

Holocene artiodactyl population histories and large game hunting in the Wyoming Basin, USA

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Received 11 May 2004; received in revised form 1 August 2004

Abstract

Regional paleoenvironmental reconstructions and data on artiodactyl response to climate change suggest that large game densities would have expanded during the late Holocene in the Wyoming Basin. Within this context, we use the prey model of foraging theory to predict a late Holocene increase in the hunting of artiodactyls, relative to lagomorphs and rodents. This prediction is then tested against 144 dated components documenting human subsistence in the Wyoming Basin. Close fits are found between the deductively derived prediction and the empirical records: significant increases in artiodactyl hunting occurred during the late Holocene. These results have implications for the interpretation of long-term increases in large-game in Holocene archaeofaunas throughout North America.

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Keywords: Artiodactyls; Holocene climate change; Middle Holocene drought; Prey model; Wyoming Basin

1. Introduction

Archaeological investigations in the oil and gas fields of the Wyoming Basin (Fig. 1) have produced an extensive dataset documenting at least 9500 years of hunter–gatherer subsistence and settlement patterns. This region thus provides an ideal laboratory for testing hypotheses about the relationship between long-term environmental change and hunter–gatherer lifeways. Indeed, given the extent of the survey and excavation conducted in the Wyoming Basin, the area may well be one of the more extensively documented prehistoric

hunter–gatherer contexts anywhere in the world. Relative to the intensity of field research however, there are few published studies incorporating the vast Wyoming Basin archaeological record into a synthetic and theoretically driven framework designed to explain patterns of human adaptation [but see 75,76,82,83, 129,130,133,132]. To begin filling this gap, we integrate the Wyoming Basin archaeofaunal record with data on artiodactyl ecology and regional paleoenvironmental information to document the relationship between climate, artiodactyl population histories and human hunting strategies in the region over the past 10,000 years.

The paleoenvironmental data we summarize suggest that precipitation varied substantially during the Holocene in the Wyoming Basin [18,33,104]. Since artiodactyl reproduction responds positively to long-term increases in precipitation [13,30,116,151], the regional moisture

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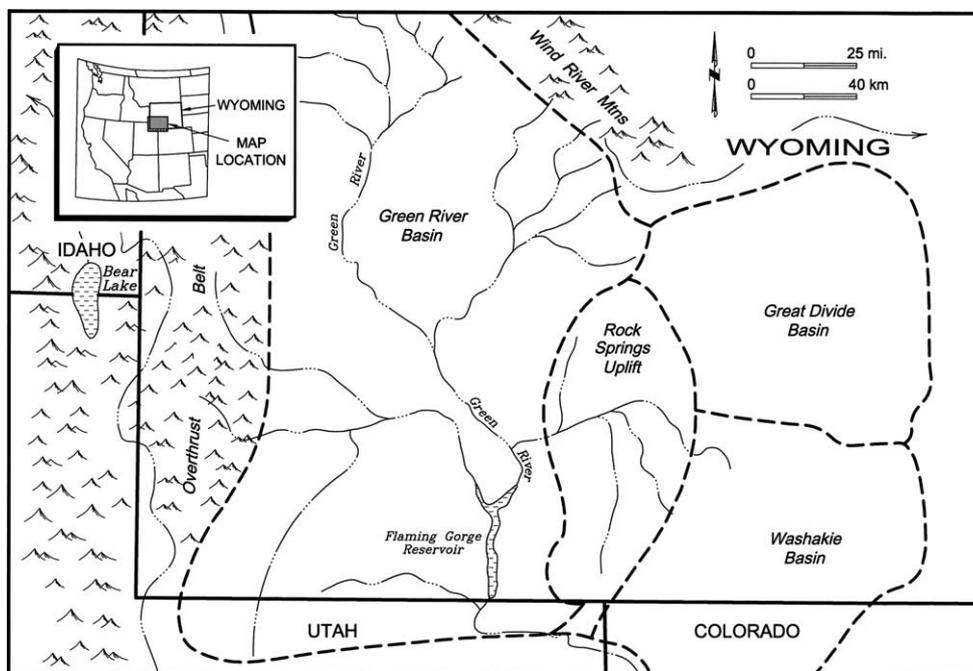


Fig. 1. Map of the Wyoming Basin and surrounding areas.

history can be used to model large-scale variation in artiodactyl abundances. These trans-Holocene patterns in the natural abundances of artiodactyls are used to leverage predictions from the prey model [137] regarding the proportionate hunting of large and small game. We then test these predictions with a rich archaeofaunal database from the Wyoming Basin. As in other areas of western North America, the Wyoming Basin experienced a dramatic ascendance of large game hunting during the late Holocene. Like the well-documented pattern in the Great Basin [19], a climate-driven increase in artiodactyl densities appears responsible for the proportionate increase in large game hunting during the late Holocene in the Wyoming Basin.

2. Wyoming Basin climate trends during the Holocene

2.1. Wyoming Basin paleoenvironmental records

While an extremely rich archaeological dataset has been generated for the Wyoming Basin over the past several decades, far less attention has been focused on the regional environmental history. As a result, only a few paleoenvironmental reconstructions are derived directly from Wyoming Basin data, and these focus almost exclusively on the Holocene history of the large dune fields found throughout the area. However, the patterns revealed by these studies and data from adjacent areas are generally consistent. This information

suggests that the Wyoming Basin was characterized by increasing xericity during the early Holocene, a hot and dry middle Holocene, and a general, but variable, trend towards more mesic conditions during the late Holocene [5,24,32,104,106,153,154].

Several examples illustrate these trends. In the southern Yellowstone and Grand Teton Park region, subalpine flora common at the end of the Pleistocene are replaced by fire adapted species which dominate during the period from 9500 and 5000 ^{14}C yr B.P. [153,154]. This pattern suggests that the area experienced frequent fires during this time. Afterwards, mesic adapted plant communities similar to those found today establish themselves in the region. Similarly, at Grays Lake, Idaho, on the Snake River plain directly west of the Wyoming Basin, pollen from *Picea* and other species adapted to cool, moist climates is abundant in late Pleistocene deposits, but declines substantially by $\sim 10,000$ ^{14}C yr B.P. [5]. Pollen from *Chenopodium*, which peaks at ~ 8200 ^{14}C yr B.P. in combination with pollen from other xeric adapted species, document a period of aridity from 10,000 to at least 7100 ^{14}C yr B.P. Increases in *Pinus* pollen at Grays Lake after this time indicate that moderate cooling, increased precipitation, or both followed for the remainder of the Holocene. In the Uinta Mountains which form the southern boundary of the Wyoming Basin, pollen records document middle and late Holocene paleoclimates. While these sequences do not extend into the early Holocene, they do show that a middle Holocene

drought terminated sometime between 6500 and 5500 ^{14}C yr B.P., with cool and/or moist conditions persisting for at least the next 2000 years [24,106].

Geoarchaeological studies have also documented Holocene trends in Wyoming Basin moisture regimes. Based on temporal patterns in the distribution of eluviated horizons identified at Wyoming Basin archaeological sites, Miller [104] suggests that the Holocene began with relatively mesic conditions, but documents an extended period of aridity characterized by eolian activity and dune formation beginning after 9500 ^{14}C yr B.P. and persisting until ~ 6000 ^{14}C yr B.P. This period was followed by ~ 2500 years of increased effective moisture resulting in region-wide dune stabilization and soil formation. Miller also documents a bloom in greasewood pollen in a number of deposits dating between 5000 and 6000 ^{14}C yr B.P., and from these data infers a general rise in water tables suggesting a trend towards a cooler, if not also moister, climate during this period.

