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**A spatio-temporal model of hunter-gatherer foraging ecology across the North
American Great Plains throughout the Paleoindian period;**

Development of theory and statistical methods to link human evolutionary biology, ecology,
and the archaeological record

A Dissertation Presented

by

Erik Roque Otárola-Castillo

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The Graduate School

in Partial Fulfillment of the

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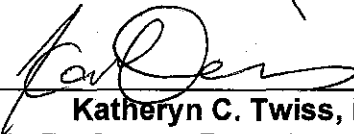
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Abstract of the Dissertation

**A spatio-temporal model of hunter-gatherer foraging ecology across the North
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Development of biological theory and statistical methods to link human
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Hunter-gatherers spread to nearly every corner of the planet in large part due to their flexible ability to forage for high-quality foods in diverse environments. The study of human foraging behavior is therefore crucial to understanding the proximate and ultimate factors that have shaped human evolutionary history. Although not necessarily in an evolutionary context, the foraging behavior of Paleoindian hunter-gatherers in North America has been studied for over a century. Researchers have paid particular attention to Paleoindian foragers' hunting of big game across the grasslands of the Great Plains, shedding light on "what" prey Paleoindians foraged, "where" foraging occurred on the paleolandscape, and "how" foraging took place. Less, however, is known about the forces shaping those foraging responses. Although prey abundance has emerged as an important factor determining predator responses, quantitative studies on Paleoindian predators' foraging decisions related to prey abundance have been less developed. In effect, only

infrequent and tenuous answers have emerged in response to the question of why archaeologically observed predator–prey interactions occurred. This dissertation addresses questions regarding Paleoindian foraging behavior by developing new tools 1) to investigate the general factors shaping hunter-gatherer foraging decisions, and more specifically, 2) to reconstruct a baseline of the bison prey abundance available to Paleoindian hunter-gatherers, particularly across the North American Great Plains. These tools are then used to test several of the current hypotheses regarding the relationship between Paleoindian predators, their environment, and their prey. These include hypotheses generated from traditional research on Paleoindian hunting, as well as hypotheses derived from foraging theory.

For my mother and father, my wife and daughter

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As a Stony Brook University undergraduate student in Dr. John Shea's Introduction to Archaeology (ANT 104), I became fascinated by archaeological science, hunters and gatherers, and stone tools. Later as a student I also discovered my fascination for computers, biostatistics, and their application to archaeological problems. Over the next several years, this fascination led me to become enthusiastically committed to learn more about the topics covered in this dissertation: 1) how organisms, including humans forage for the necessary energy and nutrients to survive and reproduce over time and space, 2) the archaeological representation of human foraging, 3) the archaeology of the Paleoindian period on the North American Great Plains, and 4) how to separate signal from noise in archaeological data to test hypotheses and make probabilistic inferences.

This dissertation is a product of that commitment. I of course did not acquire the necessary skillsets to complete this dissertation on my own. Along the way, several mentors and peers kindly contributed time and effort to help me grow along my intellectual journey. I am truly obliged to Dr. John J. Shea, who as both my undergraduate and Ph.D. adviser has observed my trajectory from a naïve Anthropology major to completing a doctoral dissertation. John taught me the soothing effects of flintknapping through his now famous "PrimTech" course, he showed me how to butcher animals with stone tools, and as a consistent mentor through the years, he has encouraged me to persist when the going got tough. John, I only hope I can guide students with a care and dedication similar to yours – I am very lucky and thankful for it. My Ph.D. committee members Kathy Twiss and Jeroen Smaers are fountains of zooarchaeological and statistical information who have been more

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CHAPTER 1: GENERAL INTRODUCTION

Overview

Homo sapiens' ability to disperse throughout the Old and New Worlds before the end of the Pleistocene was likely due to their flexible ability to procure food in diverse environments – a foraging capability most likely shaped by Darwinian natural selection and other forces of evolutionary change (e.g., genetic drift, gene flow, and cultural selection). As such, the study of human foraging, in its many expressions, is crucial to understanding the proximate (mechanistic) and ultimate (evolutionary) causes that have influenced our human evolutionary biology and ecology.

Following the 1926 archaeological discovery at Folsom, New Mexico, there was a notable increase in the scientific questions regarding the foraging dynamics of prehistoric hunter-gatherers in North America. Researchers at Folsom, and later at Clovis, NM, uncovered indisputable evidence of humans hunting large Pleistocene-aged faunas. This discovery pushed temporal estimates of the initial occupation of the North American continent to as early as the late Pleistocene (e.g., Cotter 1937, 1938; Figgins 1927, 1933; Howard 1935). Today, most of the earliest North American hunter-gatherer groups are known as Paleoindians (literally “old Indians”). Paleoindian hunter-gatherers were likely band-level social groups. This study refers to these Paleoindian foragers as groups or populations. Researchers have hypothesized that Paleoindians, beginning with the so-called Clovis culture, entered and effectively colonized the North American continent by at least 13,500 calibrated years Before Present (yCal.BP; see Dillehay et al. 2008; Hockett and Jenkins 2013; Jennings and Waters 2014; Waters et al. 2011). However, increasing evidence points to an earlier “pre-Clovis” settlement; for example, dates from the

Buttermilk Creek Complex at the Debra L. Friedkin site in Texas (13,200–15,500 BP; Jennings and Waters 2014; Waters et al. 2011) and Monte Verde in Chile (18,500 BP; Dillehay 2015) indicate that Clovis cultures were not the first colonizers of the continent. Nevertheless, Clovis and later cultures remain the most robust signatures, in terms of material remains, of human settlement in North America. For this reason, this dissertation focuses on these populations.

For the purposes of this study, the Paleoindian period encompasses the time period between approximately 13,500 and 9,000 yCal.BP, which also encapsulates the transition between the Pleistocene and Holocene geological epochs. Receding glaciers and drastic climatic and environmental changes marked this period of time, presumably affecting the spatio-temporal distribution and abundance of human food resources. Consequently, although cultural mechanisms certainly affected individual decision-making, such environmental changes must have also influenced human subsistence behaviors.

Paleoindian subsistence responses across the Great Plains and the surrounding regions seem to have been varied. The traditional view of Paleoindian hunter-gatherers is one of big-game hunters (e.g., Kelly and Todd 1988). Paleoindians indeed preyed on large game such as bison, mammoth, and mastodon. Research on big-game hunting has provided a great amount of data on bison kills (e.g., Wheat 1978:84) and generated a clearer picture of the subtleties involved in Paleoindian big-game hunting. This enhanced clarity has indicated that the Paleoindian diet was also comprised of a wide variety of other food sources, including plants, small- and medium-sized mammals, birds, and other smaller animals (e.g., Bamforth 2002b; Hill Jr. 2007, 2008; Hill et al. 2008).

Likewise, Paleoindian prey abundance, particularly bison, seems to have varied widely across the Great Plains. Researchers have often causally linked the variation in the frequency of hunted bison remains observed across kill sites to the natural abundance and distribution of the local bison population during the Paleoindian period. However, the bison population's natural abundance during this period is commonly inferred using the frequency of hunted bison remains at kill sites (e.g., Butler 1978; Cannon and Cannon 2004:56; Reher 1977:31, 1978:36). This type of inference is potentially problematic, in that, the concluding causal claim forms a critical piece of the argument's supporting evidence (e.g., "many prey were hunted here, because there were many prey to hunt here"). Therefore, it may be more desirable to use environmental and ecological principles independent of the observation to make inferences regarding the natural occurrence of prey animals.

Although inferences of bison dynamics using independent ecological causal premises exist, their quantification has been rare (e.g., Hanson 1984). In one of the few efforts to achieve this, Bamforth (1988) assessed ecological conditions and resource structures across the Great Plains in order to draw inferences regarding bison population dynamics. However, Bamforth acknowledged that his work was not quantitative in nature, and recommended that a numerical study of Paleoindian hunter-gatherer ecology in the context of bison abundance and distribution be "a second step in future research" (1988:21). Despite Bamforth's recommendation, no statistical studies have directly assessed Paleoindian hunter-gatherers' foraging responses to fluctuations in bison abundance.

Purpose and Scope of the Dissertation

The goal of this dissertation, therefore, was to revisit and invigorate this area of research by using evolutionary models of foraging behavior and reconstructing prehistoric resource distribution, specifically with respect to bison, throughout the Great Plains during the Paleoindian period. The expected outcomes of each model provided clear and testable quantitative predictions regarding the variability of Great Plains Paleoindian foraging strategies over space and time. The following questions regarding resource abundance and distribution were quantitatively assessed:

1. Did climatic variables matter for Paleoindian mobility, settlement, and subsistence decisions?
2. How was the abundance of staple resources such as bison distributed across the Great Plains during the Paleoindian period?
3. Did bison abundance variability affect Paleoindian settlement locations?
4. Are the numbers of bison at kill/camp areas associated with local bison abundance?
5. Is bison abundance consistent with zooarchaeological patterns of bison carcass butchery?

The first step was to use pollen assemblages to model paleoclimatic variables within a statistical spatio-temporal context (e.g., Cressie and Wikle 2011). The next step was to model the distribution of grass species across the North American Great Plains, using established relationships between grass morphology and their biomass concentration to generate a proxy measure for bison carrying capacity during the Paleoindian period. This proxy measure was then used to test the hypotheses regarding Paleoindian bison predation using archaeological and experimental data.

For the purposes of this study, it was important to develop the linkages between archaeological observations and dietary and evolutionary foraging inferences. For example, when modeling the reasons as to why hunter-gatherers transport prey animals in parts, the study employed the minimum number of bison killed (MNI) and the minimum number and types of bison anatomical parts (MNE) documented at several archaeological sites to make inferences about the diets of Paleoindian hunter-gatherers. To do so, it was important to understand the specific costs and caloric benefits associated with butchering different anatomical parts of a prey. Some prey animals, like bison, would have been too large for hunters to transport in their entirety after a successful kill. Instead, hunters had to make decisions as to which anatomical parts to bring home and which to leave behind. The energetic and time cost–benefit tradeoffs inherent to each anatomical part most likely informed those prey-part foraging and transport decisions. However, few statistical models have linked the anatomical parts of large game to energetic tradeoffs and foraging theory (e.g., Schoville and Otarola-Castillo 2013).

In order to interpret archaeological faunal material in the context of hunter-gatherer subsistence, zooarchaeologists have traditionally relied on the “utility” measures of anatomical parts devised by Lewis R. Binford (1978). Binford studied the hunting behavior of Nunamiut hunters in northern Alaska between 1969 and 1972, and argued that the observed skeletal element frequencies left at several functional locations reflected the element’s utility (i.e., meat, marrow, and grease) relative to its weight. Binford then developed a food utility index (FUI) to rank skeletal elements and proposed several transport strategies that corresponded with skeletal elements’ relative frequency as a

function of their utility. He categorized these transport strategies as bulk, gourmet, or unbiased.

One problem with Binford's approach is that his proposed utility curves primarily consider the energetic gains of the prey-transport tradeoff process without accounting for its costs (Metcalf and Jones 1988; Lupo 2006). This omission is significant in an evolutionary context, since models of evolutionary biology and ecology assume that the rate of net energetic return over time must be optimized over the long-term average if individuals are to maximize their reproductive potential and fitness. Therefore, when investigating questions related to human evolutionary history, it is necessary to account for the costs of obtaining resources. Factoring in processing costs causes the relative ranks of anatomical parts in Binford's ranking scale to shift. In addition, including the energetic and time costs of carrying anatomical parts from the kill site to the residential camp causes the rankings to shift even further (Schoville and Otarola-Castillo 2013). With some exceptions, transport costs between camp and kill sites are directly related to a habitat's carrying capacity and probability of encountering prey. Accordingly, this dissertation's studies build on one another to reconstruct paleoclimatic, environmental, and ecological factors influencing Paleoindian prey encounters during the Paleoindian period.

In addition, this dissertation provides much needed data with which to evaluate the foraging hypotheses related to Great Plains Paleoindians. Classical foraging theory and optimality models (e.g., Charnov 1976; McArthur and Pianka 1966) have been concerned with the energetic tradeoffs influencing the decision making of foragers. In the context of Paleoindian bison hunting, these tradeoffs consist of the energetic gains and time costs involved in extracting nutrients from bison prey. However, researchers have lacked the

energetic tradeoff data needed to make such foraging inferences with respect to bison. In light of this gap, Chapter 5 presents experimental data on the caloric benefits and costs related to bison anatomical parts. These data are the result of bison butchery experiments conducted with Andrew Boehm. These experiments involved observing professional modern butchers use stone tools to work on two bison individuals, and collecting details of the caloric gains and time costs associated with the meat and marrow of individual skeletal elements. These data, in conjunction with a proxy for bison carrying capacity, were then used to test the foraging hypotheses related to Paleoindian hunter-gatherers.

Completing this work presented several challenges. First, even though the study relied on environmental and climatic relationships for the models presented here, the actual paleoclimate or paleoenvironment could not be observed. A strategy to overcome this challenge was to use proxy measures to infer the sought-after paleoenvironmental variables. This involved comparing environmentally naïve “sub-fossil” pollen assemblages to their environmentally calibrated counterparts, inferring their environmental attributes, and then transferring those attributes from the calibrated set to the fossil set. Second, any inference based on a paleoenvironmental reconstruction is purely hypothetical, and therefore can be modified as new information, methodological developments, and theoretical paradigms emerge. This challenge is welcome, and future research should seek to modify and expand the hypotheses regarding Paleoindian foraging behavior generated in this dissertation.

