit also represents the only high-resolution, Holocene paleontological sequence of artiodactyl abundances in the Great Basin; it thus provides an ideal context in which to examine the effects of regional climatic change on artiodactyl population histories.

Homestead Cave is a wave-constructed cavern located several kilometers west of Great Salt Lake on a northwestern spur of the Lakeside Mountains (Figures 1, 4, and 5). The cave sits at an elevation of 1,406 m, midway between the Provo and Gilbert levels of Lake Bonneville. In 1993 and 1994, a 1-m² sam-

ple 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 $\frac{1}{4}$ in (6.4 mm), $\frac{1}{8}$ in (3.2 mm), and $\frac{1}{16}$ in (1.6 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. Twenty-one ¹⁴C assays were derived from the deposits. The coherency of the ¹⁴C results suggests that the deposits were laid down sequentially between ~11,300 and ~1000 ¹⁴C yr B.P. (Madsen 2000; Madsen et al. 2001).

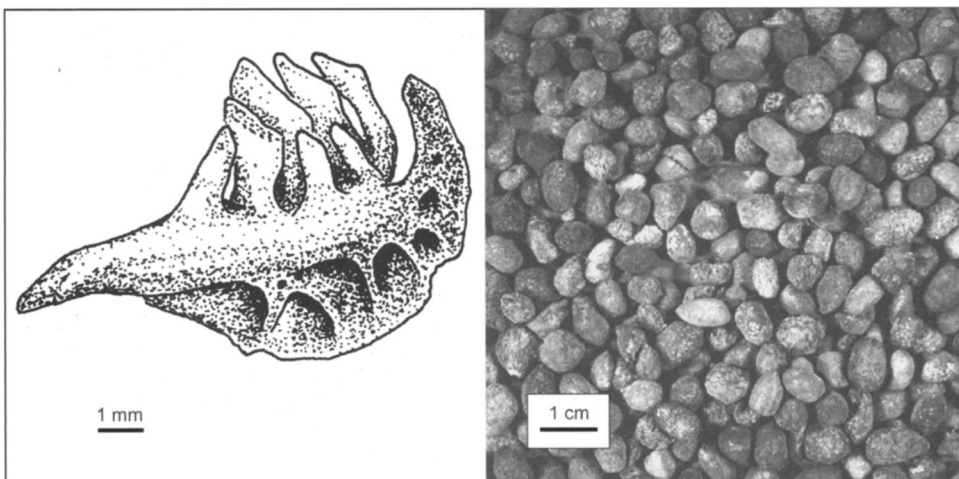


Figure 5. Key paleoenvironmental indicators from Homestead Cave used in this study: left, pharyngeal tooth of *Gila atraria*; right, artiodactyl fecal pellets.

Bonneville Basin Moisture History and the Homestead Cave Fish Record

The Homestead Cave fish record represents the most detailed, stratified, and well-dated paleontological fish sequence in the Great Basin (Broughton 2000a, 2000b). Patterns in the fish remains derived from the Holocene sequence of deposits at the cave are generally consistent with the small mammal record, summarized above, and add further insight into the nature of Bonneville Basin climate history. As with the small mammal materials derived from the cave, the fish remains were deposited by raptors, especially owls. More specifically, fish materials appear to have been deposited by owls that scavenged carcasses derived from periodic die-offs of fish that inhabited Lake Bonneville and Great Salt Lake. Spikes in fish remains in the cave deposits thus signal recessions from previous highstands in which the lakes were sufficiently deep and fresh to support fish populations (Broughton 2000a; Broughton et al. 2000). They should thus reflect regional, Bonneville Basin-wide, lake levels and precipitation regimes.

Utah chub (*Gila atraria*) is by far the most abundant fish taxon in the Holocene deposits at Homestead Cave. Although Utah chubs have never inhabited Great Salt Lake historically, this species is tolerant of moderate salinity levels and warm water temperatures and is the only member of the Lake Bonneville fish fauna that now occupies low-elevation creeks, springs, and marshes of the northern Bonneville Basin. However, genetic analyses of modern populations of Utah chub suggest that during wetter periods of the Holocene, Great Salt Lake may have become sufficiently deep and diluted to support this species (Rosenfeld 1991:89). Even if Utah chub could not have invaded Great Salt Lake during wetter cycles, the extent of local freshwater marshes should have varied with regional moisture and the elevation of the lake. In any case, change in the Holocene abundance of Utah chubs near the cave should be linked to higher elevations of Great Salt Lake and hence moister climatic episodes for the Bonneville Basin as a whole.

Figure 6 displays the changing abundances of Utah chub specimens by stratum at Homestead Cave. These data show that chub remains are relatively uncommon in the cave sediments that date to the first half of the Holocene and suggest that

freshwater habitats with sufficiently low year-round salinities and temperatures were limited during this time. However, chub remains increase dramatically in the late Holocene strata suggesting that only then did suitable freshwater habitats become widespread.² More specifically, the changing abundances of Utah chubs exhibit two marked peaks across the Holocene-aged strata of the cave: first in stratum XII and second in stratum XVII. These deposits provided radiocarbon dates of 3400 and 1020 ¹⁴C yrs B.P., respectively. These peaks in chub frequencies are in close accord with limited core and shoreline data that suggest Great Salt Lake experienced highstands around both of these times (Broughton et al. 2000; Murchison 1989).

The small mammal record from Homestead Cave suggests again that a warming and drying trend occurred across the early Holocene of the Bonneville Basin. The fish record suggests, not inconsistently, that early Holocene lake elevations and, hence, regional precipitation levels were always below the threshold required to allow chubs to successfully colonize Great Salt Lake. Both records also attest to drought conditions persisting throughout the middle Holocene with a substantial shift to cooler and wetter climate occurring at the beginning of the late Holocene.