Finally, Eckerle et al. [33] synthesize data ranging from pollen records to sediment studies from the Great Basin, northern and central Rocky Mountains, western Great Plains and southwestern Wyoming to produce a climate sequence specifically for the Wyoming Basin. Their reconstruction indicates that the period from $\sim 10,000$ to 9000 ^{14}C yr B.P. was relatively mesic. However, after this time effective moisture declines until the Holocene thermal maximum was reached sometime between 8000 ^{14}C yr B.P. and 5000 ^{14}C yr B.P. Less xeric, but still relatively warm and dry conditions persisted until 3500 ^{14}C years ago, and are followed by more mesic, but variable, conditions up to the present.

2.2. An archaeoclimatic model for the Wyoming Basin

Wyoming Basin climate simulations mirror the trends described by the paleoenvironmental proxy records. Importantly, they also provide a complete trans-Holocene reconstruction of regional climate trends in the form of point values that can be directly compared with the available archaeofaunal datasets. For instance, the archaeoclimatic model developed by Bryson and Bryson [14–18] provides a method for simulating annual temperature and precipitation values for the late Pleistocene and Holocene. These models are based on global thermodynamic and hydrodynamic patterns and their influence on the earth–atmosphere–hydrosphere–cryosphere system. These relationships in turn force the weather patterns at any time and place. The derivation of an archaeoclimate model uses information on global glacial volume, Milankovitch variations and the modulating effect of volcanic aerosol to produce a heat

energy budget for the study period. Trends in these factors are then used to model variability in meridional temperature gradients that are in turn employed to derive the latitude of the jet stream and the locations of the subtropical anticyclones through time. Finally, archaeoclimate models are calibrated with historically recorded data to produce a region-specific simulation of local rainfall and precipitation through time [e.g. 18].

Holocene temperature and precipitation values have recently been derived from an archaeoclimate simulation for the town of Green River, Wyoming, which is centrally located in the Wyoming Basin [18]. Eckerle et al. [32] adapt these data to create an “aridity index” that measures Holocene trends in soil moisture deficit. As Fig. 2 illustrates, the aridity index suggests that generally mesic conditions persisted between 10,000 and 8000 ^{14}C yr B.P., a xeric climate dominated between 8000 and 5000 ^{14}C yr B.P., and that moisture increased substantially during the later portions of the Holocene. The trends depicted by this model, we note, are generally consistent with the paleoenvironmental records from the Wyoming Basin and adjacent areas discussed above.

We also observe that the trends documented or simulated for the Wyoming Basin are generally consistent with a broad range of paleoenvironmental data from the nearby Great Basin. In this region, numerous pollen, plant macrofossil, faunal, tree-line movement, hydrological and other records document growing aridity during the early Holocene, a xeric middle Holocene, and a return to more mesic conditions during the late Holocene [47,48,65,74,87,88,103,108,121,125,135,156]. Within this paleoenvironmental context, we next consider how local artiodactyl populations would have responded to variation in the Wyoming Basin moisture regime during the Holocene.

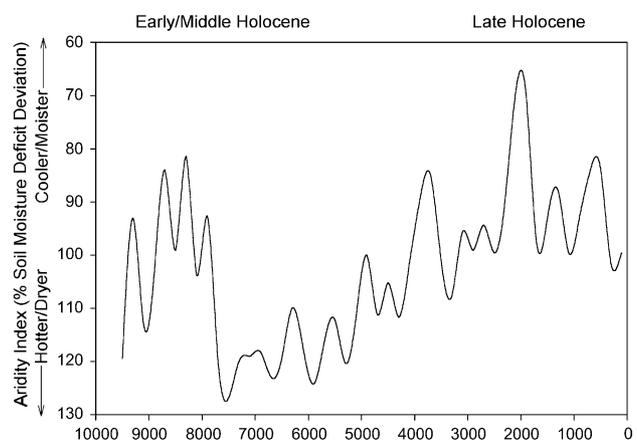


Fig. 2. Eckerle et al. [32] aridity index values plotted across the Holocene.

3. Artiodactyl response to climatic change

3.1. Climate patterns and artiodactyl reproductive ecology

Empirical research focusing on artiodactyl reproduction and recruitment in the arid West indicates that mule deer (*Odocoileus hemionus*), pronghorn (*Antilocapra americana*), elk (*Cervus elaphus*), bison (*Bison bison*) and mountain sheep (*Ovis canadensis*) are all sensitive to variation in temperature and precipitation [60,115,116,128,151]. The primary links between artiodactyl population growth and climate patterns stem from the effects of temperature and precipitation on forage quality and the availability of drinking water. In arid regions, environmental productivity and forage quality correlate positively with effective precipitation and soil moisture [e.g. 30,110]. The availability of high-quality forage, in turn, influences maternal condition, initial offspring survival, birth weight, growth rate, survival through the first winter, resistance to disease, overall recruitment rates and, ultimately, herd size [20,30,35,38,78,115,138]. The availability of high-quality forage also affects the extent that animals require free drinking water. In times of drought, low-quality forage containing little water can tether herds to scarce free water sources and eventually restrict herd size [2,91,134,150].

Several studies document the positive effects of cool and moist weather and the negative effects of hot and dry conditions on the reproductive success of artiodactyl species in a variety of contexts across the arid West [13,20,30,39,71,81,151]. Importantly, wildlife researchers have clearly demonstrated the negative influence of arid conditions on pronghorn and bison, the two most commonly identified artiodactyl species in Wyoming Basin archaeofaunas. For example, Fig. 3 illustrates the relationship between precipitation and the ratio of bison calves to cows recorded in the Henry Mountains, Utah,

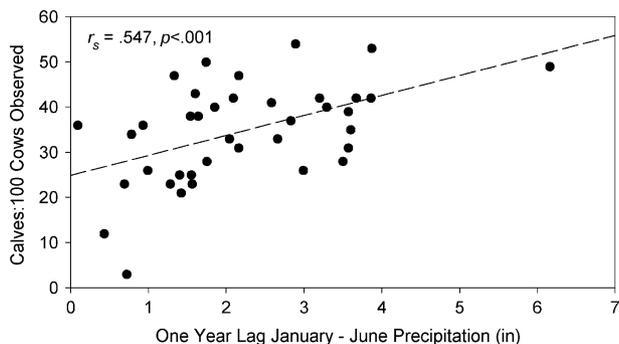


Fig. 3. The relationship between winter precipitation and bison reproduction over a 38 year period for the Henry Mountains, Utah, bison herd [data from 29,34,66–68,136,151].

herd over a 38 year period [raw data from 29,34,66–68,136,151]. Similarly, Fig. 4 presents the relationship between precipitation and reproductive success for a pronghorn herd in southern New Mexico [raw data from 13]. In both cases, the positive and significant correlation between number of offspring and precipitation clearly illustrates the importance of climatic conditions on artiodactyl reproduction.

3.2. The Homestead Cave fish and fecal pellet records: a paleontological example

The Homestead Cave paleontological record, recovered from a locality in the northeastern Great Basin (~200 km southwest of the study area), offers a unique, long-term perspective on the relationship between climate and artiodactyl reproduction [19]. The Homestead Cave deposit produced 18 well-defined strata spanning the period between ~11,300 and ~1000 ¹⁴C yr B.P. [62,86,88]. Evidence derived from stratigraphic variation in small vertebrate remains documents a shift from early/middle Holocene xeric to more mesic conditions that prevailed during the late Holocene [9,47,48,80]. Since fish populations are especially sensitive to variation in moisture, we focus on that aspect of the Homestead record here.