To make inferences about variations in foraging behavior, this dissertation compares the original data generated with data drawn from several published sources. All of the archaeological sites, data, and literature references used are detailed in the methods section

and tables within each chapter. Appendix A provides brief summaries of the geographical and archaeological characteristics of many of the key Paleoindian archaeological sites (n=70) and components (n=120) across the Great Plains. These sites include such “classic” type sites as Folsom, Blackwater Draw, Agate Basin, and Hell Gap, where key observations about Paleoindian zooarchaeological remains have been recorded.

Dissertation Organization

A primary goal of this work was to generate new hypotheses that could support and challenge existing ones through repeatable, quantitative observations and analyses. The emergent hypotheses were drawn from the large body of Paleoindian subsistence research conducted over the last hundred years. Chapter 2 briefly outlines the major tendencies in research on Paleoindian subsistence organization and settlement throughout the Great Plains.

Chapter 3 tests hypotheses regarding the magnitude and direction of climatic effects (if any) on Paleoindian foraging, demonstrating the usefulness of modern paleoenvironmental reconstruction techniques. Pollen assemblages from across the North American Great Plains are used to reconstruct multiple paleoenvironmental variables over the duration of the Paleoindian period (~14,000–9,000 years before present), including mean annual temperature, mean annual temperature variance, annual precipitation, and variance in annual precipitation. This study also adds novel methodological steps to paleoenvironmental reconstructions, in particular the use of spatio-temporal statistics to model the space–time covariance of each variable. The results of the modeling reconcile current hypotheses regarding the climatic influence on Paleoindian dietary strategies.

Chapter 4 covers three major topics. First, bioclimatic species distribution modeling (SDM) calculates the modern distribution of 116 grass species native to the Great Plains. The estimated parameters of each species model are then applied to the reconstructed paleoenvironmental variables in order to model the species' distribution during the Paleoindian period. The result is a set of maps illustrating the probability of occurrence of each of the 116 species across the Great Plains and across the 33 250-year intervals. Second, the study operationalizes McNaughton's "Grazing Lawn" concept to generate maps of Grass Biomass Concentration (GBC). GBC is a measure indicative of good grazing grounds, based on a functional relationship between grass probability of occurrence, grass morphology, and grazing response. The resulting GBC maps are able to track where bison grazers might have thrived across the Great Plains throughout the Paleoindian period. Third, the study tests several hypotheses regarding Paleoindian foraging, using data from 84 Paleoindian archaeological components in the Great Plains.

Chapter 5 describes the process of generating new data through experiments conducted with Dr. Andrew Boehm. In the North American Great Plains, bison remains comprise the most prevalent evidence of Paleoindian big game hunting. However, information on the energetic tradeoffs involved in the extraction of nutrients from bison is non-existent. Consequently, these experiments were designed to yield this necessary information. In the process of the experiments, professional butchers disarticulated and defleshed complete bison carcasses, using stone tools. The caloric gains of meat and marrow and the time costs to extract them were quantified per bison anatomical part. These data on bison butchery costs and benefits were used in conjunction with information collected from published manuscripts on Paleoindian bison kills reporting the Minimum

Number of Skeletal Elements (MNE) to generate assemblage-wide return rates. These return rates were then modeled as a function of several variables, including bison encounter rates, in order to test the hypotheses derived using the Marginal Value Theorem operationalized through Giving up Densities. Results show that Paleoindian foragers, akin to other foraging organisms, followed the predictions drawn from foraging theory

Finally, Chapter 6 provides a general conclusion and discussion of possible avenues for future research.

CHAPTER 2: REVIEW OF RESEARCH ON PALEOINDIAN SETTLEMENT AND SUBSISTENCE ORGANIZATION

In the wake of the discovery of a Folsom-type projectile point embedded in an extinct species of bison, and the subsequent acceptance of the Folsom site as evidence of human presence in North America during the Late Pleistocene (Cook 1927; Figgins 1927), archaeologists have strived to learn more about the life strategies of this prehistoric people. As part of this process, researchers have attempted to infer the strategies of bison procurement and consumption used by Paleoindian groups living throughout the Great Plains of North America during the Late Pleistocene–Early Holocene (~ 13,000–8,000 years before present). Although bison was not the sole component of the Paleoindian diet (e.g., Hill Jr. 2007; Hill et al. 2006; LaBelle 2005), most recent zooarchaeological analyses have suggested that it was a major, if not indispensable, component of their routine diet (e.g., Haynes and Hutson 2014; Byerly et al. 2005; Hill Jr. 2007; Hill 2001). It is not surprising, therefore, that researchers have often described the relationship between Paleoindian humans and bison populations according to a predator–prey dynamic (e.g., Frison 1998). Such an approach highlights the hunters’ need for sensible knowledge of their surrounding landscape and the often complex immediate and long-term behavior of their prey (e.g., Frison 1987, 1991, 2004).

These and similar inferences have been the result of decades of detailed documentation and analyses of the faunal remains recovered from archaeological sites throughout the Great Plains (e.g., Frison 1974; Hill 2001; Kehoe 1967; Todd 1983; Wheat 1972, 1979). The research conducted on Paleoindian subsistence in the early to mid-twentieth century arose in conjunction with culture-historical research and sought normative (“typical”)

modes of subsistence that corresponded with Paleoindian archaeological cultures. These modes were defined in terms of stone tool variation. For example, the Clovis archaeological culture was associated with mammoth hunting, while the Folsom culture was associated with bison hunters. In the last third of the twentieth century, researchers began to adopt more processual approaches, emphasizing ecological modeling and documenting the behavioral variability characterizing Paleoindian adaptation.

However, researchers have yet to reach a consensus on a common analytical framework with which to understand Paleoindian subsistence, landscape use, and settlement behavior. For example, early reconstructions of Paleoindian subsistence behavior were largely based on explorers' accounts during early European/Native American contact, ethnographies of the recent past, and archaeofaunal patterns of recent prehistory that may or may not have included the earlier two (e.g., Frison 1974:35-51; Sellards 1952:66; Wheat 1972:85-124). Historical and ethnographic models of native subsistence and organization, however, became problematic analogues for researchers when attempting to contextualize Paleoindians living under different environmental and ecological contexts prior to and during the Pleistocene–Holocene transition. For example, Frison (1982 cited in Todd 1991:217) noted that later prehistoric subsistence strategies involving large bison kills in the fall were geared toward accumulating food for the upcoming winter. Citing Frison (1982:200), Todd (1991:217) described the remains of more recent prehistoric bison processing as containing:

readily identifiable features and artifacts. These include stone heating pits, stone boiling pits, and piles of bone reduced to varying sizes for boiling out the bone grease. Anvil stones and hammerstones were used extensively in bone crushing and breaking processing...During the early fall, the bison are in prime condition that provides the thick layer of back fat used in pemmican manufacture. Both

dried meat and pemmican provided the necessary surpluses to insure winter survival.

This description of bison kills, their remains, and their seasonality is more representative of later prehistoric sites, such as Big Goose Creek (Frison et al. 1978), Bugas-Holding (Rapson 1990), Head Smashed In (Brink and Dawe 1989), Piney Creek (Frison 1967), River Bend (McKee 1988), Ruby (Frison 1971), and White Rock (Logan 1995, 1998). Earlier in North American prehistory, however, Paleoindian bison kills appear to show a different pattern of material remains.

Evidence from later Paleoindian periods shows regional differences between the northern and southern plains. For example, Cody Complex assemblages on the northern plains seem to reflect a fall-winter oriented pattern, whereas spring kills seem to have been more characteristic of the south (Hill Jr. 2013). With some exceptions (e.g., Byers 2002; Hill 2005), evidence of “cold marrow” bone breakage, that is, the breakage of bone solely for the purpose of marrow extraction and not for grease production (*sensu* Stiner 2003), has been rather limited. Moreover, most Paleoindian sites do not contain grease-processing pits. Rather, Paleoindian hearths appear to be mostly ephemeral features, lacking evidence that rocks were heated for grease production (e.g., Hill et al. 2011; Jodry and Stanford 1992; LaBelle 2005). To date, no Paleoindian site has yielded bones fragmented into small pieces (comminuted) – a practice observed at archaeological sites from later prehistoric periods excavated using similar recovery methods (e.g., Leechman 1951; Logan 1998; Vehik 1977). Comminuted bone has been demonstrated experimentally to be evidence of grease-rendering behavior (Church and Lyman 2003). Furthermore, unlike in later prehistoric faunal assemblages, the frequency of cutmarks on Paleoindian skeletal elements

– traditionally a reflection of the intensity of carcass butchery (although Egeland (2003) suggests that this connection is weak at best) – has been very low or non-existent.

Todd's (1987:Figures 11 & 12) comparison of skeletal element frequencies between Late-Prehistoric and Paleoindian bison kills also revealed differences in the types of animal parts the respective hunters chose to remove. According to Todd (1987:259), "it seems that a major difference between the northern Plains [Late-Prehistoric] cluster and the Paleoindian cluster is in the deletion of bones from the Paleoindian group...by complete limb units rather than by dismembered anatomical subsets" as observed in more recent prehistory. In other words, whereas Late-Prehistoric bison kills appear to show a more selective pattern of individual bone removal, Paleoindians appear to have transported bison parts as complete articulated segments. Todd argued that these differences in selectivity "may reflect the requirements of transport, scheduling, and food utility [of the selected elements] decisions" (Todd 1987:259). On the other hand, Paleoindians' less selective and more complete part transport may have been because 1) a large number of animals were taken or the workforce was too small to completely process all of the available animal products; 2) the consumer group lived nearby or moved into the kill area; 3) animal products were not selected for future-oriented storage, but instead consumed immediately; or 4) environmental or physical conditions did not allow the hunters to process all of the products. In Todd's general view, the evidence seemed to indicate that because of climatic, environmental and ecological conditions, the Paleoindian foraging system differed from that of Late-Prehistoric North Americans to the extent that archaeologists could not use the Late-Prehistoric model to explain Paleoindian behavior. Instead, a new model that

accounted for Late Pleistocene climatic and environmental conditions was necessary to describe Paleoindian behavior.

To model Paleoindian behavior, Kelly and Todd (1988) proposed that Paleoindians adapted their behavior to the short-term predictability of bison herds as moving resource patches. Relying on and tethering themselves to storage caches was probably a risky endeavor for Paleoindian groups, particularly if the positioning of bison herds throughout the year was uncertain. Therefore, according to Kelly and Todd (1988), the approach best suited to this contingency was to move from one bison kill to the next, removing easy-to-transport food packages, such as complete bison parts, and abandoning unused food products. This strategy was conducive to frequent shifts in land use ranges, and tied to the availability and immediate supply of the raw materials needed to produce the stone tools required to carry out the next kill. As a result, Paleoindians left an ephemeral and redundant material record at every site, characterized by short-term utility and limited diversity in terms of site use.

Bison kill sites, such as the Lipscomb site located in the Texas panhandle (Todd et al. 1992), appear to lend support to Kelly and Todd's (1988) theory that Paleoindians did not process bison carcasses intensively for their products. In addition, based on the analysis of stone tool raw materials, Hofman and Todd (2001:204) suggested that the hunters at Lipscomb supplied themselves with local raw materials on an as-needed basis in order to "gear up" hunting weaponry to last for an extended period or distance, while carrying enough processed food to last until their next encounter with a bison herd. Similarly, Hofman's (2003:Figures 12.4 & 12.7) analysis of the raw materials from the Nolan site in western Nebraska and from several sample locations in northeastern Colorado and

southwestern Nebraska indicated a related pattern of as-needed, on-the-go re-tooling “pit stops” prior to a kill. This “gearing-up” behavior of Paleoindians was also later observed by Sellet (2004) in the form of the mass production of projectile points at the Agate Basin site’s Folsom component. Sellet (2004:Table 4) identified the remains of 60 attempts to manufacture projectile points (38 successes, 22 failures) from mostly the same raw material (Knife River Flint), probably in anticipation of an encounter with a large number of bison.

Hofman and Todd (2001:205) commented that this pattern of “gearing-up” may only have taken place during “some seasons of most years,” suggesting that Paleoindian subsistence, land use, and settlement strategies were possibly more flexible and dynamic than a year-round kill-to-kill orientation. Hill (2001) elaborated on this apparent seasonality, based on observations made on the faunal remains at the Agate Basin, Folsom, and Hell Gap, components of the Agate Basin site in eastern Wyoming (Frison and Stanford 1982), and the Clary Ranch site fauna in western Nebraska (Myers et al. 1981). Hill’s (2001:256) results indicated that Paleoindian mobility was highly seasonal. During the summer months, Paleoindian mobility was likely unconstrained, relative to the winter months, with groups moving from one kill-butchery site to the next, effectively relocating consumer populations to resource areas. This freedom of movement probably allowed Paleoindian populations to use a “forager strategy” (Binford 1981). By contrast, during the winter months, mobility appears to have been more restricted, most likely due to unfavorable weather conditions. According to Hill, this apparent restriction in mobility probably forced Paleoindians to operate in a more logistical manner (*sensu* Binford 1980), according to which task-specific groups were charged with bringing resources to the population’s residential hub.