Regional paleovegetational records mirror these trends, although it is notable that certain early Holocene plant records suggest relatively cool and moist conditions (Wigand and Rhode 2002). The latter records, however, are typically more montane in distribution; lower elevation Bonneville Basin records typically suggest warm and dry early Holocene climates. These differences, as Wigand and Rhode (2002:349) suggest, may result from a warmer and drier early Holocene climatic regime in which mesophilic plants were lost first in lower elevations but persisted longer, perhaps under stress, in more mesic upland settings. Alternatively, an enhanced early Holocene seasonality (Davis 1999; Thompson et al. 1993) may have affected upland woodland settings differently than lowland shrub communities (Wigand and Rhode 2002:349).

The Artiodactyl Fecal-Pellet Record

Given the raptor-based origin of the Homestead vertebrate fauna, it is not surprising that artiodactyl skeletal elements are virtually nonexistent in the deposit (Grayson 2000b). However, over 21,000

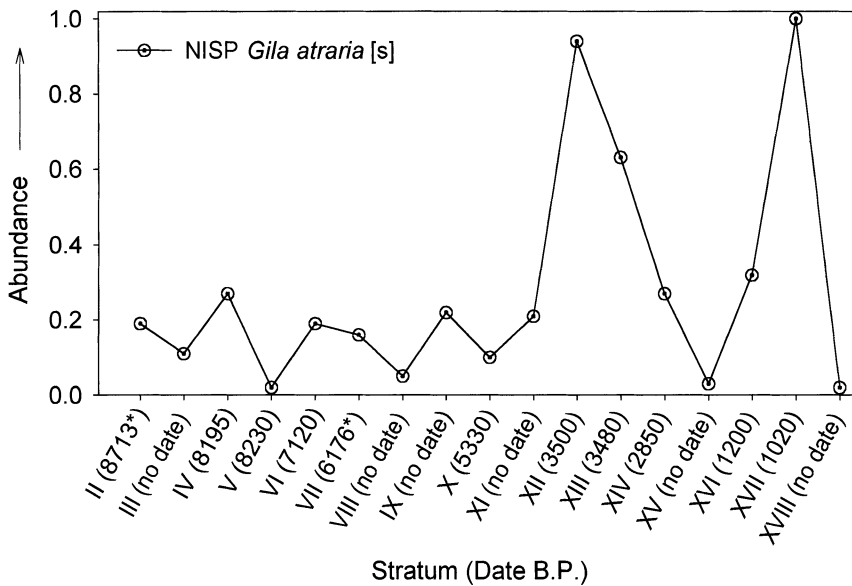


Figure 6. Changing (standardized [s]) abundances of Utah Chub specimens across the Homestead Cave sample column (exclusive of stratum I; * average of multiple dates); includes specimens identified as “Cyprinidae” (see Broughton 2000a). The highest NISP value is set at 1.0, with the remaining values scaled accordingly.

individual artiodactyl fecal pellets were identified from the site, providing the only high-resolution, Holocene paleontological sequence of artiodactyl abundances in the entire Great Basin (Hunt et al. 2000; Madsen 2000). 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 are known to have occupied the Lakeside Mountains in either recent or prehistoric times, and bighorn sheep, deer, and pronghorn are known to use caves to escape summer heat or the cold of winter (Geist 1971; Hunt et al. 2000; Krauseman 1979). Hunt et al. (2000) specifically observed pronghorn using Bonneville Basin caves. Mule deer and bighorn sheep defecate after resting and routinely leave bedding scrapes littered with pellets (Geist 1971; Linsdale and Tomich 1953).

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 in presenting the Homestead artiodactyl abundance history at the ordinal level, we are simply following the approach taken by Hunt et al. (2000) that provided the original identifications.

Figure 7 displays the changing densities of artiodactyl pellets across the Homestead Cave depositional sequence; the standardized frequencies of chub remains are included for comparison. Artiodactyl droppings are generally uncommon in both the early and middle Holocene strata (II–XI: ~8800–5000 ^{14}C yr B.P.) but are extremely abundant in many late Holocene deposits (XII–XVIII: ~3500–1000 ^{14}C yr B.P.). The range of variation here is quite dramatic with the collective sample of early and middle Holocene strata averaging 2.74 pellets per liter, while the late Holocene strata average is 13.43 pellets/liter. The patterning does not appear to be related to stratigraphic variation in pellet preservation. Indeed, *Neotoma* fecal pellets are scarce in the late Holocene deposits but occur in extremely high densities (601/liter) in the basal, terminal Pleistocene stratum of the sequence (Hunt et al. 2000).

These Holocene spikes in artiodactyl pellet frequencies also appear to align with the peaks in chub remains at Homestead Cave (Figure 7), the latter, again, an index of Bonneville Basin-wide precipitation levels. While the visual trends are striking, the peaks in chub bones and artiodactyl pellets are slightly offset, leading to an insignificant correlation ($r_s = .351$, $p = .167$).