The fish materials from Homestead Cave 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. Although fish have never inhabited Great Salt Lake historically, the Utah chub (*Gila atraria*) is tolerant of moderate salinity and warm water temperatures, and is the only member of the Lake Bonneville fish fauna that today occupies low-elevation, fresh water environments 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

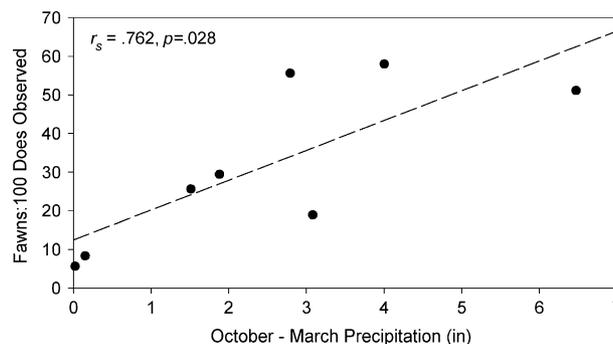


Fig. 4. The relationship between winter precipitation and pronghorn reproduction over an 8 year period for a southern New Mexico pronghorn herd [data from 13].

species [123, p. 89]. Spikes in chub remains in the cave deposits should thus signal recessions from previous high-stands in which the lakes were sufficiently deep and fresh to support fish populations [9,11]. Accordingly, changes in the Holocene abundances 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.

Homestead Cave also produced a rich fecal pellet record that offers the only fine-grained Holocene paleontological sequence of artiodactyl abundances in the arid West [62,86]. These pellets were deposited by bighorn sheep, deer, and pronghorn, all species who are known to use caves to escape summer heat or winter cold, and who routinely leave bedding scrapes littered with pellets [41,73,79]. Since the number of artiodactyl pellets recovered from any given stratum represents a time-averaged sample documenting an extended period, variation in pellets deposited in the cave during the accumulation of a specific stratum should reflect the general frequency of visits by these animals. As a result, the density of pellets (pellets/liter) can serve as a proxy measure of long-term trends in artiodactyl abundances in the nearby environment.

Fig. 5 displays the changing densities of both Utah chub remains and artiodactyl pellets across the Homestead Cave depositional sequence. Chub remains and artiodactyl pellets are generally uncommon in both the early and middle Holocene strata (II–XI: ~8800–5000 ^{14}C yr B.P.) but are abundant in many late Holocene levels (XII–XVIII: ~3500–1000 ^{14}C yr B.P.). While the visual trends are striking, the peaks in chub bones and artiodactyl pellets are slightly offset leading to an insignificant correlation ($r_s = 0.351$, $p = 0.167$). 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 [62]. Taken at face value, this record suggests that during the early and middle Holocene, low effective moisture characterized the area and, as a result, artiodactyls were uncommon in the Bonneville Basin. In contrast, a dramatic increase in artiodactyls occurs in concert with the greater effective moisture of the late Holocene. Although we do not suggest that a detailed artiodactyl population history for southwest Wyoming can be derived from a single record in the Bonneville Basin, the Homestead case does represent the only long-term paleontological dataset documenting the relationship between Holocene climate and artiodactyl population density.

The Wyoming Basin paleoenvironmental data, in combination with information on the relationship between artiodactyl reproductive ecology and climate patterns, provide a basis for modeling temporal trends in artiodactyl population histories in the region. Overall, these data strongly suggest that the xeric conditions of the middle Holocene would have limited artiodactyl populations. Conversely, the more mesic conditions characterizing the beginning of the early Holocene and much of the late Holocene would have provided an environment favorable to artiodactyl reproductive success and herd growth. The result would have been a higher density of artiodactyls on the early and late Holocene landscapes.

4. Human hunting strategies and artiodactyl abundances

Zooarchaeologists routinely use the prey model of foraging theory to evaluate prehistoric hunting decisions [e.g., 7,10,19,22,64,84] and we use it here to predict how Wyoming Basin hunters would have responded to climate-driven variation in artiodactyl abundances. Two of the most important 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 encounter rates with higher-ranked prey. It follows that increases in encounter rates with high-ranked prey will cause an increase in the overall return rate and a general narrowing of the diet, regardless of trends in the populations of lower-ranked species [137].

We also regard prey body size as the most archaeologically visible dimension of prey rank. Recent ethnographic tests of foraging models support this position by documenting that for singly handled prey, larger animals almost always produce higher return rates [8]. Further, ethnographic research on men's hunting goals underscores the emphasis that hunters

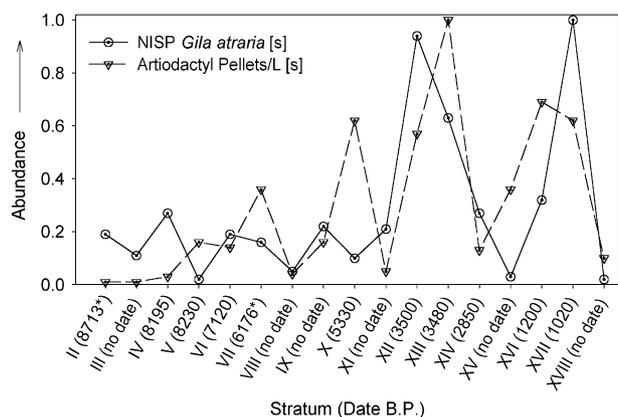


Fig. 5. Changing densities (pellets/liter) of artiodactyl fecal pellets across the Homestead Cave sample column (exclusive of stratum I; * average of multiple dates) compared with the changing abundances of *Gila atraria* remains [9,62]. The highest density is set at 1.0, with the remaining values scaled accordingly (S = standardized values).

attach to prey body size: if large game are present on the landscape, male hunters persistently seek them out [54,55,155]. The pursuit of smaller prey is far more variable and in some cases, hunters ignore small game, even when procuring them may increase an individual's overall caloric returns. Clearly, small prey move into and out of the prey set targeted by human hunters, while large-bodied animals, such as artiodactyls, are consistently pursued upon encounter. All things considered, body size would seem to be our best *archaeological* measure of prey rank using either caloric, protein, or prestige-based currencies [12].

In sum, the prey model predicts that increasing abundances of large game on ancient landscapes will result in proportionate increases in large game hunting. In the Wyoming Basin, where artiodactyls, lagomorphs, and rodents dominate archaeofaunas, it follows that patterning in an artiodactyl index [$\frac{\sum \text{artiodactyls}}{\sum \text{artiodactyls} + \text{lagomorphs} + \text{rodents}}$] should track trends in artiodactyl encounter rates. Insofar as artiodactyls were more abundant during mesic intervals of the early and late Holocene, we predict that artiodactyl index values calculated from Wyoming Basin archaeological deposits will be higher during these periods when compared to the drought-dominated middle Holocene.

5. The Wyoming Basin archaeofaunal record

5.1. The Wyoming Basin archaeofaunas

Located within the Middle Rocky Mountain physiographic province [36], the Wyoming Basin represents an extensive area of generally homogenous environment. The region consists of a series of basins and low uplifts about 16,000 km² in area that ranges from 1800 to 2400 m in elevation. High, abrupt mountain ranges surround the basin and these include the Gros Ventre Range to the north, the Wind River Mountains to the east, the Uinta Range to the south and the Overthrust Belt to the west. Cold, snowy and windy winters followed by short summers that vary from cool and moist one year, to extremely hot and dry the next, characterize the local climate [90]. Generally arid conditions in combination with short growing seasons limit vegetation to expanses of sagebrush steppe, interspersed with broad areas of mixed desert shrubland and riparian vegetation along the perennial watercourses [72].

The Wyoming Basin faunal data used in this analysis include over 88,000 specimens recovered from 144 dated components, and in all but one case, these are derived from open-air contexts (Appendix 1). With one exception (the Finley Site Paleoindian-age bison kill/processing locality [107]), all of the components included in

the sample were excavated after 1980. While all of the assemblages were screened (with the exception of the Finley Site), mesh sizes (1/4 inch, 1/8 inch) varied from site to site.