During the Pleistocene–Holocene transition approximately 10,000 years ago, the seasonal shifts in mobility Hill observed were accompanied by an overall climatic warming trend and an increase in climatic and resource seasonality (*sensu* Frison and Walker 1990:321). Similarly, Walker’s (1982) study of micromammal sympatry at the Agate Basin site in eastern Wyoming indicated that over a 400 year period, from 10,780 ± 120 B.P. to 10,445 ± 110 B.P., the annual mean temperatures in January and July increased from -13.4°C to -7.4 °C and from 9.8 °C to 15.8 °C, respectively (Hill 2001, Table 1.1). At the same time, there was a 7 cm decrease in annual precipitation and an increase in the annual frost-free period from 34 to 74 days. These changes mirror the post-Last Glacial Maximum trend of increased temperature seasonality and insolation, wherein the differences between summer highs and winter lows have been estimated to be 20% greater than in modern times (Meltzer and Holliday 2010). This sweeping climatic change may have re-engineered the environmental composition and dynamics under which Paleoindian hunter-gatherers operated, forcing them to adapt their subsistence strategies accordingly.

The seasonal pattern observed at the Clary Ranch site of a late summer-early fall kill might reflect such a change in subsistence tactics. Hill (2001, 2005) reported that a minimum of 41 animals, represented by various segmented parts, revealed a pattern of intensive butchery and thorough marrow bone breakage that had never been observed at a Paleoindian site (Hill 2001:Table 4.13 & 4.14). Hill (2001, 2005, 2008) proposed that the faunal exploitation pattern observed at the Clary Ranch site was consistent with that of a secondary processing area to which select skeletal elements were transported for processing from an as-yet-undiscovered primary kill area. This pattern appeared to reflect the initial stages of an intensification in bison processing occasioned by the onset of

relatively rapid climatic change during the Late Paleoindian period (Hill 2001:13-16). Hill's argument was based on what he called the systematic, future-oriented subsistence behavior he observed at Clary Ranch. Such behavior was characterized by the evidence of intensive exploitation of overall carcass nutrients (>3000 cutmarks and >150 impact fractures), the segregation of kill-butchery activity areas, and a kill seasonality that deviated from previously observed subsistence behaviors (e.g., Kelly and Todd 1988; Todd 1987, 1991; Todd et al. 1997). According to Hill (2001, 2005), this shift toward a subsistence strategy that included intensive butchery and thorough marrow processing was probably an adaptive response to changing resource availability under the new climatic regime. It is likely that bison availability switched from being consistent almost year-round to being seasonally restricted, mostly accessible during warmer months.

At the same time, LaBelle (2005:295) suggested that the perceived increase in resource exploitation intensity noted by Hill could be “explained by factors of length of occupation and the location of the site on the landscape, factors which would have affected local groups much more than long term evolutionary trends.” LaBelle provided a Paleoindian dataset from which he attributed similar faunal exploitation patterns to a “place-oriented” strategy, rather than a “long-term evolutionary trend” toward the intensification of resource extraction (LaBelle 2005:290, 295). He suggested that Paleoindian people most likely developed a flexible, dynamic system in which their movements revolved not only around hunting bison herds, but also around finding secure areas of relatively well-rounded resource availability to serve as residential hubs.

Such localities, usually situated in lowland valley areas, would have given Paleoindians access to a greater diversity of resources and would have been able to sustain populations

for longer periods of time. It is only logical, therefore, that these sites would leave behind more dense and diverse deposits of material remains. LaBelle argued that, by contrast, sites such as Olsen-Chubbuck (Wheat 1968, 1972) were probably task-specific places located in bison-rich upland areas. Such sites, and probably all bison kill sites, were likely to demonstrate a similar archaeological signature of low butchery and low marrow processing intensity as a result of the site's specific purpose. Due to the lack of resource diversity and availability, such task-specific sites would have been unable to sustain large groups of people over a long period time. As such, from LaBelle's perspective, the intense processing patterns witnessed at sites such as Clary Ranch were not necessarily related to questions of food-resource availability or seasonality, but rather were by-products of the site's function, location in the landscape, and length of occupation.

Locality II at the Hell Gap site (Byers 2001, 2002) also reflects this place-oriented emphasis on reoccupation rather than intensification. Although the skeletal elements at this site were not as intensely processed as at Clary Ranch, "extensive evidence for marrow extraction" suggests that the site's occupants thoroughly and continuously extracted bison products (Byers 2002:372). Behaviors at this site seem to indicate multiple occupations by Agate Basin Paleoindians ~10,000 years ago, either through relatively permanent settlement or repeated short-term occupations year-round (Byers 2002:374).

Bamforth et al. (2005) proposed similar short-term occupations, arguing for continuous use of place based on artifacts' spatial distribution at the Allen site, one of the three Medicine Creek sites in southeastern Nebraska (originally reported by Davis and Schultz 1952). According to Bamforth et al. (2005), the Allen site was persistently occupied and

reoccupied by Paleoindians between 10,800 to 8,200 RCYBP¹, roughly 3,500 calendar years. The site's persistent reuse is evidenced by the presence of numerous sequentially buried hearths (Bamforth et al. 2005:Figure 4). Moreover, according to the authors, Paleoindian groups occupied this site so frequently "that they often discarded their trash on the still visible middens of the previous occupants" (Bamforth et al. 2005:573). Although the dominant faunal remains at the site are from bison, which fits the pattern of a bison-focused adaptation, Bamforth et al. (2005) challenged other aspects of Kelly and Todd's (1988) model of the highly and unpredictably mobile, technologically sophisticated bison hunters. Instead, Bamforth et al. suggested that Paleoindians' intensive re-use of places seemed to contradict the kind of constant long-distance travel proposed by Kelly and Todd's model (1988). This argument was largely driven by the dominant presence of Niobrara jasper, a local raw material used for manufacturing stone tools, at the Allen site. In light of these observations, Bamforth (2002a; 2005) argued that late Paleoindians were more territorially aware and more predictable than Kelly and Todd (1988) had proposed; they often returned to known places in the landscape and possibly relied on trade networks to acquire exotic raw materials. The place-oriented hypothesis suggests that the archaeological pattern of continuous occupation leaves behavioral signatures that mirror the intensive butchery of bison. Other place-oriented evidence suggests that late Paleoindians were indeed territorial, sticking to relatively small ranges and persistently occupying and reoccupying the same "places" for over a few millennia (e.g., Bamforth 2007; Bamforth et al. 2005). In sum, place-oriented advocates argue that the patterns

¹ Radiocarbon Years Before Present

resulting from the intensive use and re-use of places have generated data that archaeologists might mistakenly interpret as butchery intensification over time.

The “diet-breadth hypothesis” uses place orientation as a feature of its explanatory framework (Hill Jr 2008, 2007b; Hill Jr.2007a:432-433), alongside intensification over time due to deteriorating climatic conditions and declining bison abundance during the Pleistocene–Holocene transition. However, the intensification trend observed is not related to more intensively butchered bison, but to Paleoindians broadening their diet breadth over time by increasing the proportion of smaller game included in their diet (e.g., Hill Jr 2008, 2007b; Hill Jr.2007a:432-433). This process is similar to other archaeologically documented human diet expansions, for example, in the Mediterranean Basin 50-40kya and 13-10kya during the Natufian period in the Levant (Stiner and Munro 2002).

Yet another proposed explanation of Paleoindian subsistence and settlement is the Paleoindian “generalist hypothesis.” This hypothesis questions the traditional Paleoindian dietary focus on bison, arguing that “Paleoindian economies were not focused on large game (mammoth or bison), but rather included, likely in significant quantities, a wide variety of plant and animal resources” (e.g., Kornfeld 2007:56; Kornfeld and Larson 2008). Kornfeld (2007) and Kornfeld and Larson (2008) introduced an impressive amount of empirical evidence to show that the frequencies of bison are relatively small when compared to those of smaller mammals. In their opinion, bison was not, in fact, the staple food of the Paleoindian diet, but rather an artifact created by inadequate sampling focused on the archaeological remains of large mammal bonebeds.

As detailed above, many predictions of Kelly and Todd’s Paleoindian model have been refined and/or refuted over time. However, the emergent hypotheses challenging Kelly and

Todd's model have often been in conflict and not fed back into a consistent body of theory capable of explaining all observed archaeological patterns. With some exceptions, this incompatibility has been largely due to the geographically limited nature of each interpretation. Moreover, attempts to extrapolate these temporally and spatially limited patterns to broader scales have only confounded the problem further.

Paleoindian settlement and subsistence organization was most likely not homogeneous or governed by a single strategy. Instead, the strategies employed surely reflected variations in seasonal and long-term climatic contexts across a broad spatial and temporal ecological gradient. In other words, processes that affected the abundance and distribution of key resources, including bison, likely shaped the organization of hunter-gatherer subsistence and settlement strategies. Unfortunately, knowledge of bison abundance and distribution during the Paleoindian period is incomplete at best.

Todd (1987) noted that, based on skeletal element assemblages of bison, Paleoindians probably operated according to different ecological rules than their ethnographic and even later prehistoric counterparts. Particularly due to different climatic conditions, it is possible that bison abundance and distribution during Paleoindian times were quite different from those of their more recent counterparts. However, to avoid circular reasoning, inferences of the effect of bison abundance and distribution on Paleoindians should not be drawn from Paleoindian-mediated zooarchaeological assemblages. Rather, independent ecological causal premises should be used to infer bison spatio-temporal distribution models. Therefore, to address Bamforth's (1988:21) call for a "second step in future research," this dissertation reconstructed the paleoclimate and bison distribution across the Great Plains throughout the Paleoindian period, and then used the results of those quantitative studies

to test several hypotheses related to Paleoindian foraging within a predictive modeling framework.

CHAPTER 3: DID CLIMATE VARIABILITY AFFECT THE FORAGING STRATEGIES OF PALEOINDIAN HUNTER-GATHERERS?

A Spatio-Temporal Model of Reconstructed Paleoenvironmental Variables across the North American Great Plains

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Chapter Overview

Hunter-gatherer patterns of land use and foraging strategies are strongly influenced by their ecology and the environmental features of their surroundings. As the literature review in Chapter 2 highlighted, studies of Paleoindian foragers have often made hypotheses regarding climatic influences on dietary strategies, but rarely tested those hypotheses empirically. This lack of explicit hypothesis testing has been partly due to a dearth of operationalized paleoenvironmental variables. Although paleoenvironmental reconstructions have been abundant, particularly those based on pollen, they have mostly been qualitative. Moreover, existing quantitative reconstructions have not accounted for spatial or temporal autocorrelation. This paper demonstrates the usefulness of modern paleoenvironmental reconstruction techniques, testing hypotheses regarding climatic effects on Paleoindian hunter-gatherers' foraging behavior. The hypotheses tested were specifically related to the magnitude and direction of climatic effects (if any) on Paleoindian foraging. This study used pollen assemblages from across the North American Great Plains to reconstruct multiple paleoenvironmental variables – mean annual temperature, mean annual temperature variance (seasonality), annual precipitation, and variance in annual precipitation (seasonality) – during the Paleoindian period (~14,000–9000 years before present). This study also added novel methodological steps to paleoenvironmental reconstruction by applying spatio-temporal statistics to model the space–time covariance of each variable. Using spatio-temporal kriging, the reconstructed variables within the data range were estimated for times during the Paleoindian period and in areas across the Great Plains. The results have important implications for the understanding of Paleoindian foraging and subsistence within the context of

paleoenvironmental and nutritional resource reconstruction. Specifically, this study reconciles current hypotheses regarding the climatic influence on Paleoindian dietary strategies.

Introduction

Hunter-gatherer land use and foraging strategies are strongly influenced by the ecological conditions and environmental features of their surroundings. For modern hunter-gatherers, environmental attributes, such as mean annual temperature, annual precipitation, and their respective seasonal patterns, have significant effects on subsistence organization and strategies (e.g., Kelly 1995; Binford 1980; 2001; Marlowe 2001; Burnside et al. 2012). For example, investigating whether seasonal patterns affect the manner in which hunter-gatherer populations organize themselves, Binford (1980: 15) found that hunter-gatherers' reliance on food storage correlates with the length of the annual growing season across latitude. Binford reasoned that, as harvestable resources decrease throughout the year, hunter-gatherer dependence on storage increases in order to compensate for potential food shortages. Similarly, Kelly (1995: 65-73) found that the dietary composition of hunter-gatherer groups, as determined by hunting, gathering, and fishing activities, fluctuates with changes in effective temperature (ET). Researchers have observed similar environmental effects on the underlying differences in the proportional caloric contributions by males and females to modern hunter-gatherer diets (Marlowe 2001).

Paleoanthropologists have applied similar environmental analyses to infer the ecological causes of evolutionary patterns in prehistoric hunter-gatherer and non-human primate populations (e.g., Elton 2008). However, since prehistoric ecological dynamics and environmental attributes cannot be measured directly, paleoanthropologists use proxy measurements, (e.g., pollen and phytoliths) to reconstruct past climates and environments, and then use those proxies to infer the ecologies of the study populations. The resulting

paleoecological reconstructions have played a key role in understanding the ecological mechanisms affecting Paleoindian populations (e.g., Holliday 1997; Balakrishnan et al. 2005). Paleoenvironmental inferences have contextualized Paleoindian responses to several climatic events, including the opening of the ice-free corridor and the human colonization of the North American continent at the end of the Pleistocene (Elias et al. 1996; Mandryk et al. 2001; Elias 2002; Dixon 2013); the Younger Dryas cooling event around 11,000–10,000 years BP (Meltzer and Holliday 2010; Ballenger et al. 2011; Holliday et al. 2011; LaBelle 2012); the so-called “8,200-year” cooling event (Dean et al. 2002; Ellison et al. 2006; Meltzer 2009); and the prehistoric global warming period known as the Altithermal (Meltzer 1999; Seebach 2002; Sheehan 2002; Nordt et al. 2008).