In sum, this record suggests that artiodactyl

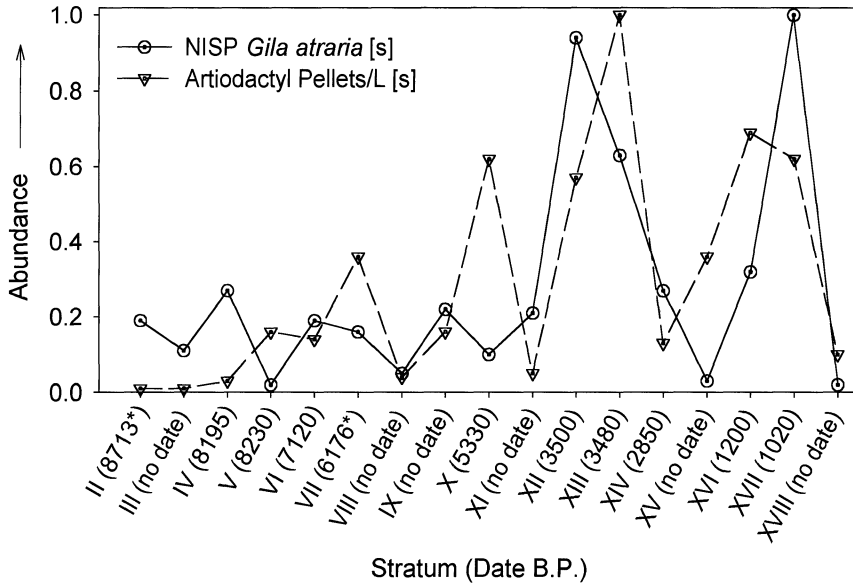


Figure 7. Changing densities (pellets/liter) of artiodactyl fecal pellets across the Homestead Cave sample column (exclusive of stratum I; * average of multiple dates). The highest density is set at 1.0, with the remaining values scaled accordingly (data from Hunt et al. 2000:53). Utah Chub frequencies, from Figure 6, are provided for comparison.

abundances responded predictably to regional climate change. They were relatively uncommon throughout the early Holocene, a time characterized by growing warmth and aridity and, perhaps, amplified seasonality. Populations remained depressed during the hot and dry middle Holocene, but increased dramatically with the climatic amelioration of the late Holocene. Such a trend has clear implications for changes in human hunting strategies in this area.

Human Response to a Late Holocene Artiodactyl Increase in the Great Basin

The prey model of foraging theory is now routinely used in zooarchaeological analyses of ancient hunting behavior (e.g., Broughton 1994, 2002; Cannon 2000; Janetski 1997; Lupu and Schmitt 1997), and we use it here to predict how Bonneville Basin hunters would have responded to the apparent late Holocene increase in artiodactyl abundances. Two of the most straightforward predictions of the prey model are: (1) the highest-ranked prey are always taken upon encounter; and (2), the inclusion of lower-ranked prey in the diet depends not on their own abundance but, instead, on the encounter rate with higher-ranked prey. It follows that increases in the encounter rate with high-ranked prey should

cause an increase in the overall return rate and a general narrowing of the diet to include fewer lower-ranked prey (Stephens and Krebs 1986).

We also regard prey body size as the most critical, archaeologically recoverable, dimension of hunter preference ranking. This position has, in fact, been supported by recent ethnographic tests of foraging models that show that for singly handled prey, the largest animals almost always produce the highest return rates (Broughton 1999). Although the relationship between body size and return rates is strong, it is clearly imperfect, and individual small-sized prey items, when collected en masse, can sometimes produce higher returns than large prey captured singly (e.g., Madsen and Schmitt 1998).

Recent ethnographic research on men's hunting goals (e.g., Hawkes 1991, 1993; Weissner 2002), however, underscores the overriding significance that hunters attach to prey body size: if large game are present on the landscape, male hunters persistently seek them out. The pursuit of smaller prey is far more variable. In fact, many hunters ignore small game, even when pursuing them would increase their overall caloric returns. Clearly, small prey move into and out of the set of targeted prey for human hunters, but large game is invariably included within it. Body size really does seem to



Figure 8. View west to the portal of Hogup Cave.

be the truest general measure of hunter preference ranking (Broughton and Bayham 2003).

In sum, implications from the prey model and recent tests of it with human foragers provide a strong basis to predict that increasing abundances of large game on ancient landscapes will result in proportionate increases in large-game hunting. In the Great Basin context, where artiodactyls and lagomorphs dominate mammalian archaeofaunas, it follows that patterning in the artiodactyl index ($\sum \text{artiodactyls} / [\sum \text{artiodactyls} + \sum \text{lagomorphs}]$) should track the paleontologically derived trends in artiodactyl abundances. More specifically, we predict that artiodactyl index values calculated from archaeological deposits should increase substantially at the middle-late Holocene transition, but should also parallel the apparent fluctuations in artiodactyl populations within the late Holocene. We conduct tests of this hypothesis below using two of the richest, longest, and best-dated archaeological faunal sequences in the Bonneville Basin: Hogup Cave and Camels Back Cave.

Hogup Cave

Hogup Cave is a limestone cavern located along the southern end of the Hogup Mountains, only 48 km northwest of Homestead Cave (Figures 1 and 8). The cave sits at an elevation of 1,433 m, midway between the Provo and Stansbury shorelines.

Aikens (1970) opened several trenches in 1967 and 1968 within the archaeologically rich cave deposits and excavated 16 stratigraphic units in sediments that reached over 4 m in depth. One-quarter-inch screens were used to collect not only an enormous sample of faunal remains, but also an extensive record of perishable artifacts, including, textiles, nets, and moccasins (Aikens 1970; Durrant 1970). Twenty-three ^{14}C dates place the human occupation of the cave between ~ 8400 to ~ 500 ^{14}C yr B.P.