A number of different investigators identified the archaeofaunal materials reported here (Appendix 1). While these analysts routinely attempted to assign specimens to the genus or species level, the highly fragmentary nature of the assemblages resulted in the identification of most specimens only to body size categories [e.g., 141]. Unfortunately, because relatively few specimens have been identified to specific taxa, we did not pursue species-level analyses of the data. Instead, we grouped the faunal data into four size-based classes: artiodactyl sized, lagomorph sized, rodent sized and “small mammal”. In order to use as much of the data as possible, we lumped specimens identified simply as large mammal, artiodactyl or to a specific artiodactyl taxon (e.g. pronghorn or bison) into a single category. Our totals for lagomorphs and rodents were derived in a similar fashion, while our “small mammal” category contains those specimens identified by the original analysts only as representing taxa lagomorph sized or smaller. We excluded carnivores and specimens identified to broad size classes (e.g., “dog to bison-sized” or “small to medium mammal”).

While rodent remains are often non-cultural in origin, in some instances in the Wyoming Basin, people clearly exploited these species in substantial numbers. For example, Reust et al. [120] recovered 869 burned specimens identified as “rodent/rodent-very small mammal” from component 1 at 48UT375. Moreover, the entire assemblage ($n = 3175$) is composed of specimens lagomorph sized or smaller and 98% of the total sample was recovered from cooking features. Given the obvious anthropogenic origin of rodents in some contexts, we took the following approach in dealing with the potentially adventitious small mammal data included in these collections. If the original investigator specifically considered such factors as context, bleaching, burning, digestive damage, articulation/skeletal completeness, and weathering in determining whether rodent bones represented food remains or were intrusive, and adjusted rodent species counts accordingly, then we used those data here. Many of the collections in the sample were studied in this way. We omitted the rodent remains from those collections not reported in this manner.

We use the number of identified specimens (NISP) as a measure of taxonomic abundance in the analyses that follow. Although clearly imperfect, NISP is the least contrived and arguably the least problematic, available measure. This is especially so in contexts such as this one, where a nearly endless set of aggregation decisions would be required to otherwise quantify the sample [44]. Components were included in the study if they contained NISPs of 25 or more. These numbers were chosen

as a way of including as many assemblages as possible, while at the same time reducing the bias inherent in very small samples. We also only included assemblages if they were associated with at least one radiocarbon date. For components with multiple dates, averages were calculated using the Calib 4.4.2 software [139]. Finally, since the ultimate goal of this study is to monitor artiodactyl encounter rates whatever the context, we included data from all of the qualifying components from throughout the Wyoming Basin.

5.2. Temporal variation in artiodactyl abundances

In order to evaluate the relative contribution of artiodactyls relative to smaller, lower-ranked species in each assemblage, an artiodactyl index for each component was constructed using NISP counts and these values were then plotted by uncalibrated ^{14}C date. Fig. 6 displays a scatterplot of these data. While middle Holocene (~ 8000 to 5000 ^{14}C yr B.P.) artiodactyl index values are typically low, those for the early ($\sim 10,000$ to 8000 ^{14}C yr B.P.) and late Holocene (~ 5000 ^{14}C yr B.P. to present) are highly variable, ranging from values of 0, which represent a focus on small game, to values of 1, which document assemblages composed exclusively of artiodactyls. Although the visual pattern suggests that early Holocene artiodactyl index values are in general higher than those from the middle Holocene, these samples are not statistically different (mean early = 0.23, mean middle = 0.26, $t = -0.178$, $p = 0.860$, $df = 35$). In contrast, mean artiodactyl indexes are significantly higher for late Holocene components (mean late = 0.62) when compared to those from either the early Holocene ($t = -2.638$, $p = 0.010$, $df = 111$), middle Holocene

($t = -5.130$, $p < 0.001$, $df = 136$) or the combined early/middle sample (mean early/middle = 0.25, $t = -5.537$, $p < 0.001$, $df = 142$). Due to the lack of statistical difference between the early and middle Holocene datasets, we combined them into a single analytical unit for the analyses that follow.

To further clarify the overall pattern represented by the point data (Fig. 6), a running mean was calculated from the entire sample of artiodactyl index values by averaging them across overlapping 700 year periods spaced at 200 year increments beginning at 9500 ^{14}C yr B.P. For example, the value plotted at 5100 ^{14}C yr B.P. represents the mean value for all assemblages dating to between 5450 and 4750 ^{14}C yr B.P. The 700 year interval was chosen as a compromise between displaying as much short term variability as possible, while at the same time averaging samples large enough to clearly demonstrate the overall pattern. Fig. 7 presents these data as a line graph illustrating the trans-Holocene trend in artiodactyl abundances. Fig. 8 shows this same trend arrayed against Eckerle et al.'s [32] aridity index. As the visual relationship suggests, there is a significant rank-order correlation between the two datasets ($r_s = 0.411$, $p = 0.004$), suggesting that Wyoming Basin foragers hunted proportionally more artiodactyls during mesic periods and more small game when it was hot and dry.

5.3. Potential biases in the Wyoming Basin artiodactyl index

Several agents including counting methods, screen size, the taxa employed to create the artiodactyl index and sample size may all to some extent condition our results and each of these issues is addressed in turn here.

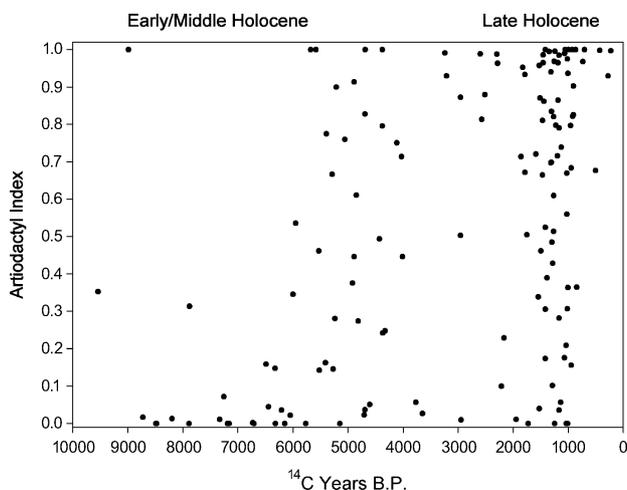


Fig. 6. Wyoming Basin artiodactyl index defined in text plotted as point values. Each point represents a single component.

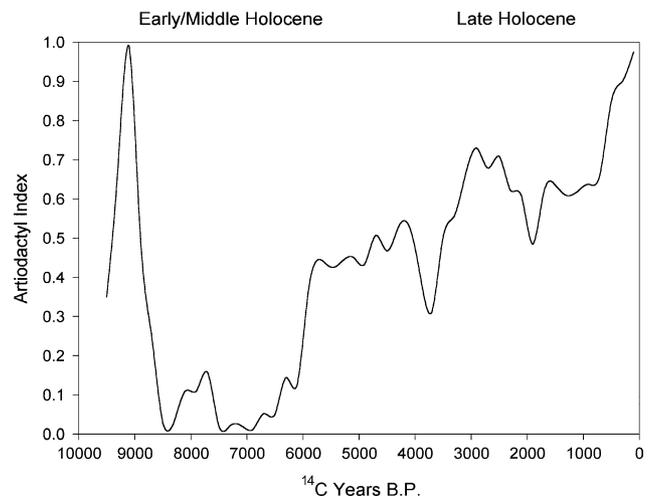


Fig. 7. Wyoming Basin artiodactyl index values plotted as a 700 year running average calculated at 200 year intervals.