Clearly, extensive research has been conducted to understand the environmental drivers of Paleoindian ecology and foraging behavior. However, hypotheses regarding the effects of climatic and environmental changes on Paleoindian foraging behavior and diet are difficult to quantify and test. Moreover, evaluating hypothesized effects of individual climatic variables on the diet of these hunter-gatherers is a difficult task. Consequently, questions germane to these hypotheses remain unanswered. The purpose of this study was to test several current hypotheses regarding the effects of climatic change on the foraging behavior and diet of Paleoindian hunter-gatherers of the North American Great Plains. To accomplish this goal, novel spatio-temporal analytical methods were developed to reconstruct quantitative paleoenvironmental variables, while accounting for the statistical problems inherent to these data.

Background

The effect of climate on Great Plains Paleoindian foraging

Paleoenvironmental reconstructions of the Great Plains have shown an overall trend of increased warming and climatic and resource seasonality during the Pleistocene–Holocene transition (e.g., Frison and Walker 1990:321). For example, Walker’s (1982) study of micromammal sympatry at the Agate Basin site in eastern Wyoming indicated that within a 400-year period, from $10,780 \pm 120$ B.P. to $10,445 \pm 110$ B.P., the annual mean temperatures for January and July increased from -13.4 °C to -7.4 °C and from 9.8 °C to 15.8 °C, respectively (Hill 2001: Table 1.1). At the same time, annual precipitation decreased by 7 cm, and the annual frost-free period increased from 34 to 74 days. These changes were accompanied by a post-Last Glacial Maximum trend of increased temperature seasonality and insolation, with differences between summer highs and winter lows estimated to be 20% greater than in modern times (Meltzer and Holliday 2010). These climatic changes may have forced an adaptive change in the subsistence strategies employed by Paleoindian hunter-gatherers. Evidence of these potential changes in subsistence behavior has come from several archaeological sites on the Great Plains.

According to Hill (2001), the faunal exploitation patterns observed at Clary Ranch (a Paleoindian secondary bison butchery and processing area) had a systematic and future-oriented character. Hill argued that these patterns reflected the initial intensification of bison processing that resulted from the relatively rapid increase in seasonality; this seasonality created uneven annual resource distribution and thus resource bottlenecks in the winter months on the Great Plains during the Late Paleoindian period (Hill 2001: 13-16). Evidence of the intensive exploitation of nutrients (NISP = 1584, MNI = 41; >3000 cutmarks and 150+ impact fractures) and the spatial segregation of kill/butchery activities

diverged from previously observed Paleoindian subsistence behavior (Wheat 1972; Kelly and Todd 1988). Hill (2001) suggested that the intensive processing of a single large species (e.g., bison) might have been this late Paleoindian population's chosen adaptive response to subsistence-related problems, as opposed to the increase in diet breadth observed at Paleoindian sites from similar time periods (e.g., the Medicine Creek sites; Bamforth 2002).

According to LaBelle (2005: 295), however, Hill's evidence of resource intensification can be "explained by factors of length of occupation and the location of the site on the landscape, factors which would have affected local groups much more than long term evolutionary trends." Using a large Paleoindian dataset focused on the Central Plains, LaBelle (2005: 290, 295) interpreted similar patterns of faunal exploitation as "place-oriented" strategies, rather than a "long term evolutionary trend" of resource intensification. By this, LaBelle referred to Paleoindian groups becoming more regionalized and occupying a smaller territorial range. Such regionalization would have led Paleoindians to adapt to and reoccupy known habitats for subsistence (*cf.* Kelly and Todd 1988: 236).

For LaBelle (2005), occupation density evidence (i.e., the frequency of lithic materials and a survey of extant faunal remains) suggested that Paleoindian people had been able to develop a flexible system within which they sought out not only bison herds, but also "places" with predictable availability and diversity of resources to use as residential campsites. Such localities or residential places were usually situated in lowland valley areas that would have been able to sustain populations for longer durations. As a result, more diverse and dense deposits of material remains can be found at these sites. Furthermore,

LaBelle proposed that intensive processing activities, such as those observed at Clary Ranch, were to be expected at sites located near residential sites, where Paleoindians could afford to engage in longer term forays, such as intensive processing activities. By contrast, sites such as Olsen-Chubbuck (Wheat 1972) were probably task-specific places (e.g., a kill site in the case of Olsen-Chubbuck) and not campsites. The lack of resource diversity and availability at these sites would have made them unsuitable for sustaining large groups of people over a long period of time; as a result, these sites would have functioned poorly as camps. Therefore, minimal processing was to be expected at places like Olsen-Chubbuck because “transport costs would have prohibited exhaustively processing and carrying large bulky remains back to distant camps” (LaBelle 2005: 295). LaBelle argued that the homogeneous archaeological signatures found at these sites suggested that they had been used for specific purposes within the subsistence system. Accordingly, the intense processing patterns observed at sites such as Clary Ranch were not related to questions of food-resource availability or climatic change, but rather to a site-specific location and/or function.

Subsequent studies by Hill Jr. (2007, 2008) analyzed the variability of food-resource exploitation by monitoring the breadth in the Paleoindian diet across large spatial and temporal scales (n=69; 11 states; time range = 11,500-7,200 rcybp). Hill Jr. examined diet breadth at different types of “places,” and measured diet-breadth patterns across time as a proxy for climatic and environmental change. His results partially validated the hypotheses proposed by both Hill and LaBelle. On the one hand, Hill Jr. found support for LaBelle’s place-oriented model, discovering that the degree of food-processing intensity depended on landscape location and habitat. Food processing behaviors indeed had different diet-

breadth signatures in sites located in alluvial valleys, plains, and foothill/mountain settings. On the other hand, Hill Jr.'s results showed that the effect of a temporal trend was "most definitively seen in foothill/mountain settings during the Paleoindian period." Moreover, he found "limited evidence for subsistence change over time in either plains/rolling hills or alluvial valleys" (Hill Jr. 2007: 432). Hill Jr. speculated that climate-triggered environmental changes observed during the Pleistocene–Holocene transition likely caused this change in the diet of foothill/mountain Paleoindians (in line with previous work, e.g., Albanese and Frison 1995; Holliday 1997; Olson and Porter 2002; Davis et al. 1986). Nevertheless, the specific climatic and environmental factors affecting variability in the Paleoindian hunter-gatherer diet across space and time remain unknown.

Although the place-oriented model provides a plausible interpretation of Paleoindian hunter-gatherers' subsistence, in order to reject Hill's causal model of resource-intensification over time due to environmental reorganization, environmental variables need to be shown as diachronically constant or at least with no directional effect on the Paleoindian diet. Doing so is problematic, however, because the results of Walker's (1982) micromammal sympatry study indicate that key environmental components (e.g., climate) were not constant across the North American Great Plains during the Paleoindian period. Studies by Hill Jr. (2007, 2008) further explored this context by including the effect of time as a proxy for climatic and environmental change on various types of habitats. Using time as a proxy for climate is also problematic, however, because it confounds the effect of several climatic and non-climatic factors. While variation in foraging behavior over time might have been a response to multiple climatic factors, for example, mechanisms underlying cultural evolution could also explain a portion of this variation (e.g., Boyd and

Richerson 1985; Henrich and McElreath 2003; Boyd and Richerson 2005). In addition, identical habitat types, such as alluvial valleys, can often be climatically dissimilar during the same time period, and therefore climatic effect signals might also be confounded.

As a result, the question of how Paleoindian hunter-gatherer behavior was affected by climatic and environmental changes has been left unanswered. The nature of these competing models and their implications for understanding hunter-gatherer behavior is compelling. However, only the precise isolation and measurement of climatic variables and their effects on the observed subsistence patterns of early-Holocene humans can answer the following research questions: with habitat and site function held constant, did climatic shifts indeed influence the behavioral signature variability, specifically the resource-exploitation strategies, of Paleoindian hunter-gatherers? In addition, what were the diachronic and synchronic effects of climate, and changes in temperature, precipitation, and seasonality on Paleoindian hunter-gatherer subsistence? Answering these questions requires a formal, quantitative reconstruction of the paleoenvironment associated with Paleoindian hunter-gatherers across the Great Plains during the Pleistocene–Holocene transition.

The purpose of this paper was to evaluate the individual effects of “place” (habitat type) and diachronic and synchronic climatic trends on Paleoindian hunter-gatherers’ foraging strategies by using new analytical techniques to reconstruct paleoenvironmental variables and to model their spatio-temporal characteristics. This study focused on the North American Great Plains, an important setting with a diverse record of hunter-gatherer foraging ecology. Results of the spatio-temporal paleoenvironmental modeling assigned climatic attributes to Paleoindian sites across time and space. To make paleoenvironmental

reconstructions, a method known as the modern analogue technique (MAT) (defined below) was employed along with a very large sample of microbotanical information (see Methods). The goal was to reconstruct four paleoenvironmental variables across the Great Plains throughout the Paleoindian period: mean annual temperature, mean annual temperature variance (seasonality), annual precipitation, and variance in annual precipitation (seasonality). The reconstructed variables were then used to assess their influence on the dietary strategies of Paleoindian hunter-gatherers.

Quantitative paleoenvironmental reconstruction

In general, most paleoenvironmental inferences related to prehistoric human response have not been based on quantitative estimates of climatic attributes (e.g., annual temperature, precipitation, or seasonality). Although the fossil and sub-fossil data used to infer paleoclimate are intrinsically quantitative, a vast number of the resultant inferences have been qualitative environmental and climatological descriptions (Nordt et al. 1994; Whitlock et al. 1995; Worona and Whitlock 1995; Connin et al. 1998; Muhs et al. 1999; Allen and Anderson 2000; Armour et al. 2002; Meltzer and Holliday 2010; Ballenger et al. 2011; Holliday et al. 2011; Krause and Whitlock 2013). For example, some researchers have relied on pollen assemblages in their studies, as such pollen data are some of the most ubiquitous. Pollen assemblages contain crucial records of past climates and environments and how they have changed. However, while such plant pollen's relative frequency in core samples offers a quantitative measurement of vegetation abundance over time, the climatic inferences drawn from the assemblages have been largely qualitative in nature (Meltzer and Holliday 2010; Arsuaga et al. 2012; Krause and Whitlock 2013). More recently, semi-quantitative land cover reconstructions have used pollen data to assess the level of

anthropogenic impact on local vegetation (e.g., Broothaerts et al. 2014; Bunting et al. 2016). Although these are exciting steps in the quantitative modeling of paleoenvironmental change, these latter studies do not focus on reconstructing the climate or climatic variables. In effect, the lack of numerical climatic reconstructions has made it difficult to assess explicitly quantitative models.

This quantitative gap is not a new problem in paleoclimatological research. In the late 1960s, paleoclimatologists sought to remedy this issue by calibrating mathematical functions that could link climatic attribute measurements to several measurements of fossil data, including pollen counts (Cole 1969; Webb and Bryson 1972), marine plankton (Imbrie and Kipp 1971), and tree-ring morphology (Fritts et al. 1971). The use of transfer functions and multivariate distance analyses in paleoenvironmental modeling have since led to computerized developments such as the MAT (Figure 3.1; Overpeck et al., 1985; Jackson and Williams, 2004). Across the Great Plains, there has been some degree of paleoclimatic research using transfer functions in the context of the Late Quaternary, but this has been limited to temperature only (Elias 1996; Fredlund and Tieszen 1997; Hoppe et al. 2006; Nordt et al. 2007) with methods that have not been widely replicated. Nonetheless, these analytical tools enable researchers to develop statistically rigorous paleoclimatic reconstructions using environmentally calibrated datasets, while assessing the reconstruction's degree of uncertainty and precision (Viau et al. 2006).

The MAT (Overpeck et al. 1985; Jackson and Williams 2004) is a statistical method that can be used to infer past environments (Davis 2000). The technique relies on transfer functions derived from modern calibration datasets in which the environmental attributes are known (e.g., climatic and vegetation variables) to infer the environments of samples

with unknown environmental characteristics (e.g., the fossil or sub-fossil sample). Researchers have commonly used this technique to extract past environmental information (vegetational and climatic) from sub-fossil pollen across several temporal and spatial scales (Guiot et al. 1993; Gajewski et al. 2000; Williams et al. 2001), for example, to reconstruct canopy variation since the Last Glacial Maximum in the North American continent (Williams 2003), and to make global reconstructions of several paleoclimatic variables during the mid-Holocene (around 6 ka) and Last Glacial Maximum (around 21 ka) (Bartlein et al. 2011: Table 3).

The MAT has also been used on smaller spatial scales to reconstruct vegetation cover at the Last Glacial Maximum (Newnham et al. 2013) and seasonality during the early Holocene of New Zealand (McGlone et al. 2011). In addition, the MAT has been used to make temporally longer reconstructions of vegetation and climate history, for example, in the late Pleistocene of easternmost Beringia (Fritz et al. 2012). The success of the MAT has prompted an increase in the number of statistical tools and programs enabling users to conduct paleoenvironmental reconstructions (Sawada 2006; Juggins 2007; Simpson 2007).