Figure 9 displays the artiodactyl index values across the Hogup Cave strata. As predicted, artiodactyl abundances show a dramatic increase at the middle-late Holocene transition. The difference in the mean artiodactyl index values between the middle Holocene (strata 1–7) and late Holocene (8–16) strata is, in fact, highly significant ($F = 15.159$, $p = .002$, $df = 15$). Not only are artiodactyls significantly more abundant in the collective set of late Holocene strata compared to those of the middle Holocene, but the specific fluctuations within the late Holocene are well-aligned with the artiodactyl pellet spikes at Homestead Cave. Both data sets show dramatic peaks in artiodactyl specimens between about 4000 and 3000 ^{14}C yr B.P and again at about 1000 B.P.

While the taphonomic history of this set of deposits is clearly complex and people were only one of many predators that introduced bones into

Table 1. Bone Modifications of the Hogup Cave Lagomorphs (data from Hockett 1994).

Strata Sets	Total NISP	Human Modified Specimens	Raptor/Carnivore Modified Specimens	Human/Raptor-Carnivore Ratio	Artiodactyl Index
15 to 16	303	2	14	.14	.14
12 to 14	2,146	33	65	.51	.15
9 to 11	1,139	17	97	.18	.19
1 to 8	14,620	158	1,119	.14	.05
Total	18,208	210	1,375	.15	

the cave (Hockett 1993, 1994), several lines of evidence suggest that the trend in the artiodactyl index is truly reflecting variation in human hunting behavior. These are based on both taphonomic analyses of the Hogup Cave lagomorph materials as well as temporal patterns in the associated tools likely used to hunt artiodactyls and lagomorphs.

First, 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. If so, we would expect that the proportion of bones with human modifications should increase within the upper strata of the deposit. Hockett's (1993, 1994) taphonomic analysis of the Hogup Cave lagomorph remains suggests, however, that this is probably not the case. Although Hockett was unable to identify the depositional agent for the vast majority of lagomorph specimens, there is no correlation between the artiodactyl index and the ratio of human to carnivore/raptor modified specimens among the four stratigraphic aggregates in which

the taphonomic data were provided (Table 1; $r_s = .738$, $p = .262$).

Additional evidence comes from the percentage of burned lagomorph specimens identified and reported for each of the Hogup Cave strata (Hockett 1993). We assume here that a greater human presence in the cave would result in higher fire frequencies and, hence, a higher proportion of burned sediments in general. If so, the proportion of burned to unburned bones can be used as a crude measure of change in the relative contribution of human deposited animal remains.³ In this case, the percentage of burned lagomorph specimens varies little through time (Table 2; middle vs. late Holocene aggregates $F = 1.615$, $p = .224$, $df = 15$) and there is no correlation between the proportion of burned bones and the artiodactyl index ($r_s = -.190$, $p = .480$). When viewed together, these taphonomic data suggest that the relative contributions made by human and nonhuman predators to the Hogup Cave lagomorph assemblage did not vary markedly through time, and, thus, changes in the artiodactyl

Table 2. Distribution of Burned Lagomorph Specimens by Stratum at Hogup Cave (data from Hockett 1993).

Stratum	Number Burned	Total Lagomorph NISP	Proportion Burned	Artiodactyl Index
1	15	954	.02	.04
2	10	1,656	.01	.04
3	125	2,474	.05	.07
4	111	3,525	.03	.05
5	131	4,285	.03	.04
6	152	5,285	.03	.04
7	60	3,791	.02	.04
8	97	3,405	.03	.07
9	31	797	.04	.12
10	14	569	.02	.28
11	1	216	.00	.30
12	17	2,159	.01	.10
13	10	525	.02	.18
14	20	666	.03	.23
15	2	107	.02	.10
16	7	397	.02	.15
Total	803	30,811	.02	

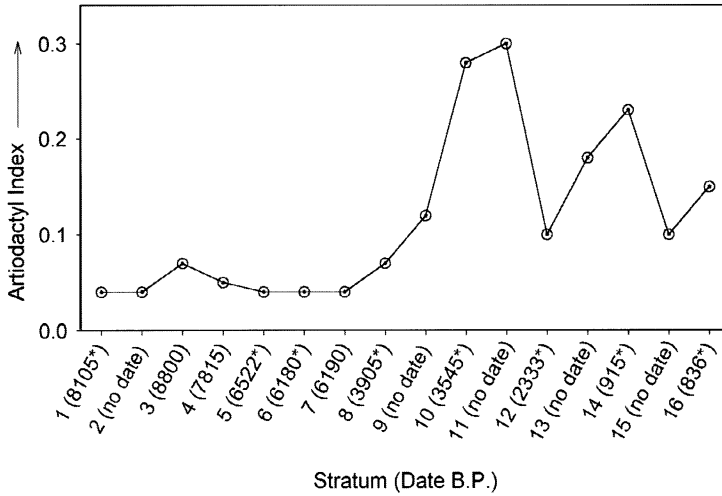


Figure 9. Changing artiodactyl index values across the Hogup Cave strata. Values are based on the MNI (minimum number of individuals) data provided in Durrant (1970:242-243; * average of multiple dates); dating is from Aikens (1970:26-30).

index probably do not merely reflect proportionate increases in the human use of the cave.