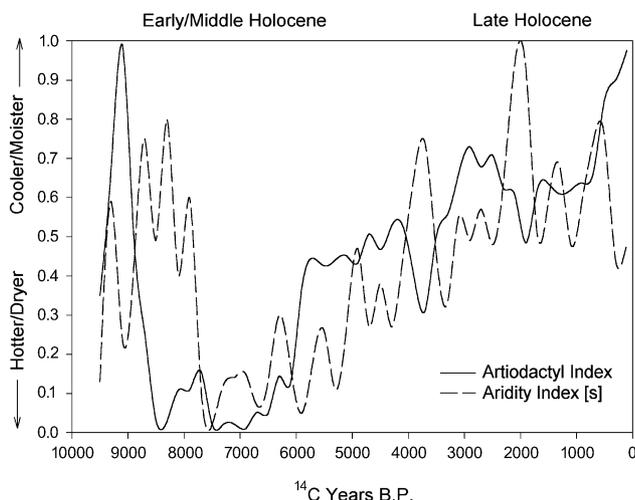


Fig. 8. Wyoming Basin artiodactyl index values arrayed against the Eckerle et al. [32] aridity index. To make the two datasets comparable, the highest aridity value is set at 1.0, with the remaining values scaled accordingly.

We recognize that differential fragmentation resulting from variation in taxon specific or seasonal processing strategies can potentially bias NISP based measures [85]. To evaluate the robustness of the NISP based artiodactyl index used here, each assemblage was coded to simply document the presence or absence of artiodactyls in each component. Assemblages consisting exclusively of large game received a value of 1, while those containing only the remains of small animals were given values of 0. Assemblages representing both large and small game species were assigned values of 0.5. Using this coarse-grained approach immune to the effects of fragmentation, mean artiodactyl index values once again demonstrate a statistically significant increase from 0.39 in the early/middle Holocene to 0.52 in the late Holocene ($t = -3.226$, $p = 0.002$, $df = 142$). While differential fragmentation may subtly condition Wyoming Basin artiodactyl indexes, this factor is nonetheless, not responsible for the overall trend.

To evaluate the possibility that the screen-sizes used to collect the faunal materials may have influenced the pattern [21,63], a sub-set of the total sample was chosen for further analysis. Specifically, we focused on 14 components that together span the period from ~9000 B.P. to ~230 ^{14}C yr B.P. and that were all collected with 1/8 inch hardware cloth under the direction of the same investigator [119,120]. As Fig. 9 displays, this sub-set produced a pattern very similar to the one displayed by the overall sample, with mean artiodactyl index values increasing significantly from 0.08 in the early/middle Holocene to 0.53 in the late Holocene ($t = -2.736$, $p = 0.018$, $df = 12$). Given these results, it would appear that the overall pattern does not stem from variation in recovery methods.

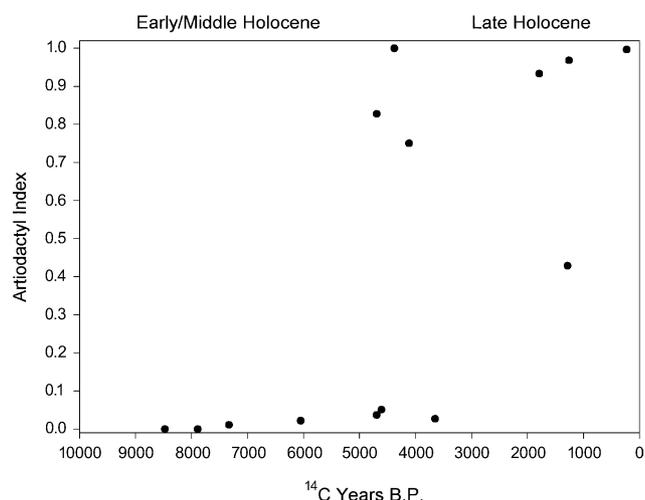


Fig. 9. Artiodactyl indexes from 14 components spanning the Holocene that were all excavated under the direction of the same primary investigator and all screened with 1/8 inch hardware cloth [119,120].

To assess the possibility that the documented trend results from the inclusion of potentially non-cultural rodent remains, artiodactyl indexes were recalculated using only artiodactyls and lagomorphs for assemblages containing at least 25 specimens ($n = 129$). With the rodent materials omitted, mean artiodactyl index values once again increase significantly, in this instance from 0.34 in the early/middle Holocene to 0.74 in the late Holocene ($t = -5.930$, $p < 0.001$, $df = 127$). Moreover, when the artiodactyl indexes calculated using just the artiodactyl and lagomorph remains are plotted as a running average (Fig. 10), they demonstrate a significant

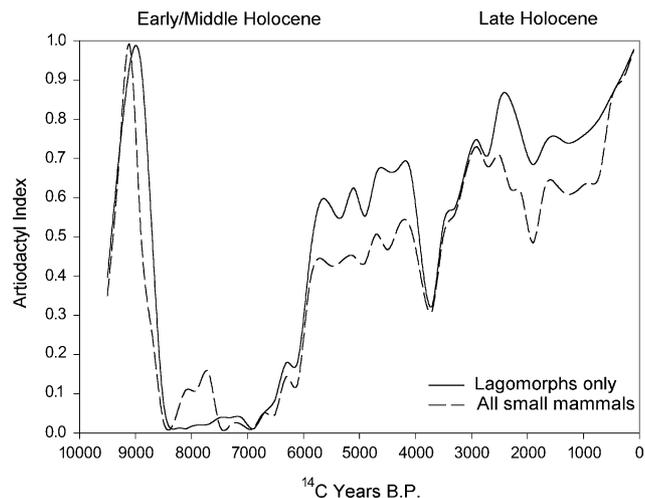


Fig. 10. Wyoming Basin artiodactyl index values calculated from only artiodactyl and lagomorph sized specimens arrayed against values that include all small mammal remains. Both trend lines are plotted as 700 year running averages calculated at 200 year intervals.

and positive correlation with those derived from the entire assemblages of small mammal remains ($r_s = 0.936$, $p < 0.001$).

Finally, because many assemblages with relatively small sample sizes were included in this study and because such samples could potentially bias the results, the dataset was evaluated yet again, this time using only components with NISP > 500 ($n = 40$). In this case, plotting the reduced sample size required a 1000 year running average. Fig. 11 illustrates the resulting trend line. Although the trend fluctuates more dramatically within the late Holocene compared to the previous analysis, artiodactyl index values for the modified data set nonetheless increase significantly from 0.29 in the early/middle Holocene to 0.70 in the late Holocene ($t = -2.792$, $p = 0.008$, $df = 38$). Given the overwhelming consistency of these results, we conclude that a climate-driven increase in large game hunting occurred during the late Holocene in the Wyoming Basin.

6. Artiodactyl population histories in nearby regions of the arid west

The Wyoming Basin artiodactyl population history presented here does not stand alone and similar trends have been documented in archaeological deposits from throughout western North America [19]. Take for instance the record from Hogup Cave, located in the Bonneville Basin of northwest Utah [1], where the faunal data document over 9000 years of human subsistence patterns. As Fig. 12 illustrates, artiodactyls are more abundant in late Holocene levels than in the early or middle Holocene portions of the sequence ($t = -2.893$, $p = 0.002$, $df = 14$; Table 1). A review of the evidence from a number of other Great Basin sites

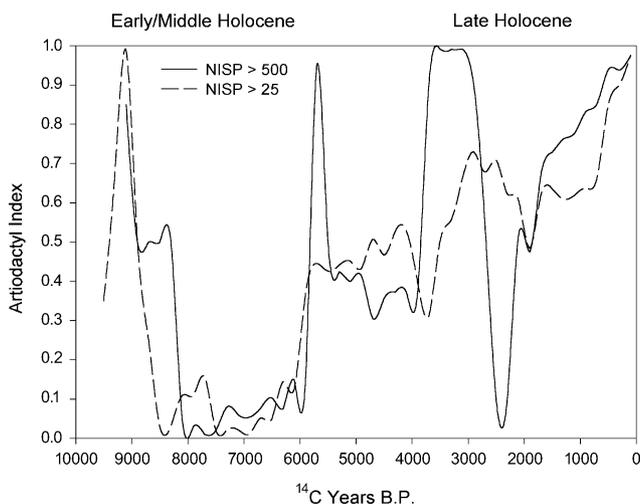


Fig. 11. Wyoming Basin artiodactyl index values for assemblages with NISP > 500 plotted as a 1000 year running average calculated at 200 year intervals.