Paleoenvironmental data and lack of spatio-temporal independence

Despite the success of the MAT, current paleoenvironmental reconstructions face a challenge in that, like variations in modern environmental measurements, paleoenvironmental proxy measurements are dependent upon their spatial location and temporal occurrence. Tobler's rule, the first law of geography, states: "Everything is related to everything else, but near things are more related than distant things" (Tobler 1970, 2004). In this context, the qualities implied by "near" and "distant" apply to the measurements (the "things") recorded across space and time. For example, temperature

measurements across sampling locations in middle latitudes will be more similar to each other than to measurements in northern latitudes, and temperature measurements across middle latitudes taken today will be more similar to each another than to measurements at the same sampling locations recorded 10 years ago. The values of these measurements are thus dependent upon their particular spatial and temporal locations and, as such, violate the assumption of independence required for standard statistical analyses (see Hulbert 1984 for discussion). This spatial and temporal dependence applies to climate measurements both in the present and in the past, and includes measurements derived from paleoenvironmental climate reconstructions.

Analyzing non-independent samples as independent replicates is known as pseudoreplication, defined as “the use of inferential statistics to test for treatment effects with data from experiments where either treatments are not replicated (though samples may be) or replicates are not statistically independent” (Hulbert 1984). Due to the problematic nature of pseudoreplication, the parameter estimates in question might not reflect true variation. For example, increasing pseudoreplicates in a set of samples will decrease the error of the measured population parameters, such as their mean. However, the statistical danger is that the mean differences due to sampling error may be mistaken for true differences between populations. Therefore, the results of statistical analyses that include pseudoreplicates are not reliable.

To account for this spatial and temporal autocorrelation, developments in the field of spatio-temporal statistics can be applied (Cressie 1993; Cressie and Wikle 2011; Sherman 2011). Spatio-temporal statistics offers several methods with which to model and account for the spatial and temporal dependence of measurements from locations sampled

throughout the spatial and temporal extent of the population in question. Several spatial interpolation and prediction procedures such as kriging (see Cressie 1993) can be extended to generate measurement predictions across unsampled locations in space and time.

Spatio-temporal research has examined environmental measurements, such as sea surface temperature (Beltrán et al. 2012); air quality particles such as nitrogen dioxide, ozone, and particulate matter (Finazzi et al., 2013); and oceanographic variables of interest to maritime safety research, such as ocean wave heights (Vanem et al. 2012). Very recently, health researchers have turned to space–time analysis to investigate the prevalence, etiology, transmission, and treatment of many diseases (Richardson et al. 2013). In addition, promising and exciting research in paleoclimatological reconstruction has identified similar problems and is currently following a similar trajectory (see Tingley et al. 2012).

In light of these challenges, this study closes a significant gap in our knowledge by answering questions regarding the effects of place, time, and climatic change on the subsistence behavior of Paleoindian hunter-gatherers. Here, the method involved using the MAT in conjunction with radiocarbon-dated lake pollen core counts to obtain measurements of four key paleoenvironmental variables (i.e., mean annual temperature, mean annual temperature variance, annual precipitation, and variance in annual precipitation) across the Great Plains of North America. These measurements were used to compute observed spatial, temporal, and spatio-temporal covariances (i.e., the dynamic between spatial and temporal patterns). The spatio-temporal covariances were used to generate predictions with respect to the paleoenvironmental variables at unsampled locations in space and time (spatio-temporal kriging). Unsampled locations are Paleoindian

archaeological sites that contain published information on their spatial location (latitude and longitude coordinates), temporal location (radiometric date), and dietary behaviors. The latter is a measure of Paleoindian diet breadth/diversity independent of the paleoenvironmental predictions generated through kriging. Finally, the Paleoindian diet data were modeled as a response to habitat setting (alluvial valleys, foothills/mountains, and plains/rolling hills settings) and to the temporal and spatial effects of the estimated paleoenvironmental variables.

Methods

The modern analogue technique (MAT)

To reconstruct paleoenvironmental variables, this study made use of available pollen records and the MAT. Pollen was the paleoclimatic proxy of choice largely because the pollen record is one of the most ubiquitous assemblages of paleoenvironmental proxies available. In addition, few Paleoindian studies have made paleoclimatic reconstructions using pollen assemblages and the MAT. Comparative studies have shown that, for making paleoenvironmental inferences, the MAT is as accurate and precise as other methods, including more sophisticated Bayesian hierarchical models (Bartlein and Whitlock 1993; Malmgren and Nordlund 1997; Ohlwein and Wahl 2012). The MAT measures the dissimilarity in multivariate composition, known as d_{ij} , between a “target” fossil (or sub-fossil) assemblage (i) and a modern reference assemblage (j ; see Figure 3.1). This measure of dissimilarity is then repeated for each assemblage in the modern reference dataset and target (fossil) dataset. Subsequently, the environmental characteristics of the most similar modern (reference) samples are compiled and inferred to belong to the target fossil sample. Usually, researchers use the arithmetic mean when computing averages, but the

environmental variable of similar assemblages from the modern reference sample can be weighted using the measured dissimilarity coefficient (see Lytle and Wahl 2005; Williams and Jackson 2007). This technique generates a weighted average.

The MAT uses a dissimilarity threshold (T) that is predetermined and computed using the modern reference sample. This threshold is the cutoff point at which d_{ij} is too large to belong within a given geographic extent or landscape analytical unit (e.g., biome). A target sample is considered to have no modern analogue if the dissimilarity to the modern sample is greater than the threshold T . If this is the case, no environmental inference can be made. In this context, therefore, the best modern match to a fossil assemblage is the assemblage that is the least dissimilar to the reference sample (as measured by the dissimilarity coefficient). The best matching assemblage's environmental characteristics are then assigned to the spatio-temporal coordinates of the fossil assemblage under comparison. Although not explicit, one key assumption of the MAT is that there are mechanistic biological links between the variability of the variables of interest and variations in assemblage composition. Furthermore, it is assumed that environmental conditions similar to those that shaped the fossil assemblage can be found within the limits of the reference sample (Williams and Jackson 2007).

Researchers have usually quantified the dissimilarities between the reference and fossil pollen samples using well-known multivariate dissimilarity coefficients (Legendre and Legendre 2013; Overpeck et al. 1985; Williams and Jackson 2007). This study quantified the dissimilarity between assemblages using the square chord distance coefficient (SCD). The SCD is a robust signal-to-noise coefficient that can be used when measuring dissimilarities between pollen samples (Overpeck et al. 1985; Gavin et al. 2003).

MAT reconstructions using terrestrial pollen have commonly applied the SCD (Sawada et al. 2004; Williams and Jackson 2007). Algebraically, the SCD can be described as:

$$(1) \quad d_{ij} = \sum_{k=1}^n [(\sqrt{p_{ik}} - \sqrt{p_{jk}})^2]$$

where d_{ij} is the multivariate distance between pollen assemblage i and pollen assemblage j . A total of n taxa make up each assemblage, and k is each individual taxon; p_{ik} is the proportion of pollen taxon k in sample i (the fossil pollen); and p_{jk} is the proportion of pollen taxon k in sample j (the modern pollen). The SCD ranges from zero, indicating no dissimilarity, to a maximum value of two. In sum, this study made use of pollen-based MAT (using the SCD) to reconstruct climatic and environmental contexts and to determine their association to the foraging behavior of Paleoindian hunter-gatherers.

Sample selection

Modern pollen calibration data were obtained from the Modern Pollen database (Whitmore et al. 2005). This database houses a calibration dataset comprised of over 4,800 pollen assemblages composed of 134 pollen taxa on a reasonably densely sampled spatial scale. In addition, the database provides climatic and plant species composition information for each site. The Neotoma database supplied target/fossil pollen assemblage samples that were filtered to include only those samples located in habitats within or immediately surrounding the Great Plains between 25–52 decimal degrees (DD) North, and -111 – -93 DD East (Figure 3.2). All selected samples had radiocarbon dates ranging from 15,000 to 8000 before present ($n = 2,184$ assemblages). The multivariate distance between each fossil (i) and modern pollen (j) assemblage was calculated using the SCD, resulting in a modern-x-fossil distance matrix.

Modern analogues

The assemblages best suited to be modern analogues are the modern assemblages within a certain distance below the threshold at which assemblage matches from the same biome can occur by chance. Methods to decide on the cutoff distance range from the use of low percentiles (Anderson et al. 1989) to the application of more sophisticated Monte Carlo simulations (Sawada et al. 2004). The latter technique randomly draws reference assemblage pairs and computes their distances. Once a distribution of distances has been generated, the cutoff distance can be identified as those SCDs that happen infrequently (e.g., $\leq 5\%$ of the time). This study determined the threshold distance by generating the full distribution of pairwise distances using every modern pollen assemblage within its respective biome (*cf.* Sawada 2004; see Table 3.1). The cutoff values for the threshold distance in each biome were distances occurring $\leq 5\%$ of the time. This facilitated a false-positive threshold of $\leq 5\%$; $p \leq 0.05$. Once all biome-specific threshold distances were calculated, the average threshold multivariate distance among all biomes was computed as 0.20, meaning that, on average, distances greater than 0.20 occurred within individual biomes less than 5% of the time. In terms of prairies, this calculation was actually conservative, since the 5% cutoff for prairies is 0.23 (see Table 3.1 for all individual biome threshold computations).

Analogue environmental attributes

Following the selection of the candidate analogue for each fossil assemblage, environmental variables were attributed to their respective candidates. Environmental

variables were drawn from the Modern Pollen database (Whitmore et al. 2005), and a weighted average was then calculated for the candidate variables. The weights used were 1 minus the SCD distance, standardized as a proportion of the sum of all candidates.

Adjusting for potential radiocarbon date bias

The radiocarbon dates associated with several pollen assemblages in this study were derived using conventional (bulk) ^{14}C samples. Grimm et al. (2009) empirically demonstrated that there are crucial differences between accelerator mass spectrometry (AMS) and conventional (bulk carbon) radiocarbon methods (see Appendix B, Figure B.1). In general, because AMS requires less carbon amounts to calculate a date, researchers can date a single piece of organic material with exceptional spatial provenance. AMS radiocarbon dating is therefore considered to be a more precise method than the conventional dating of bulk carbon samples. To show this, Grimm et al. compared AMS-based radiocarbon dates with conventional radiocarbon dates obtained from sediments derived from pollen cores at four lakes in Illinois, South Dakota, Wisconsin, and North Dakota. The results showed that conventional ^{14}C dates derived from bulk samples were on average older than ^{14}C ages computed using the AMS methods. At its most extreme, this overestimation was as great as almost 2,000 years.

One possible reason for the discrepancy between dates is that considerable amounts of old carbon had been incorporated into the conventional samples from geological sources. Although the bias in Grimm et al.'s (2009: 305; Appendix B, Figure B.1) bulk samples was constant (i.e., systematically older than the AMS results), this might not always be the case if the depositional processes for lake layers change. Moreover, this bias depends on the

carbon's source. In order to account for this discrepancy, this study modeled the bias observed (in Grimm et al.'s 2009 study) in the relationship between conventional radiocarbon dating and AMS methods associated with pollen assemblages in order to obtain a correction (details in Appendix B). A test application on the temporal location of the Younger Dryas showed optimal performance (see description in Appendix B and Figure B.3). All conventional dates in the study sample were corrected using this method.

Space–time prediction across the Great Plains

Geostatistical methods are designed to model spatial processes and to use such models to predict values for unobserved locations. These predictions account for the autocorrelation of values distributed across space. The inherent presence of a temporal component in paleoenvironmental data implies an additional source of autocorrelation, the behavior of which can differ widely from spatial processes. There are several approaches to statistically modeling space–time correlation. This study used spatial and temporal semivariograms (defined below; see Figure 3.3 caption) to model the spatial and temporal dependence of the paleoenvironmental variables reconstructed via the MAT (Cressie 1993: 90-104; Cressie and Wikle 2011; Sherman 2011). This approach could account for both the trend of the model and the stationary temporal and spatial components. The space–time covariances resulting from the semivariogram modeling were then used to generate space–time kriging predictions at 250–500 year intervals. These prediction maps were benchmarked using maps derived from independent geological data.

From the simpler spatial perspective, a semivariogram describes the degree of spatial dependence as a function of spatial distance, where s_i is the i th spatial location (e.g.,

x , y , or x , y , z) of some value of interest z (e.g., elevation, temperature, precipitation, etc.), and where $i= 1, \dots, m$ and h is the spatial lag from s_i . Here, the variance of z at each lag (2γ) can be estimated to create an empirical variogram. Thus, the variance of z at location s with distance lag h can be represented as:

$$(2) \quad 2\gamma(s, h) = \sigma^2(z(s) - z(s + h))$$

and its spatial covariance:

$$(3) \quad \text{Cov}(z(s), z(s + h))$$

Traditionally, researchers use semivariograms (illustrating γ , 1/2-the variance) instead of variograms (depicting 2γ , the variance). However, for the purposes of this description, the terms variogram and semivariogram refer to a model of spatio-temporal autocorrelation and are used interchangeably. Empirical variograms can be optimally modeled using several functions to depict the structure of spatial dependence, including three general parameters: the nugget, the sill, and the range (as well as other parameters, see Figures 3.3a and 3.3b). The nugget is the height of the jump at the point where the variance should be zero. The discrepancy between zero-variance and the nugget is usually due to measurement error. The sill is the limit of the variogram model. It is the point at which the increase in variance as a function of distance is negligible. The variogram's range is the distance lag at which the sill is reached. Thus, it represents the distance at which the strength of spatial dependence comes close to zero (see Cressie 1993 for more detail).