Yet far more convincing are trends in subsistence technology that occur across the Hogup Cave strata. If in fact the artiodactyl index truly monitors the widening and narrowing of the diet breadth in relation to variation in artiodactyl abundances, then temporal trends in subsistence technology observed at the site should parallel trends in the faunal data. Insofar as nets and snares were commonly used to capture lagomorphs and projectile points were

associated with weaponry designed to kill artiodactyls, then a projectile point index (\sum projectile points/ \sum projectile points + \sum cordage) should track the artiodactyl index. Figure 10 shows the two indices plotted together across the Hogup Cave strata. The two variables appear well-aligned and a rank-order correlation analysis confirms this impression ($r_s = .841, p < .001$). Further, late Holocene values of the projectile point index are significantly higher than those of the middle Holocene ($F = 19.084, p < .001, df = 15$).⁴

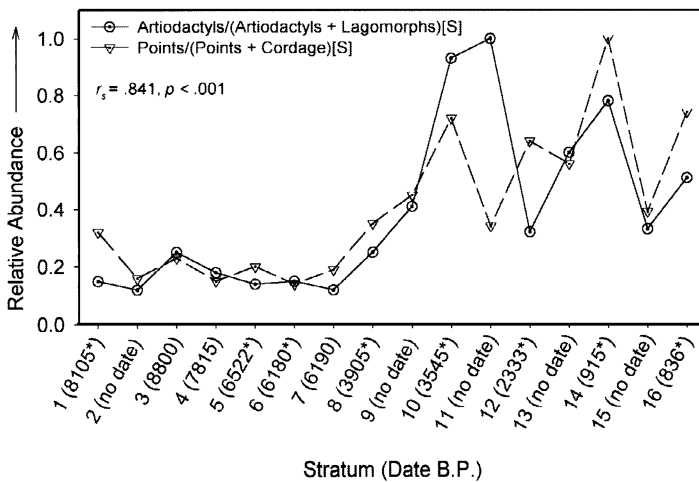


Figure 10. Changing relative abundances of projectile points and cordage across the Hogup Cave strata; data from Aikens (1970:34, 120; * average of multiple dates). The artiodactyl index values are plotted for comparison. For both indices, the highest values are set to 1.0, and the remaining ones are scaled accordingly.

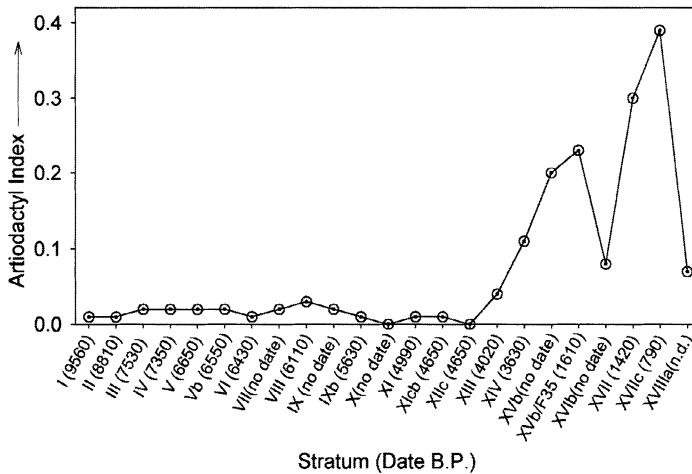


Figure 11. Changing artiodactyl index values across the Camels Back Cave strata (data from Schmitt and Lupu 2002: Table 7.7).

In sum, the lack of any trends in bone modifications coupled with the striking patterns in subsistence technology suggest that variation in the artiodactyl index is truly reflecting variation in the hunting of artiodactyls. The patterning in this index, we observe again, closely parallels Bonneville Basin moisture history and variation in artiodactyl pellet frequencies at Homestead Cave (Figure 6). More artiodactyls on the landscape led to proportionate increases in both the hunting of artiodactyls and the manufacture of tools used to take them.

Camels Back Cave

Camels Back Cave is a small cave located in the south end of Camels Back Ridge, about 84 km from the southwest margin of Great Salt Lake (Schmitt and Madsen 2002). Between 1996 and 1998, excavation of a ~2-x-4 m unit uncovered a well-defined stratigraphic sequence documenting 33 alternating cultural and noncultural layers. A huge collection of faunal materials, exceeding 51,000 specimens, was recovered by sieving the sediments with both $\frac{1}{4}$ in and $\frac{1}{8}$ in screens (Schmitt et al. 2002, 2004; Schmitt and Lupu 2002). Twenty-one ^{14}C dates indicate that people occupied the cave intermittently over the last 7,500 years. Given the precise stratigraphic and temporal control and the enormous faunal collection that it provided, Camels Back Cave offers a very fine-grained record of middle and late Holocene hunting behavior in the Bonneville Basin.

Much like the record drawn from Hogup Cave, a dramatic late Holocene increase in the artiodactyl index occurs at Camels Back Cave (Figure 11). A comparison of artiodactyl index values for the collective set of middle Holocene strata (I–X) compared to those of the late Holocene (strata XI–XVIII) indicates the difference is significant ($F = 9.258$, $p = .006$, $df = 22$). During the late Holocene, artiodactyl indices show especially dramatic peaks between about 4000 and 3000 ^{14}C yr B.P. and 1500 and 1000 ^{14}C yr B.P. While there are clearly differences in the details, the general pattern closely matches both the faunal record from Hogup Cave and the Homestead Cave fecal pellet record.

Camels Back Cave undoubtedly experienced a complex formational history as well, receiving bones from both human and nonhuman agents across the Holocene. Although we cannot conduct an analysis of variation in subsistence technology because artifacts such as cordage did not preserve here (Schmitt and Madsen 2002), a relatively comprehensive taphonomic analysis of the fauna has been conducted (Schmitt and Lupu 2002). From that analysis, two particular lines of evidence suggest that the trend in the artiodactyl index accurately reflects variation in human prey selection. Both of these involve patterning in the proportion of burned lagomorph and artiodactyl specimens across the Camels Back strata. Burned bone, including both charred and calcined specimens, was extremely