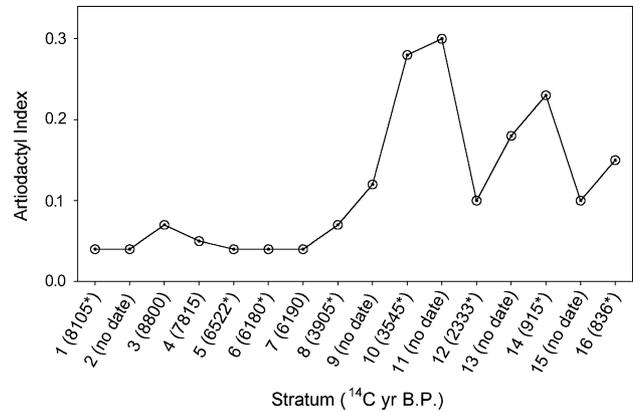


Fig. 12. Changing artiodactyl index values across the Hogup Cave strata. Values are based on the MNI (minimum number of individuals) data provided in Durrant [31, pp. 242–243; * average of multiple dates]; dating is from Aikens [1, pp. 26–30].

further emphasizes the widespread nature of this phenomenon (Table 1). Throughout the Great Basin, artiodactyls are more abundant in late Holocene components than in those dating to the early and/or middle Holocene. Given this evidence, the pattern documented in the Wyoming Basin appears to represent one case of a much broader artiodactyl population expansion that occurred throughout the arid west during the late Holocene.

7. Early Holocene artiodactyl abundances

While the ascendance of artiodactyl hunting in the late Holocene follows as expected from our climate-based predications, the relationship between artiodactyl abundances and early Holocene climate is less clear. Although there is no statistical distinction between the early and middle Holocene samples, the visual trends illustrated above hint that artiodactyls may have in fact been more numerous in the earlier period (Figs. 6, 7). Indeed, the artiodactyl index values generally follow the trend represented by Eckerle et al.'s [32] aridity index during the early Holocene (Fig. 9). Moreover, many paleoenvironmental records suggest that the initial part of the early Holocene was relatively mesic. Given these observations, the lack of statistical difference may simply be a function of the relatively small datasets under comparison. Conversely, the single artiodactyl index value of 1.0 (the Finley Site bison kill), which strongly influences the visual trend line in the early Holocene (Fig. 8), may represent an extremely rare event during this time in the Wyoming Basin. If this is true, then the low numbers of artiodactyls during the early Holocene are consistent with trends observed in the nearby Great Basin, where artiodactyls are decidedly rare in early Holocene deposits [19]. In the Great Basin

Table 1

Relative abundances of lagomorphs and artiodactyls by Middle and Late Holocene stratigraphic units for selected archaeological sites in the Great Basin and Wyoming Basin

Site	NISP		Artiodactyl Index	χ^2	<i>p</i> -Value	Analytical units	Reference
	Lagomorphs	Artiodactyls					
Camels Back Cave							
Middle Holocene	16 226	281	0.02	1056.78	<0.000	Strata I–X	
Late Holocene	12 880	1480	0.10			Strata XI–XVIII	[124]
Danger Cave							
Middle Holocene	574	72	0.11	60.39	<0.000	Stratum III	
Late Holocene	553	213	0.28			Stratum V	[46]
Dirty Shame Rockshelter							
Middle Holocene	1399	34	0.02	255.08	<0.000	Strata III–VI	
Late Holocene	634	193	0.23			Strata I–II	[42]
Gatecliff Shelter							
Middle Holocene	276	15	0.05	25.71	<0.000	Horizons 12, 14, 15	[43]
Late Holocene	4906	951	0.16			Horizons 1–11	[142]
Hogup Cave ^a							
Middle Holocene	1085	54	0.05	29.34	<0.000	Strata 1–7	
Late Holocene	901	111	0.12			Strata 8–16	[1]
Last Supper Cave							
Middle Holocene	426	62	0.13	68.17	<0.000	Stratum 4	
Late Holocene	354	189	0.35			Strata 2 and 3	[46]
O'Malley Shelter							
Middle Holocene	167	10	0.06	21.23	<0.000	Stratum I	
Late Holocene	935	233	0.20			Strata II–VII	[37]
Pie Creek Shelter							
Middle Holocene	200	234	0.54	21.70	<0.000	Component IV	
Late Holocene	813	1551	0.66			Components I–III	[23]
Wyoming Basin Aggregate ^b							
Middle Holocene	9378	6691	0.41	18063.47	<0.000	> 5000 ¹⁴ C yr B.P.	Appendix 1
Late Holocene	15 133	56 930	0.79			< 5000 ¹⁴ C yr B.P.	

^a MNI based counts.

^b Includes all small mammals.

however, a number of paleoenvironmental reconstructions indicate mesic conditions at least for the *early* early Holocene [45,47,48,87] and insofar as moisture is a critical variable, artiodactyls should have been abundant during this period.

The apparent lack of artiodactyls in the early Holocene may well be a function of enhanced seasonality during this time. 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 [70]. In addition to the negative influence of arid conditions on artiodactyl reproduction demonstrated in this paper, several studies have documented the negative effects of cold, snowy winters on artiodactyl populations [6,113]. If the early Holocene of the arid West was characterized by hot, dry summers followed by cold, wet winters, then extreme intra-annual variation in temperature and precipitation may have had a greater effect on artiodactyl populations than long-term averages of these variables. Recent stable isotope analyses of artiodactyl specimens from Mummy Cave, northwest Wyoming [61], buttress this argument. Here, oxygen and nitrogen

isotope data obtained from bighorn sheep remains indicate cooler summer temperatures during the late Holocene, while similarly derived oxygen isotope records suggest warmer winters during this time. While it is unclear when during the middle Holocene the climate shift occurred, these data suggest a late Holocene decrease in seasonality when compared to the early/middle Holocene, at least in northwest Wyoming. While Mummy Cave presents an intriguing example, future work on early Holocene climatic regimes in this context, including the seasonality of precipitation, is clearly required to clarify these issues.

8. Settlement strategies and artiodactyl indices

While the results presented above follow predictably from the prey model-based hypothesis that relative increases in artiodactyl hunting during the late Holocene should result from a climate driven expansion of large game populations, several factors, such as site function, spatial variation and settlement patterns may have played an important role in shaping the pattern observed in the Wyoming Basin faunal data. Unfortunately,

a rigorous evaluation of either spatial factors or site function falls well beyond the scope of this paper. We can however, comment on the influence of temporal changes in settlement strategy on the Wyoming Basin sample. Within this context, late Holocene increases in artiodactyl abundances may perhaps signal a shift in settlement and mobility patterns. If so, then a new pattern of site type differentiation should be noticeable at approximately the same time that artiodactyl abundances increase. Bayham [4,140], for example, proposes that a dramatic late Holocene increase in artiodactyls at Ventana Cave in southern Arizona resulted from reorientations of regional settlement patterns and functional changes in the use of upland caves, from residential bases to logistical hunting camps associated with distant permanent village sites. In the Wyoming Basin context however, there is little evidence for a fundamental late Holocene restructuring of settlement patterns. Specifically, the trend towards sedentism, horticulture and permanent villages seen in other areas of the West did not happen in the Wyoming Basin.