Modeling the temporal dependence of a variable of interest z employs similar computations. For example, the equation

$$(4) \quad 2\gamma(t, r) = \sigma^2(z(t) - z(t + r)),$$

describes 2γ , the variance of variable z , as a function of the difference between its value at time t_j , where $j = 1, \dots, k$, and its value at time t_j plus a temporal lag r . In addition, z exhibits a temporal covariance:

$$(5) \quad \text{Cov}(z(t), z(t + r)),$$

Similarly, the space–time dependence of the variable of interest $z(s_i, t_{ij})$ can be depicted by its variance structure across space and time:

$$(6) \quad 2\gamma(s, h; t, r) = \sigma^2(z(s, t) - z(s + h, t + r))$$

and by its spatial covariance:

$$(7) \quad \text{Cov}(z(s, h), z(t, r)) = z(s, t), z(s + h, t + r)$$

In the case of separable spatial and temporal covariances, the space–time covariance is described by:

$$(8) \quad \mathbf{C}_Z = \text{Cov}(z(s, h), z(t, r)) = \text{Cov}(z(s, h)) \otimes \text{Cov}(z(t, r)),$$

where the \otimes operator denotes the Kronecker product.

Once the separable space–time covariance has been modeled, space–time kriging can be used to make optimal predictions for unknown points in space and time. This study also considered the case where $\mathbf{Z}(\cdot)$ has an unknown but constant mean μ , which can be estimated using the generalized least squares estimator

$$(9) \quad \hat{\mu}_{gls} = (\mathbf{1}^t \mathbf{C}_Z^{-1} \mathbf{1})^{-1} \mathbf{1}^t \mathbf{C}_Z^{-1} \mathbf{Z},$$

where $\mathbf{1}$ is a vector of 1 of length k . The kriging prediction of Y , \hat{Y} , at location s_0 and time t_0 is

$$(10) \quad \hat{Y}(s_0, t_0) = \hat{\mu}_{gls} + \mathbf{c}_0^t \mathbf{C}_Z^{-1} (\mathbf{Z} - \hat{\mu}_{gls} \mathbf{1})$$

Here, \mathbf{c}_0 is the covariance of $\hat{Y}(s_0, t_0)$ and the observation \mathbf{Z} . The observed measurements over space and time can be plotted on a spatio-temporal grid. These locations can then be

used as the points over which to make predictions $\hat{Y}(s, t)$. In order to estimate C_Z , the space–time covariance matrix data, this study employed a least-squares procedure to impute missing values based on the temporal trend at each spatial location.

By estimating the spatio-temporal covariance of the paleoclimatic variables reconstructed via the MAT, this study dynamically describes the relationship between spatial patterns across time. Spatio-temporal kriging can generate estimates of the paleoclimatic variables at unsampled locations, such as Paleoindian sites containing dietary remains. The resulting climatic estimates can then be used as covariates and tested for their effects when modeling the variability of Paleoindian diet breadth over space and time.

Measuring the Paleoindian diet breadth

Diet breadth refers to an optimal foraging model useful to predict the number of types of prey a predator will include in its diet (Kelly 2013:47; Bettinger 2009:1-20). Imagine a predator has a diet composed of N types of prey. Individual prey of type “ i ” are hunted ranked on their rate of caloric returns over the time taken to handle it (see below). Caloric returns (E_i) refer to the net amount of calories obtained from hunting the i^{th} prey type. The foraging time for that prey type (T_i) is classified into search-time (T_{is}), time spent until prey $_i$ is encountered, and handling-time (H_{it}), the post-encounter time spent acquiring, killing, and processing prey $_i$ for consumption. The foraging return rate, E_i/T_i , indicates the amount of calories a predator obtains per unit of time spent foraging the i^{th} prey. The diet return rate E/T includes the caloric returns and foraging times of all N prey types in the diet. The model predicts that a predator should add a new prey type “ j ” to its diet if the j^{th} post-encounter caloric return rate, E_j/H_{jt} , is greater than the current diet’s foraging return

rate, E/T . Assuming that post-encounter return rates are fixed, variation of a predator's diet breadth, between broad and narrow, is ultimately related to its prey search time and encounter rate on a landscape.

A narrow diet breadth results in few types of prey included in a predator's diet, while a wide diet breadth results in many types of prey included. To assess the Paleoindian diet breadth across space and time, this study recorded data depicting Paleoindian diet from 53 components in 25 published reports of archaeological sites in the North American Great Plains and surrounding regions (Figure 3.4, Table 3.2). Data collected were in the form of counts of faunal species abundance represented by the number of identified specimens (NISP) recovered from archaeological sites of appropriate age. Faunal specimens depicted as "cultural fauna" by published reports (e.g., Johnson and Pastor 2003) were accepted as components of the Paleoindian diet. One potential limitation here is that if all specimens did not belong to the Paleoindian diet, but were accepted as such, the measure of diet breadth (eq. 11) will yield an overestimate of the true Paleoindian diet breadth. This effect would be more pronounced on smaller samples. Figure 3.5 illustrates the proportional composition of these fauna at each site and component. There were several reasons for selecting the specific archaeological sites. First, these sites have reported spatial coordinates and associated radiocarbon dates – the latter of which were needed to estimate the paleoclimatic variables at the site's position in space and time. Second, research has designated these sites as residential camps, yielding faunal remains related to Paleoindian dietary behavior (see references in Table 3.2). The faunal remains from residential camps are likely to provide a more complete view of the Paleoindian diet than task-specific sites

such as bison kills (Hill Jr. 2007: 429). Having a more complete sample of the overall Paleoindian diet is a key element when comparing diet breadth across space and time.

Species richness is a measure of diversity that accounts for the number of different species in an organismal assemblage or sample. To quantify species richness and infer Paleoindian diet breadth and variability this study used D_{Mg} , the Margalef diversity index (Magurran 2004: 73-74, Hill and Knell 2013). D_{Mg} is an index of species richness that attempts to account for sampling intensity across samples containing multiple species by standardizing species richness by sample size:

$$(11) \quad D_{Mg} = \frac{S-1}{\ln(N)}$$

Here, S is species richness (number of species), and N is the sum of the total number of individuals in the sample; $\ln(N)$ is the natural logarithm of N . In addition, D_{Mg} provides a good comparative measure because it has been used in previous studies of Paleoindian diet (Hill and Knell 2013: 197). To avoid arithmetic problems inherent to small sample sizes (e.g., dividing by zero), the quantities S and N were augmented by adding “1” to their totals prior to the calculation of D_{Mg} .

This study modeled diet breadth as a response to several predictors, including habitat (e.g., alluvial valley, plains, or foothills) and estimated climatic variables. The effect of time (radiocarbon date) was also of interest to this study. However, since climatic variables are highly correlated with time, modeling diet breadth as a response to climate and time without accounting for their correlation would have confounded estimates of their individual effects. To account for this problem, the temporal autocorrelation of climatic variables was modeled and removed using techniques developed in the analysis of time-

series data. Residuals from an auto-regressive integrated moving average model (ARIMA) were used as climatic variables uncorrelated with time (Box and Jenkins 1976; Box et al. 1994). This approach allowed for the individual and uncorrelated effects of time and climate to be estimated. ARIMA residuals were computed in the R programming environment v. 3.3.1 (R Core Team 2016).

As discussed earlier, traditional modeling methods (e.g., analysis of variance (ANOVA)) assume that data are independent. However, spatial autocorrelation resulting from closely positioned locations can cause residuals to violate the statistical assumption of independence (Hulbert 1984; Cressie 1993). To account for spatial autocorrelation, this study used generalized least squares (GLS) to estimate parameters. GLS introduces a distance covariance matrix created from an exponential model of spatial dependence (Figure 3.3A and 3.3B; Anselin and Griffin 1988; Cressie 1993; Shabenberger and Gotway 2006:144). Several models of spatial dependence exist (e.g., Shabenberger and Gotway 2006:143-152). Because the exponential model is one of the simplest and frequently used models, it was used in this study. In the future, other spatial dependence models might be useful or a better fit to these data. This procedure was able to account for any bias in parameter estimates resulting from the close proximity of locations. GLS was modeled using the nlme package in R (Pinheiro et al. 2014).

Twenty-nine individual models, including permutations of the predictor variables, were assembled and evaluated. Akaike's information criterion (AIC), derived from Information Theory and now common in likelihood modeling, was used to evaluate best fit between models (Akaike 1974; Burnham and Anderson 2002; Schoville and Otárola-Castillo 2014).

$$(12) \quad AIC = -2 \cdot \log(L) + 2k$$

Here, $\log(L)$ is the natural logarithm of the likelihood function, L , of a model, while k stands for the number of estimated parameters in the model. AIC can account for the increase in explanatory power when there are more parameters (or variables) by including the model's likelihood. As a tradeoff, this criterion also penalizes a model for increasing the number of parameters without adequately increasing the estimated variance. Thus, AIC guards against over-fitting. As a result, this approach identifies the best model from among several possible models, explaining the available data. The best models are those with the lowest AIC values. Models are considered equable in terms of their fit to the data if the difference between AIC values is not substantial, that is, if $\Delta AIC < 2$ (delta AIC; Burnham and Anderson 2002: 70). Likelihoods and AIC values were computed in R.

Results

MAT paleoenvironmental reconstruction

The environmental variables reconstructed using the MAT were mean annual temperature, mean annual temperature variance (seasonality), annual precipitation, and variance in annual precipitation (seasonality) (Figure 3.6). The estimated values of these variables appear to be qualitatively similar to other models of paleoenvironmental reconstruction (e.g., Fredlund and Tieszen 1997; Meltzer 2006; Nordt et al. 2007). For example, the reconstruction of mean annual temperature reflected the Younger Dryas, a short cooling interval at the end of the Pleistocene, as reconstructed by Nordt et al. (2007; dated between 11,000 and 10,000 before present; see Figure 3.6). In addition, the annual

precipitation decreased after 10kbp, supporting a shift to more arid conditions after the Pleistocene (e.g., Frison and Walker 1990; Meltzer and Holiday 2010). Similarly, these reconstructions render a picture of increasing mean annual temperature seasonality, which also supports the results of previous investigations (e.g. Meltzer and Holiday 2010).

Space–time modeling and prediction

This study used reconstructed mean annual temperature to construct empirical variograms of space and time. A matern model for space and an exponential model for time generated empirical variograms. Matern is a model of covariance commonly used in spatio-temporal statistics to describe measurement variation within samples as a function of their dependence on spatial and temporal similarity (for full description of matern model see Cressie and Wikle 2011; Figure 3.4). Figure 3.7 illustrates the empirical (3.7A) and modeled (3.7B) semivariance resulting from the space–time models. The color scale in Figure 3.7 depicts the semivariance or the degree of similarity as the spatial and temporal distance increases. The semivariance model, for example (Figure 3.7B left), shows that as time and distance increase, so does the semivariance and thus the dissimilarity between sites. After fitting the model, the resulting parameters were used to calculate the space–time covariance matrix according to equation (8). This technique allowed for predictions across time and space to be generated using ordinary space–time kriging.

Ordinary space–time kriging was conducted using equations (9) and (10). Figure 3.8 shows the results of the ordinary kriging over the grid surrounding the data at 15,000 years before present. For benchmarking purposes, the resulting prediction map was overlaid on a digitized map of glacial conditions also at 15,000 years before present (from Dyke 2004: 378). The benchmarking of the temperature predictions across space was

successful, as the temperature contours of the predictions follow the southern border of the Laurentide ice sheet as expected, and as described by Dyke (2004). The coldest contours (blue) match Dyke's outline depicting the James and Des Moines lobes. Following the benchmarking procedure, the space–time covariance matrix was again used in ordinary kriging to create a space–time, multi-panel map to illustrate predictions of mean annual temperatures across the Great Plains between 15,000 and 7000 years before present at 250-year intervals (Figure 3.9).

Site-specific climatic variables

Climatic variables at each site were reconstructed using its respective estimated space–time covariance. Each individual site's spatial and temporal location was input into an ordinary kriging system (equation 10). The site's climatic variables were then used as predictors in a model of Paleoindian diet breadth response. This response was quantified using the Margalef index (equation 11).

Effects of habitat, climate, and time on Paleoindian diet breadth

Paleoindian diet breadth was quantified using the Margalef index (eq. 11) and modeled as a response to habitat, climate, and time. This study constructed several models to estimate the effects of these variables on Paleoindian hunter-gatherers across the Great Plains and the immediate surrounding regions. The models accounted for the temporal and spatial autocorrelation inherent in the data (see Methods section). This statistical technique helped to reduce the possible bias in parameter estimates due to an overabundance of sites

sharing similar temporal or spatial conditions. The best models given for the data were arbitrated using AIC (Table 3.3).

The best model for the data, according to AIC values, included mean annual temperature, mean annual temperature seasonality, total annual precipitation, time, and habitat type (Figure 3.10; Table 3.4; AIC = 96.83; Δ AIC = 2.591). The parameter estimates shown in Table 3.4 suggest that time had a small effect on diet breadth ($\beta = -0.00014$). The negative coefficient indicates that for every increase in unit of time (per year), the Margalef coefficient decreased by 0.014% (holding other effects constant). This means that as the value of time in RCBP decreased toward the present, diet breadth increased by 0.014%.

The results showed that environmental variables had large effects on Paleoindian diet breadth. Mean annual temperature, for example, had the greatest positive effect ($\beta = 0.1909$), followed by precipitation ($\beta = 0.0174$). In other words, for every unit increase in mean annual temperature and annual precipitation, diet breadth increased by approximately 19% and 1.7%, respectively. Temperature seasonality, on the other hand, had a relatively large, negative effect on diet breadth ($\beta = -0.677$). As the standard deviation surrounding mean annual temperature (annual seasonality) increased in degrees Celsius, the Paleoindian diet breadth decreased by close to 68%. The effect of this variable is interesting and potentially critical.