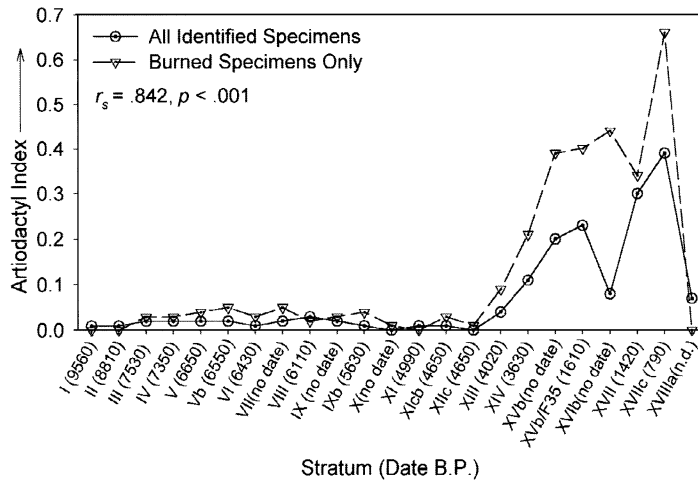


Figure 12. Changing artiodactyl index values across the Camels Back Cave strata derived from all identified specimens and just those that exhibited evidence of burning (data from Schmitt and Lupo 2002: Tables 7.7 and 7.8).

abundant in the deposit and was recovered throughout the cave sediments (Schmitt and Lupo 2002).

First, an evaluation of the percentage of burned versus unburned lagomorph bones in the collective set of middle Holocene strata compared to those of the late Holocene shows no difference between the two groups ($F = .946$, $p = .342$, $df = 22$). This suggests that the relative contributions of lagomorph materials by human and nonhuman predators did not vary markedly between these sets of deposits.

Second, and more convincingly, we calculated the artiodactyl index for each stratum using only artiodactyl and lagomorph specimens that exhibited burning. As Figure 12 shows, a dramatic increase in artiodactyl abundances occurs again during the late Holocene. Indeed, the two indices—one calculated with the entire assemblage of artiodactyl and lagomorph bones, and one calculated using just the burned specimens—are themselves highly correlated ($r_s = .743$, $p < .001$). While we recognize the potential for bones that were deposited by raptors or carnivores to become subsequently burned by human fires, this seems unlikely to be a serious issue here since the extremely rich, largely owl-deposited, small rodent assemblage shows minimal evidence of burning (Schmitt and Lupo 2002).

Other Great Basin Archaeofaunal Records

We have focused on the Bonneville Basin because

it is represented by an exceptionally detailed paleoenvironmental record—including the only high-resolution paleontological record of artiodactyls in the Great Basin—and a set of fairly fine-grained, trans-Holocene records of human hunting behavior. Insofar as the Holocene climatic conditions and artiodactyl abundance history documented in detail for the Bonneville Basin can be generalized to other regions of the Great Basin, we anticipate a similar human response. That is, faunal records from other settings in the Great Basin should show significant late Holocene increases in the proportional representation of artiodactyl bone.

While many other faunal records have been generated from the Great Basin, coarse-grained temporal control or taphonomic issues preclude all but the most coarse-grained assessments. Still, as Table 3 shows, many records reveal trends very similar to those derived from the Bonneville Basin. This suggests that the pattern identified in the eastern Great Basin may, in fact, be a very general one.

Discussion

Temporal Variation in Great Basin Settlement Patterns

While the prey model predicts relative increases in artiodactyl hunting during the late Holocene under conditions of expanding large game populations, this model makes several important assumptions

Table 3. Relative Abundances of Lagomorphs and Artiodactyls by Middle and Late Holocene Stratigraphic Units for Selected Archaeological Sites in the Great Basin.

Site	NISP Lagomorphs	NISP Artiodactyls	Artiodactyl Index	X ²	P-Value	Analytical Units	Reference
<i>Danger Cave</i>							
Middle Holocene	574	72	.11	6.39	<.000	Stratum III	Grayson 1988
Late Holocene	553	213	.28			Stratum V	
<i>Dirty Shame Rockshelter</i>							
Middle Holocene	1,399	34	.02	255.08	<.000	Strata III - VI	Grayson 1977
Late Holocene	634	193	.23			Strata I - II	
<i>Gatecliff Shelter</i>							
Middle Holocene	276	15	.05	25.71	<.000	Horizons 12, 14, 15	Grayson 1983 Thomas 1983
Late Holocene	4,906	951	.16			Horizons 1 - 11	
<i>Last Supper Cave</i>							
Middle Holocene	426	62	.13	68.17	<.000	Stratum 4	Grayson 1988
Late Holocene	354	189	.35			Strata 2 and 3	
<i>O'Malley Shelter</i>							
Middle Holocene	167	10	.06	21.23	<.000	Stratum I	Fowler et al. 1973
Late Holocene	935	233	.20			Strata II - VII	
<i>Pie Creek Shelter</i>							
Middle Holocene	200	234	.54	21.70	<.000	Component IV	Carpenter 2003
Late Holocene	813	1551	.66			Component I-III	

about the real world situations to which it is applied. Perhaps most important in this context, the prey model assumes that foragers search through a relatively homogenous or fine-grained habitat pursuing and consuming prey as they go. Thus, the prey model takes no accounting of the fact that many predators travel far from central places to hunt and transport prey back to such locations to consume them. Travel and transport costs to and from central places to foraging patches are thus not considered by the prey model but could, theoretically, influence the economics of hunting behavior and ultimately the taxonomic composition of archaeological faunas (Bayham 1982; Bird and Bliege Bird 2000; Broughton 1999, 2002; Cannon 2000, 2003). A shift in the regional settlement pattern is one of the most obvious ways in which such costs can be altered and so could potentially be a variable causally linked to the established trends in Great Basin archaeological faunas.