The appearance of housepit structures during the period from 6000 to 3500 ^{14}C yr B.P. does however suggest some degree of variation in residential mobility patterns and site function in the area. Yet, in the Wyoming Basin these sites likely represent a trend not towards long-term, semi-sedentary occupations, but instead to a more stable mobility pattern where the same locations were reused for a series of short occupations over an extended period [130]. Regardless, housepit sites constitute only a small fraction of the analyzed assemblages ($n = 10$) and at most represent seasonal occupations. The 7% of the overall Holocene sample representing the housepit phenomenon notwithstanding, the overwhelming majority of Wyoming Basin sites throughout the Holocene represent short-term, open-air residential camps occupied by highly-mobile hunter-gatherers [146]. As such, shifts in settlement patterns and site function appear to have little to do with the faunal pattern documented here.

9. Summary

The goal of this paper was to explore the relationship between Holocene climate change and variability in artiodactyl abundances documented in the Wyoming Basin zooarchaeological record. Paleoenvironmental data in combination with climate simulations derived from an archaeoclimate model both indicate a general, region-wide shift towards xeric conditions during the early Holocene that was followed by a period of extreme aridity during the middle Holocene. Relatively more mesic conditions, perhaps with reduced seasonality, return to the Wyoming Basin sometime between 5000

and 6000 years ago and persist with some variability into the present. Against this background, we predicted that Wyoming Basin archaeofaunas would reflect the subsequent elevation in encounter rates with artiodactyls during the more mesic early and late periods of the Holocene. The apparent complexities of the early Holocene notwithstanding, the vast archaeological dataset of over 88,000 specimens used here clearly supports this prediction for the late Holocene.

The more mesic environment of the late Holocene appears to have provided higher encounter rates with the artiodactyl species inhabiting the Wyoming Basin. Interestingly, while late Holocene components on average document greater artiodactyl abundances, these assemblages range from exclusively small mammal remains to those comprised entirely of artiodactyl remains. It would seem that while artiodactyls were present in significantly greater numbers during the late Holocene, and at many times Wyoming Basin foragers were able to narrow their diet to the general exclusion of small mammals, in many other instances artiodactyls were rare and broad diets were thus required. This observation suggests that while environmental conditions were improving as a function of climate at the end of the middle Holocene and thereafter, throughout the region artiodactyls were nonetheless encountered inconsistently.

This study is not the first to identify a relationship between climate change at the middle/late Holocene transition and artiodactyl encounter rates. Similar patterns have been documented previously in the Great Basin [19], California [12], and most recently in the Midwest [157]. In those cases where increases in the proportionate hunting of artiodactyls have been documented in detail, rises in large game abundances occur in concert with increasing late Holocene effective moisture in otherwise unremarkable archaeological contexts. This is not to say that increasing artiodactyl densities and the enhanced environmental productivity that lie at its root did not ultimately have far-reaching implications for human demography, technology, the sexual division of labor, and many other aspects of the human adaptive systems in the arid west. Indeed, important modeling work on these issues is well underway [e.g., 149,158] with significant archaeological implications. Accordingly, future research in the Wyoming Basin incorporating the region's rich stone tool, cooking technology, plant macrofossil [131], and site location records would undoubtedly prove fruitful.

Acknowledgements

We thank Judson Finley, Bill Eckerle, Pat Lubinski, Michael Cannon, Susan Hughes and two anonymous reviewers for their helpful comments on earlier drafts of the manuscript.

Appendix 1

Sites and associated data used in this analysis

Site	Component	Mean date ¹⁴ C yrs B.P.	Artiodactyl sized	Lagomorph sized	Rodent sized	Small mammal	Total	AI	Reference
48CR1790	2A	6320	0	335	28	0	363	0.000	[111]
48CR1790	2B	6730	1	490	52	0	543	0.002	[111]
48CR3961	II	1420	459	0	0	0	459	1.000	[112]
48CR4139	I	4693	573	34	69	16	692	0.828	[119]
48CR4681	I	7332	3	136	4	129	272	0.011	[119]
48CR4681	II	6050	7	160	18	139	324	0.022	[119]
48CR4681	III	4607	26	317	40	124	507	0.051	[119]
48CR4681	IV	3649	13	221	3	251	488	0.027	[119]
48CR4686	I	4696	14	10	6	353	383	0.037	[119]
48FR1602	1	4850	116	2	0	72	190	0.611	[92]
48FR1602	2	4330	252	23	0	743	1018	0.248	[92]
48FR2330	Subfeature 2	5770	0	2	15	175	192	0.000	[118]
48FR2330	Subfeature 3	7160	0	0	0	46	46	0.000	[118]
48LN0350	Bone bed	1060	5509	0	0	0	5509	1.000	[95]
48LN0373 ^a	2	4380	176	45	0	0	221	0.796	[152]
48LN0373 ^a	3	4030	142	57	0	0	199	0.714	[152]
48LN0373 ^a	4	2960	138	20	0	0	158	0.873	[152]
48LN0373 ^a	5	1590	132	51	0	0	183	0.721	[152]
48LN0373 ^a	6	1200	111	44	0	0	155	0.716	[152]
48LN0373 ^b	2	6000	9	17	0	0	26	0.346	[152]
48LN0373 ^b	3	5530	18	21	0	0	39	0.462	[152]
48LN0373 ^b	4	5240	16	41	0	0	57	0.281	[152]
48LN0373 ^b	7	4011	17	21	0	0	38	0.447	[152]
48LN0373 ^b	9	2960	77	76	0	0	153	0.503	[152]
48LN0373 ^b	10	1860	35	14	0	0	49	0.714	[152]
48LN0373 ^b	11	1790	45	22	0	0	67	0.672	[152]
48LN0373 ^b	12	1170	125	33	0	0	158	0.791	[152]
48LN0373 ^b	13	1030	14	11	0	0	25	0.560	[152]
48LN1286	3	1471	123	62	0	0	185	0.665	[152]
48LN1286	2	1515	27	4	0	0	31	0.871	[152]
48LN1334	1	5952	15	13	0	0	28	0.536	[152]
48LN1334	2	5290	30	15	0	0	45	0.667	[152]
48LN1334	3	5060	19	6	0	0	25	0.760	[152]
48LN1468	III	2516	44	0	0	6	50	0.880	[131]
48LN1468	IV	1500	60	15	2	53	130	0.462	[131]
48LN1468	V	1310	137	14	0	45	196	0.699	[131]
48LN1468	VI	1170	48	11	3	108	170	0.282	[131]
48LN1468	VII	960	106	12	0	15	133	0.797	[131]
48LN1733	2	1250	0	9	9	50	68	0.000	[58]
48LN1738	1	5410	25	0	0	128	153	0.163	[58]
48LN1880	I	7879	11	0	0	24	35	0.314	[96]
48LN1880	II	5271	6	0	0	35	41	0.146	[96]
48LN2068	Locus A	1170	16	424	0	0	440	0.036	[99]
48LN2068	Locus B	1421	72	342	0	0	414	0.174	[99]
48SU0846	Locality B	5680	139	0	0	0	139	1.000	[144]
48SU0595	1	4920	56	89	4	0	149	0.376	[147]
48SU0595	2	4372	453	1328	92	0	1873	0.242	[147]
48SU0867	5	737	8088	84	0	185	8357	0.968	[143]
48SU0867	6	280	676	47	0	4	727	0.930	[143]
48SU1006	V	5583	4685	1	0	0	4686	1.000	[105]
48SU1006	VII	4690	164	0	0	0	164	1.000	[105]
48SU2094	Structure B	6445	2	42	0	0	44	0.045	[97]
48SU2324	Structure B	6707	0	42	0	0	42	0.000	[98]
48SU2630	*	869	200	0	0	0	200	1.000	[50]
48SW00005	*	8988	1055	0	0	0	1055	1.000	[127]
48SW00097	II	2600	268	1	2	0	271	0.989	[102]
48SW00097	III	1460	145	0	2	0	147	0.986	[102]
48SW00097	IV	707	1585	0	0	0	1585	1.000	[102]
48SW00155	I	1020	312	8	0	0	320	0.975	[102]
48SW00211	III	2286	163	1	1	4	169	0.964	[102]