The habitat in which Paleoindian groups lived also had an influence on diet breadth. As shown in Figure 3.11, the results revealed the greatest diet breadth in sites in alluvial valleys (mean $D_{Mg} = 1.71$), followed by sites located in the foothills/mountains (mean $D_{Mg} = 1.18$) and sites in the plains/rolling hills (mean $D_{Mg} = 0.57$). In terms of the model, holding all variables constant at zero, the diet breadth in alluvial valleys was estimated at

3.27 (as measured by D_{Mg}). Diet diversity decreased by about 83% for sites in the foothills and mountains, while in the plains/rolling hills habitat, diet breadth decreased by 133% (Table 3.4).

Discussion

The paleoenvironmental reconstruction and spatio-temporal modeling pipeline

These findings have several implications. First, this study used a novel conceptual and methodological approach to discern the effects of climatic variability on prehistoric hunter-gatherers. The MAT served as the paleoenvironmental inference technique, as research has shown it to have high accuracy and precision in reconstructing paleoenvironmental variables similar to the ones in this paper (see Overpeck et al. 1985; Gavin et al. 2003; Viau et al. 2006). Combining this method with spatio-temporal modeling and statistics is also a novel approach in this context. Doing so provided a more dynamic view of the spatial and temporal variability of environmental variables across the Great Plains during the Late Pleistocene–Holocene transition. The benchmarking work conducted here and other attempts to validate the predictions resulting from these paleoreconstruction methods indicate that the variables inferred in this study are in line with current knowledge of these processes.

However, this approach is not without its shortcomings. One problem is empirical, in that, the strength of the predictions is dependent upon the sampling efforts across time and space. Therefore, caution should be used when interpreting predictions made outside the boundaries of the data. Naturally, increasing the number of samples can reduce the standard error of the predictions, rendering them more precise. Another potential problem

is associated with error across multiple levels of the analytical hierarchy, from radiocarbon date estimations through to space–time predictions. Explicitly modeling all possible sources of error can mitigate this issue. However, this paper did not address the compounding of error across the multiple levels of analyses. Future MAT reconstructions should address this issue by using empirical or Bayesian hierarchical models in which the error can be modeled along with the data (e.g., Tingley et al. 2012). In addition, care should be used in the assignment of site function typologies to archaeological sites (e.g., residential camps or kill sites). Rather than reflecting discrete types, archaeological sites might be part of an occupation continuum (Binford 1982; Shott 2010). Nevertheless, the site function designations used here are generally accepted and have been used in previous research (e.g., Hill Jr. 2007, 2008).

What was the effect of climate on Paleoindian diet diversity?

The main question of this study was: what effect did time and climate have on the diet breadth of Paleoindian hunter-gatherers across the North American Great Plains? The best model generated by this study answered this question, finding that, although time had a small effect, most but not all climatic variables were associated with fluctuations in diet. Of course, compounding the time effect across several millennia of Paleoindian living, the effect adds up. Climatic variables such as mean annual temperature, temperature seasonality, and annual precipitation had large effects on the diet choices of Paleoindian hunter-gatherers. However, annual precipitation seasonality did not appear to have an influence on Paleoindian diet diversity.

The magnitudes of these environmental drivers of diet breadth were matched and varied by the Paleoindian foragers' location in the landscape. Indeed, Paleoindian hunter-gatherers' habitat had a great influence on their dietary choices. As discussed by Hill Jr. (2007, 2008), alluvial valleys probably had the greatest faunal richness followed by foothills and mountain settings and lastly by grassland environments. The results of the present study support the notion that habitat and location in the landscape shaped the dietary strategies of Paleoindian hunter-gatherers in conjunction with climatic trends. As such, this finding helps to reconcile LaBelle's (2008) and Hill's (2001) hypotheses.

The fact that the order of habitat effects matches that of previous work seems to be a good measure of the reliability of this analysis. However, this study's estimates of those habitat effects in terms of percentage increases and decreases in diet breadth are new to Paleoindian research. Furthermore, this study's most novel and notable finding lies in the estimation of climatic effects on Paleoindian hunter-gatherer diets. Estimating the effects' magnitude and direction is an important step in ensuring a strong inference approach (i.e., Platt 1964) that will hopefully prove useful for future research.

Why might climatic variables have affected the Paleoindian diet?

Perhaps a more interesting question than whether climate had an effect on the Paleoindian diet, and in what direction and by how much, is what was the reason for this effect? Looking at the effects of temperature and precipitation: They were both positive and large, meaning that as precipitation and temperature increased, so too did the diet breadth of these Late-Pleistocene humans. There are several potential reasons for this pattern, some of which are to be expected. One set of answers is ecological. As

demonstrated by well-established measures of habitat productivity, indices such as net primary productivity (NPP) and organismal diversity increase as temperature and precipitation increase (Kelly 1999; Binford 2001). Potentially, increases in resource productivity and diversity in habitats where Paleoindians dwelled positively covaried with these foragers' dietary niche. As proposed by the "place-oriented" strategy in previous studies (e.g., LaBelle 2005; Hill Jr. 2007, 2008), a broader archaeological dietary signature should be found at Paleoindian camps situated in more productive habitats with higher resource diversity.

Interestingly, although the effect of temperature seasonality was quite large, it negatively affected Paleoindian diet diversity at residential campsites. All other variables held constant, Paleoindian diet breadth decreased by nearly 68% per unit of temperature as the annual temperature seasonality increased. This represents by far the greatest effect among the environmental variables. It is unclear as to why hunter-gatherers would follow a more restricted dietary strategy in response to increased seasonality. However, this narrowing of diet breadth might be more a matter of perception than a reality. Given that in highly seasonal environments select food resources are only available during limited portions of the year, the dietary signal at residential camps should correlate with seasonal food abundance and related activities (Binford 1982: 15-16). Therefore, while the dietary signal might appear to be more specialized, it may simply be indicative of these hunter-gatherers' versatility in exploiting a wide range of resources year-round.

Conclusions

This study responded to a pressing question in Paleoindian studies: what were the effects of climate and climatic change on the dietary choices of Paleoindian foragers? To answer this question, this study operationalized and evaluated related hypotheses by recording the archaeological remains of Paleoindian dietary strategies from 53 components in 25 published reports of archaeological sites encompassing the North American Great Plains and surrounding regions (Table 3.2) and measuring their diversity. The study also used a novel approach to reconstruct quantitatively tractable paleoenvironmental variables (i.e., mean annual temperature, mean annual temperature variance (seasonality), annual precipitation, and variance in annual precipitation (seasonality)). To evaluate the magnitude and direction of the climatic effects on the Paleoindian diet, these data were modeled within a GLS framework to account for spatial and temporal sampling bias. Different hypotheses were arbitrated using criteria drawn from Information Theory, as outlined in the Methods section.

The results showed that time as a covariate had a small effect, and most of the climatic variables were associated with fluctuations in diet. Mean annual temperature, temperature seasonality, and annual precipitation had large effects on the diet choices of Paleoindian hunter-gatherers. Specifically, temperature seasonality had the greatest effect on Paleoindian diet diversity. In addition, the magnitude of these environmental variables varied according to Paleoindian foragers' location in the landscape. These results indicate that habitat and landscape location in conjunction with climatic trends shaped Paleoindian hunter-gatherers' dietary strategies. As such, these results help to reconcile several existing hypotheses on Paleoindian dietary change. Moreover, the present work brings together several methodological advances to evaluate the effect of climate and climatic change on

prehistoric hunter-gatherer foraging. Further evaluation will unravel more details of this phenomenon.

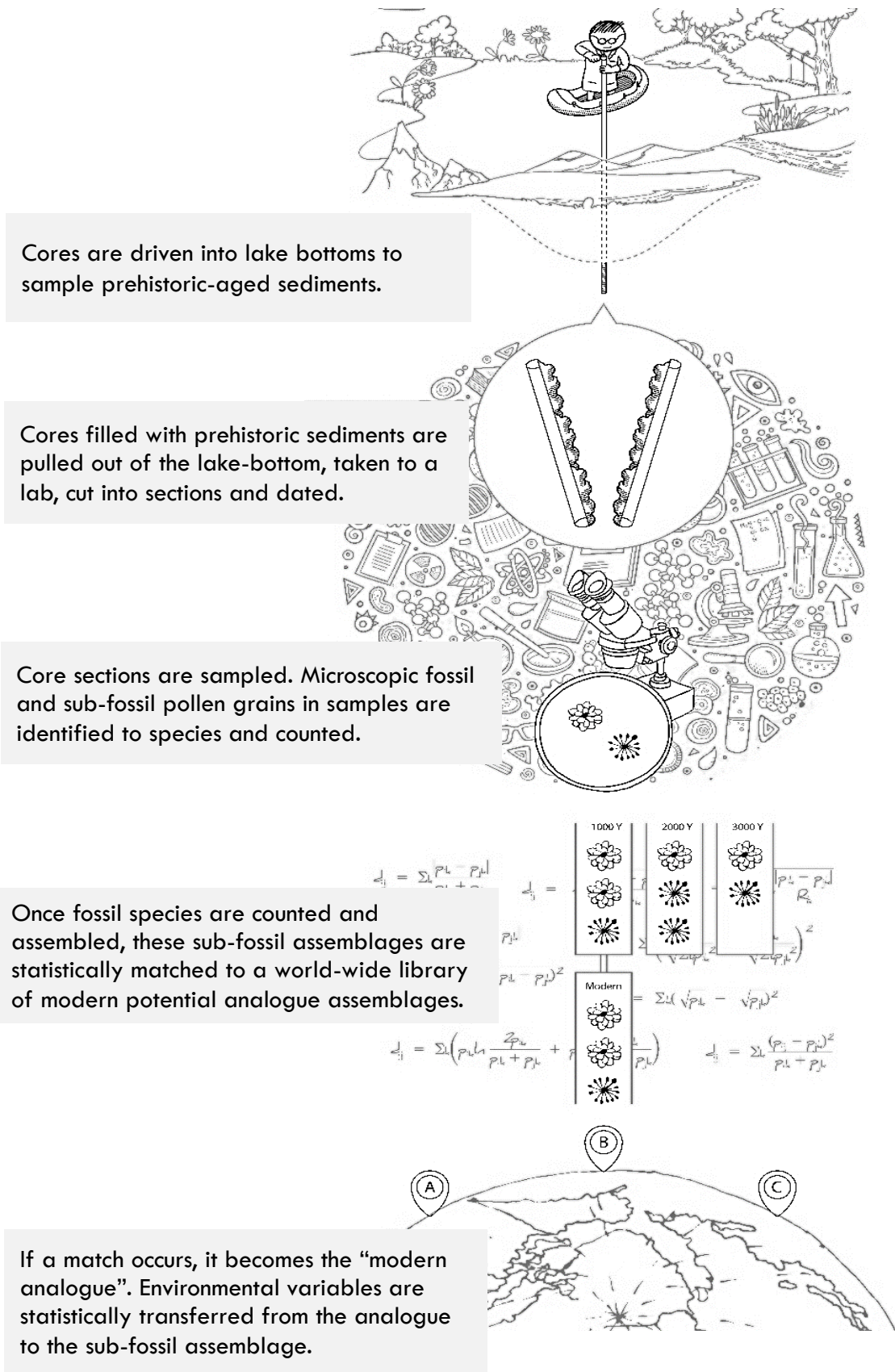


Figure 3.1. Diagram of the process behind the modern analogue technique (MAT), illustrating its use for pollen-based quantitative paleoenvironmental reconstruction .

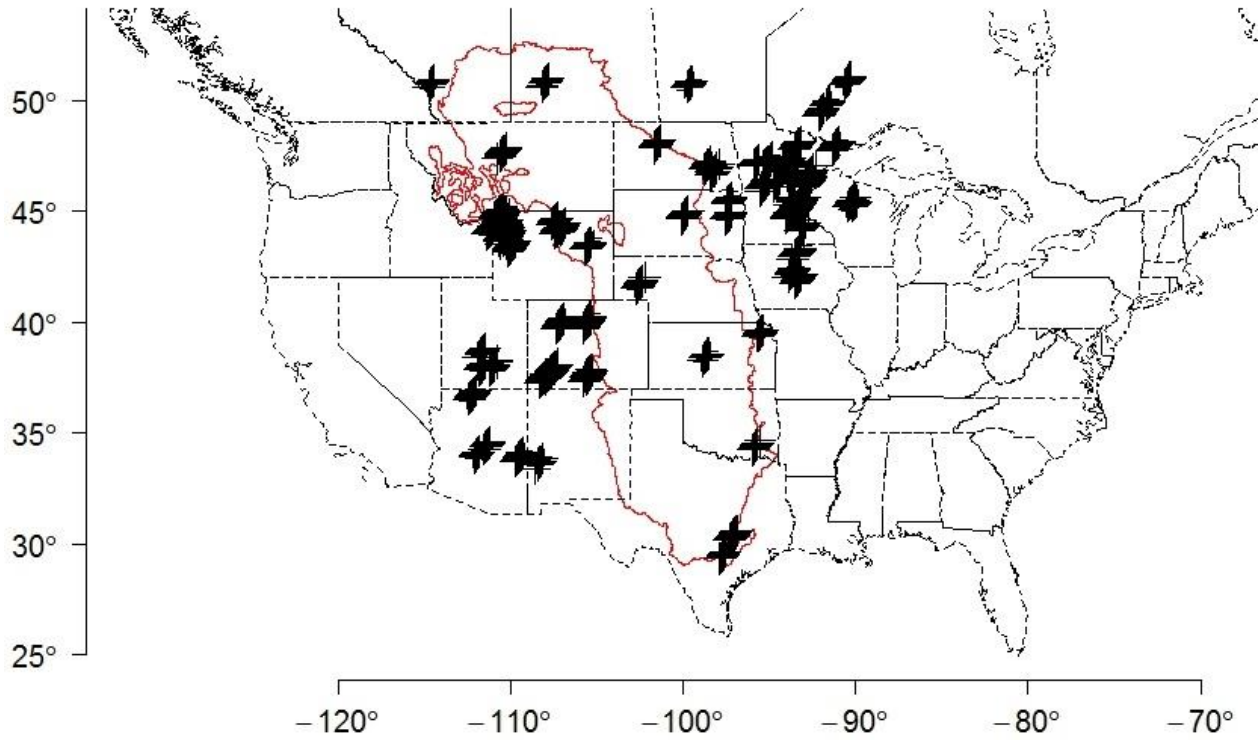


Figure 3.2. Spatial distribution of locations containing paleoenvironmental proxy data (pollen assemblages). Locations have been “jittered” to give a sense of samples across time.