Bayham (1982; Szuter and Bayham 1989), for example, proposed that a dramatic late Holocene increase in artiodactyls at Ventana Cave in southern Arizona was a response to reorientations of regional settlement patterns and functional changes

in the use of upland caves.⁵ In particular, Bayham argued that this cave was initially used as an Archaic short-term residential locality but later shifted to a logistical hunting camp. This change accompanied the establishment of sedentary, agriculturally based Hohokam villages in distant lowlands. Since the earlier residential occupations of the shelter were relatively more intensive, they would have had a greater impact on local artiodactyl populations, compared to the cave's later, more ephemeral use as a hunter's camp. In addition, with the substantial increases in travel costs required to reach the cave for Hohokam hunters, overall returns and large game abundances would have to have been sufficiently high to justify its use (see Cannon 2000, 2003). Hohokam hunters could thus only be expected to visit Ventana Cave in especially game-rich months, seasons, or years; higher proportions of artiodactyls in Hohokam-aged deposits follow accordingly.

An analogous scenario in the Bonneville Basin context would be one where early and middle Holocene Archaic foragers used sites such as Hogup and Camels Back caves as short-term residential bases, whereas later on they served as logis-

tical camps for hunters derived from agricultural villages associated with the "Fremont Complex" (Janetski 1997; Madsen and Simms 1998). This hypothesis makes fairly straightforward predictions about trends in anatomical part representation in relation to economic utility, but systematic analyses of this sort have yet to be conducted. Short of this, several lines of evidence make this scenario seem unlikely in the Bonneville Basin setting.

First, most of the larger Fremont sites in the northern Bonneville Basin are located on its eastern margin, often within easy reach of the mesic and, hence, relatively game-rich Wasatch Mountains. Settings such as Hogup Cave and Camels Back Cave would thus seem to be far too remote and relatively unproductive to be logistical outposts for Fremont hunters (Janetski 1997:1082). But more significantly, dramatic increases in the relative abundances of artiodactyls are first registered in these Bonneville Basin caves at about 3500 B.P., some 1,500 years before the emergence of the Fremont (Madsen and Simms 1998). If the increase in artiodactyls is reflecting the increasing logistical use of these sites, Great Basin archaeologists have yet to identify the complementary suite of residential bases that they served.

Regional Variation and Anthropogenic Depressions of the "Later" Late Holocene

Although we expect proportional increases in artiodactyl hunting to characterize many settings in the late Holocene Great Basin, there are good reasons to anticipate regional or site-specific exceptions as well. Insofar as particular spatiotemporal contexts during the early and middle Holocene were characterized by moister climate, they may also have supported higher densities of artiodactyls. 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 (2,267 m) mesic upland site located in central Utah, shows consistently high artiodactyl index values (>.87) across the site's entire occupational history, spanning from about 8000 to 3000 B.P. (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 also emphasize 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 detailed predictions about variation in artiodactyl abundances and the subsequent human hunting response at any particular spot on the landscape requires careful attention to high-resolution, locally derived paleoenvironmental records. Overall environmental productivity was, of course, not the only factor influencing the prehistoric abundances of artiodactyls in the Great Basin. 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 (Grayson 1991a, 2001; Janetski 1997). Such anthropogenic depressions have now been documented in some detail in several other areas of western North America, including California (e.g., Broughton 2002; Hildebrandt and Jones 2002), the Southwest (Cannon 2000, 2003), and the Pacific Northwest (Butler 2000). In these settings, expanding densities of late Holocene human populations appear to have caused the depression of a wide diversity of large, high-ranked prey taxa, from elk to sturgeon (*Acipenser* sp.). It may thus be telling that the strongest cases for late Holocene depressions of artiodactyls in the Great Basin have been derived from spatiotemporal contexts that appear to have supported some of the highest human population densities in the region.

Grayson (1991a, 2001), for instance, has documented significant declines through time in the relative abundances of bighorn sheep from late Holocene archaeological sites in the White Mountains of the far western Great Basin (Figure 1). These sites are directly upslope from the well-watered Owens Valley, a setting that, according to Steward (1938), supported one of the highest early historic period human densities in the entire Great Basin.

The Fremont occupation of the eastern Great

Basin represents another context characterized by relatively high human population densities, which appear to have increased considerably between about 1500 and 900 B.P. (Madsen and Simms 1998; Massimino and Metcalfe 1999). While moist conditions favorable to artiodactyls characterized much of Fremont times (Figure 7), expanding human population densities appear to have ultimately depressed local herds. As Janetski (1997) has documented, artiodactyl index values are exceptionally high (.98–.82) in the earliest Fremont occupations but decline substantially through time after that.⁶

Overall, these patterns not only show that indigenous human impact on animal populations was highly variable in the Holocene Great Basin, but also provide insight into what demographic and ecological factors influence that variation. As we have noted, artiodactyl populations appear to have increased dramatically nearly as soon as environmental conditions improved at the close of the middle Holocene. Such a population irruption may have been possible then, as human populations themselves had been kept thin by middle Holocene drought. Later depressions of artiodactyls occurred in entirely different contexts. Again, both the Fremont and the late prehistoric Owens Valley appear to have been characterized by high human population densities fueled by high levels of subsistence productivity—the latter being derived from either a rich array of wild resources or agriculture. In such contexts, like much of California west of the Sierra Nevada, prehistoric peoples may have had the resource substrates to allow their expansion, despite the continual depression of the most attractive prey resources (Broughton 2003; see also Winterhalder and Golland 1991; Winterhalder and Lu 1997).