Appendix 1. (continued)

Site	Component	Mean date ¹⁴ C yrs B.P.	Artiodactyl sized	Lagomorph sized	Rodent sized	Small mammal	Total	AI	Reference
48SW00211	IV	1530	323	3	6	5	337	0.958	[102]
48SW00211	I	4890	93	14	39	62	208	0.447	[102]
48SW00212	I	4431	772	118	61	613	1564	0.494	[102]
48SW00270	II	1318	3649	180	47	0	3876	0.941	[102]
48SW00390 ^c	1	1270	96	21	0	0	117	0.821	[122]
48SW00390 ^d	1	1308	218	43	0	0	261	0.835	[122]
48SW00390 ^d	2	1830	41	2	0	0	43	0.953	[122]
48SW00998	I	1790	1854	116	0	16	1986	0.934	[119]
48SW00998	II	1260	63	0	1	1	65	0.969	[119]
48SW01242	2	2170	8	4	0	23	35	0.229	[56]
48SW01242	3	1547	192	115	0	259	566	0.339	[56]
48SW01560	Lower	1470	86	20	0	0	106	0.811	[59]
48SW01612	1	1950	1	2	64	23	90	0.011	[145]
48SW02302	*	1320	30	13	0	0	43	0.698	[148]
48SW02590	I	6325	181	249	0	794	1224	0.148	[52]
48SW02590	II	4818	485	506	0	781	1772	0.274	[52]
48SW02590	III	2215	74	248	0	420	742	0.100	[52]
48SW02590	IV	1140	30	109	0	389	528	0.057	[52]
48SW02613	I	230	291	1	0	0	292	0.997	[119]
48SW03604	*	1000	595	0	0	0	595	1.000	[77]
48SW04381	2	1390	32	39	10	1	82	0.390	[40]
48SW04491	1	5520	5	30	0	0	35	0.143	[26]
48SW05019	1	6150	0	171	0	0	171	0.000	[26]
48SW05019	3	1070	1988	20	0	0	2008	0.990	[26]
48SW05057	2	1445	318	31	0	20	369	0.862	[51]
48SW05057	3	1267	141	17	0	73	231	0.610	[51]
48SW05215	1	5150	0	26	6	644	676	0.000	[93]
48SW05215	2	1040	0	9	0	39	48	0.000	[93]
48SW05222	Middle	1230	1675	424	0	0	2099	0.798	[49]
48SW05222	North	850	221	384	0	0	605	0.365	[49]
48SW05352	1	3241	581	5	0	0	586	0.991	[100]
48SW05649	1	1300	361	383	0	0	744	0.485	[100]
48SW05655	1	1289	45	398	0	0	443	0.102	[100]
48SW05734	1	9540	42	64	2	11	119	0.353	[69]
48SW05734	2	8198	1	53	6	15	75	0.013	[69]
48SW05734	3	7256	21	200	6	66	293	0.072	[69]
48SW05734	4	6210	3	41	7	33	84	0.036	[69]
48SW05982	II	4379	36	0	0	0	36	1.000	[119]
48SW06324	EV	1190	276	6	37	0	319	0.865	[102]
48SW06324	EVI	430	1711	2	1	0	1714	0.998	[102]
48SW06324	WI	2573	57	9	3	1	70	0.814	[102]
48SW06324	WII	1010	776	29	1	22	828	0.937	[102]
48SW06324	WIII	921	709	110	13	31	863	0.822	[102]
48SW06454	1 (occ. 1)	1010	12	2	4	15	33	0.364	[114]
48SW06454	1 (occ. 2)	1270	130	21	66	136	353	0.368	[114]
48SW06595 ^d	I	1753	54	43	4	6	107	0.505	[101]
48SW06777	1	5215	242	0	0	27	269	0.900	[53]
48SW06926	3	1420	22	8	0	42	72	0.306	[27]
48SW07107	III	1285	72	11	1	84	168	0.429	[119]
48SW07933	A2	1072	13	61	0	0	74	0.176	[28]
48SW07933	A1	4710	5	209	0	0	214	0.023	[28]
48SW07991	II	1420	73	58	0	8	139	0.525	[102]
48SW08000	II	3769	2	23	1	9	35	0.057	[102]
48SW08594	1	6490	121	639	0	0	760	0.159	[28]
48SW08842	1	1730	0	19	0	0	19	0.000	[117]
48SW08842	2	2950	2	190	0	0	192	0.010	[117]
48SW08842	3	5150	0	66	0	0	66	0.000	[117]
48SW08842	4	7190	0	582	0	0	582	0.000	[117]
48SW08842	5	8490	0	147	0	0	147	0.000	[117]
48SW09251	2 (occ. 2)	1020	98	71	141	9	319	0.307	[114]
48SW09251	2 (occ. 1)	1030	523	161	96	1	781	0.670	[114]

(continued on next page)

Appendix 1. (continued)

Site	Component	Mean date ¹⁴ C yrs B.P.	Artiodactyl sized	Lagomorph sized	Rodent sized	Small mammal	Total	AI	Reference
48SW09251	3 (occ. 1)	1530	30	490	207	15	742	0.040	[114]
48SW10233	1	1190	777	0	10	18	805	0.965	[114]
48SW10248	3	3212	106	0	0	8	114	0.930	[114]
48SW10888	3 (occ. 3)	950	39	1	17	0	57	0.684	[114]
48SW10888	3 (occ. 4)	910	28	3	0	0	31	0.903	[114]
48SW10888	3 (occ. 5)	950	59	60	259	0	378	0.156	[114]
48SW10888	3 (occ. 6)	1041	33	124	1	0	158	0.209	[114]
48SW13156	I	8725	3	0	0	169	172	0.017	[25]
48UT0035	I	1350	1041	5	0	0	1046	0.995	[159]
48UT0199	I	930	1069	0	0	0	1069	1.000	[3]
48UT0199	Area A	1460	625	23	0	0	648	0.965	[126]
48UT0199	Area B	4890	85	8	0	0	93	0.914	[126]
48UT0370	*	5394	31	9	0	0	40	0.775	[126]
48UT0375	I	8476	0	15	1404	1756	3175	0.000	[120]
48UT0375	II	7890	0	0	20	6	26	0.000	[120]
48UT0375	III	4116	130	0	0	43	173	0.751	[120]
48UT0390	*	1246	11237	43	0	0	11280	0.996	[126]
48UT0401	2	2300	254	0	3	0	257	0.988	[57]
48UT0445	*	1013	0	14	0	20	34	0.000	[126]
48UT0779	3	1130	207	73	0	0	280	0.739	[126]
48UT1186	2	910	280	56	0	3	339	0.826	[94]
48UT1186	1	1170	1268	0	0	19	1287	0.985	[94]
5MF2631	*	505	111	42	0	11	164	0.677	[109]

*Single undesignated component.

^a 1000N, 1000E.

^b 100N, 1000E.

^c Block A.

^d Block B.

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