Summary and Conclusions

Paleoenvironmental records from the Bonneville Basin suggest that artiodactyl populations expanded substantially with the cooler and moister climatic conditions of the late Holocene. As predicted from the prey model, the diet breadth of human hunters narrowed and smaller lagomorph prey entered the targeted resource set less frequently. The relative importance of the tools manufactured to hunt artiodactyls and lagomorphs shifted in turn: the abundance of cordage used to make rabbit nets and snares decreased at the

expense of the projectile points required to kill ungulates. These patterns were revealed from a set of relatively high-resolution archaeological records from the northern Bonneville Basin, but more coarse-grained data from throughout the Great Basin suggest the trend may be far more widespread. These patterns may extend to other regions of North America, such as California (Broughton and Bayham 2003; Hildebrandt and McGuire 2002), Wyoming (Byers et al. 2003), and perhaps even portions of the Eastern United States (see Purdue 1989).

Shifts in the regional settlement pattern do not appear to drive these patterns, although a more definitive evaluation of this issue must await systematic analyses of artiodactyl anatomical part representation. And while we are quite skeptical that the archaeological record will permit us to detect to what degree prestige or nutritional motivations underlie large game hunting in any particular context in the past (see Broughton and Bayham 2003; Hildebrandt and McGuire 2002), there were clearly more artiodactyls to go around for either purpose, at least during the early part of the late Holocene. These good times for hunters certainly did not uniformly characterize all spatiotemporal contexts of the late Holocene and would not last in certain places where they did. In several settings characterized by high human population densities, artiodactyl herds were ultimately depressed by intensive human hunting during the *later* late Holocene.

These conclusions, and the general research strategy used to reach them, follow a long-standing Great Basin tradition wherein environmental change is viewed as providing an essential baseline from which to understand variation in the human record. Yet, in spite of this tradition, there have been few systematic attempts to use evidence of paleoenvironmental change to understand long-term variation in human hunting behavior (but see Lupo and Schmitt 1997). In fact, two of the most visible zooarchaeological analyses that have specifically addressed human hunting variation in the Great Basin have been conducted within contexts where environmental change was effectively held constant (Grayson 1991a; Janetski 1997). Several factors appear to have prevented the merging of long-term paleoenvironmental records with archaeological data on human hunting behavior.

First, only very recently have extremely detailed,

well-dated environmental records been amassed from locations closely adjacent to comparably detailed records of human hunting behavior. We are referring specifically here to the unprecedented paleoenvironmental record recently provided by Homestead Cave and its close proximity to the archaeological sequences of Hogup Cave and Camels Back Cave.

Second, attempts to address Holocene trends in human hunting behavior have been tempered by a deep appreciation of the taphonomic challenges that confront the analysis of faunas derived from the settings that provide the longest, deepest records: caves and rockshelters (e.g., Grayson 1983, 1991b; Hockett 1993; Schmitt and Lupo 1995). It may be telling here again that two of the most notable diachronic analyses of hunting behavior in the Great Basin were based on archaeological vertebrate data derived, not from caves, but from open sites (Grayson 1991a; Janetski 1997). However, it now seems that guided by explicit, theoretically derived predictions, we can work through the taphonomic thickets that may have seemed impenetrable a short time ago. It is both a testament to the utility of the basic prey model of foraging theory and a tribute to the detailed paleoenvironmental and taphonomic work that has been conducted over the last several decades that a serious attempt at explaining Holocene trends in human hunting behavior from Great Basin cave faunas is possible.

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Notes

1. Arguments for late Pleistocene megafaunal extinctions, for example, focus on the seasonal swings in temperatures, or a “loss of equability,” as the critical climatic variable, rather than simply changes in average annual temperature. Extreme interannual variation in temperature and precipitation may also have greater effects on artiodactyl populations than long-term averages of these variables.

2. The ability of Utah chubs to invade Great Salt Lake may depend more on the seasonal amplitudes of the lake than the average annual depths; extremely low summer depths could eliminate populations even during times of relatively

high average annual lake elevations.

3. We do not assume here that a burned bone indicates that a person deposited it. We only suggest that substantial changes in the intensity of the human use of a cave should be reflected by changes in the proportion of burned versus unburned cave sediments in general. See Grayson (1988) and Hockett (1993) for details on the complexities involved in interpreting burned specimens from Great Basin cave deposits.

4. Although Bonneville Basin foragers obviously used cordage for many purposes beyond trapping small game, the overall abundance of cordage should nonetheless increase with a rise in the manufacture of nets and snares, other things being equal. Moreover, we might also expect technologies associated with the exploitation of other lower-ranked resources to be more abundant at times when artiodactyls were generally uncommon. We observe in this context that if the Hogup Cave millingstone fragments are substituted for cordage in the Projectile Point Index, the measure is still positively correlated with the artiodactyl index ($r_s = .642$, $p = .007$), and significantly higher index values exist for the late Holocene strata compared to those of the middle Holocene ($F = 15.273$, $p = .002$, $df = 15$).

5. Grayson and Cannon (1999:151) note that the trend in the artiodactyl index at Ventana Cave is complicated by the fact that it is correlated with sample size. However, a Cochran's test, which evaluates trends in sample relative abundances while directly controlling for variation in sample sizes (see Cannon 2001), shows the trend in these data to be highly significant ($X^2_{\text{trend}} = 260.53$, $p < .000$).

6. These extremely high proportions of artiodactyls in early Fremont contexts suggest high artiodactyl population densities and high hunting returns. This seems to run counter to Barlow's (2002) elegant model that predicts intensive maize agriculture should result from low foraging returns. It is unclear to us why this is the case, but it may suggest the need to decouple hunted resources from gathered-cultivated ones in finer-grained analyses of prehistoric subsistence behavior.

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