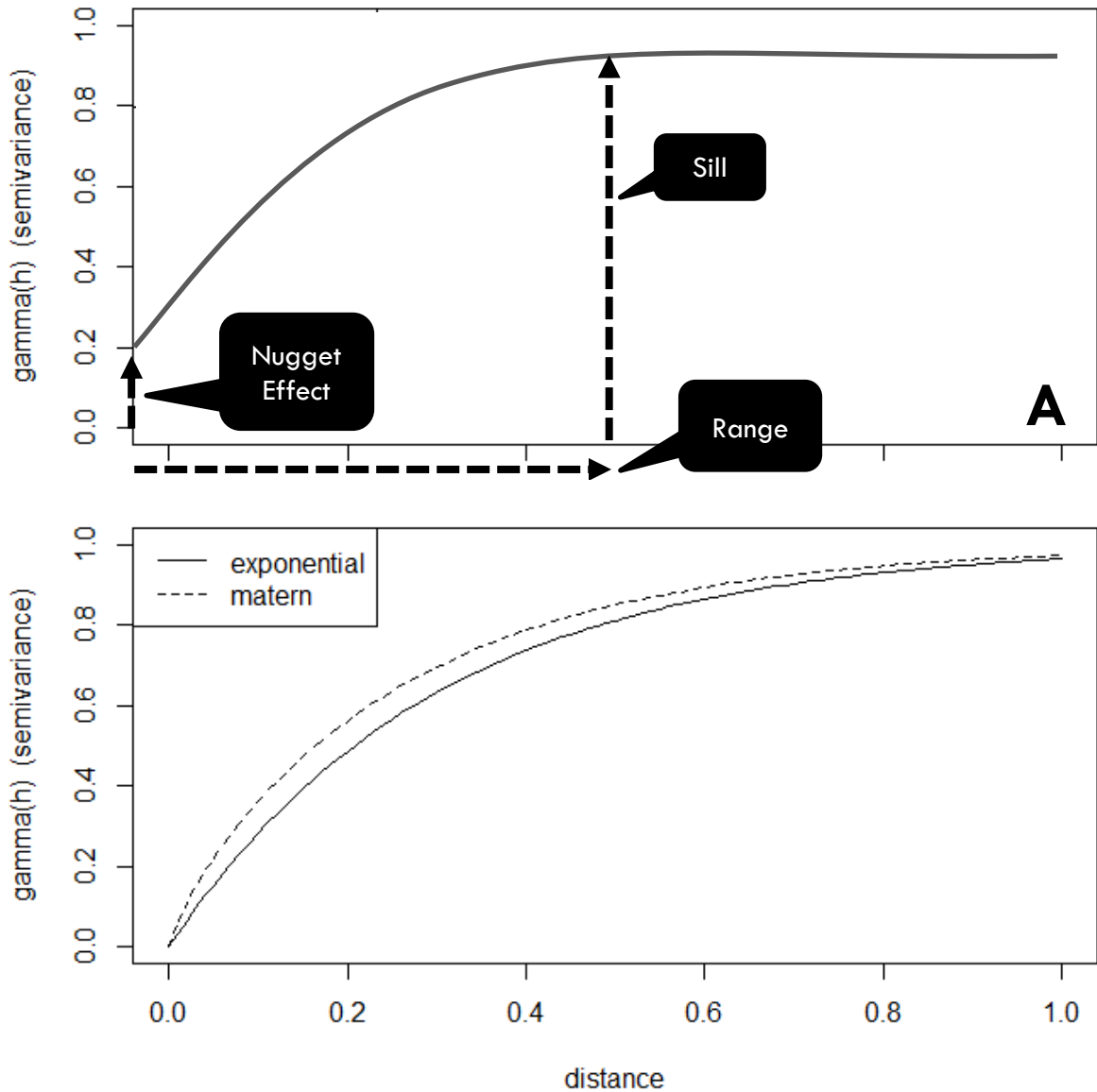


Figure 3.3. Idealized semivariograms. A) anatomy of a semivariogram model representing spatial dependence. The x-axis depicts pairwise distances between samples, while the y-axis shows the “semivariance”, a measure of variability (1/2 of the variance). The implication here is that, as the distance between samples decreases from right to left on the x-axis, their variability decreases on the y-axis, as does the dissimilarity between samples. This is, in effect, an operationalization of Tobler’s first rule of geography: “things closer together are more similar than things farther apart.” The shape of the spatial dependence curve is process-dependent and based on a parametric model. Parameters of the spatial dependence curves are highlighted (nugget, sill, and range). Parameters are usually fit to the data through maximum likelihood or least squares. B) Depicted for example here are the “matern” and “exponential” curves with identical “sill” and “range” parameters, but different “kappa” smoothing parameters.

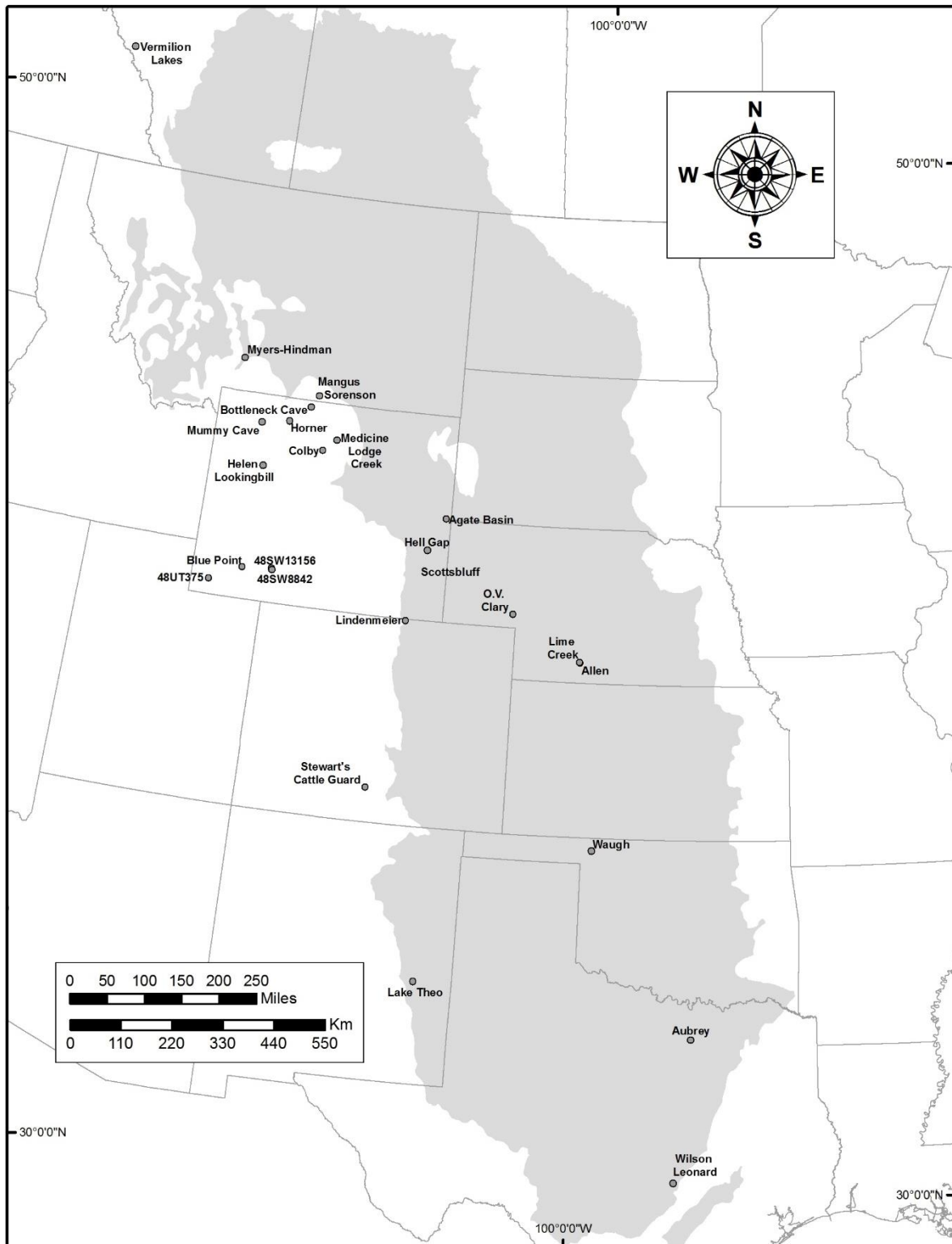


Figure 3.4. Geographic distribution of archaeological sites discussed in this chapter.

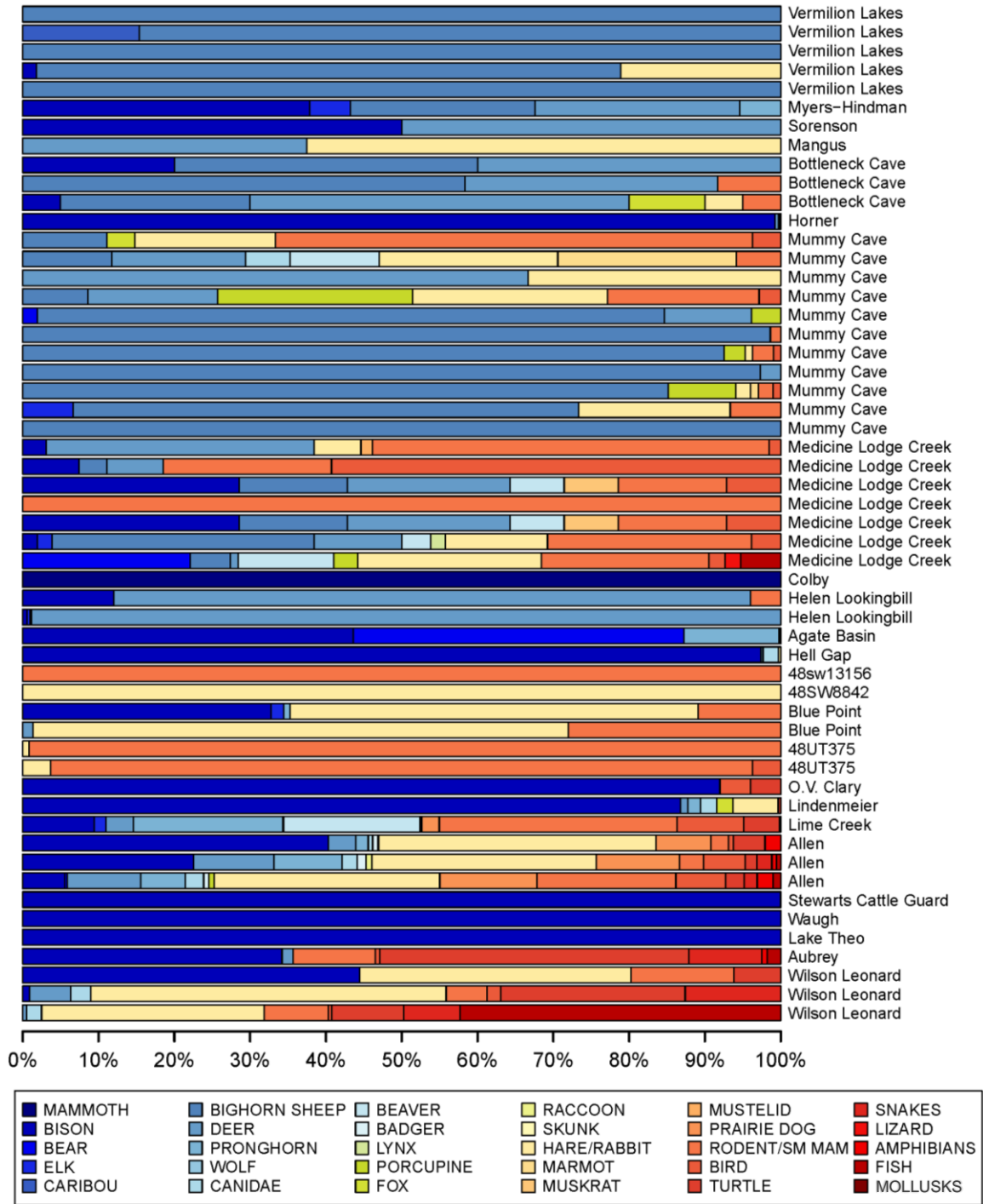


Figure 3.5. Illustration of percentage distributions of cultural fauna by component/site used in this study. Archaeological sites are arranged in north-to-south order from top to bottom.

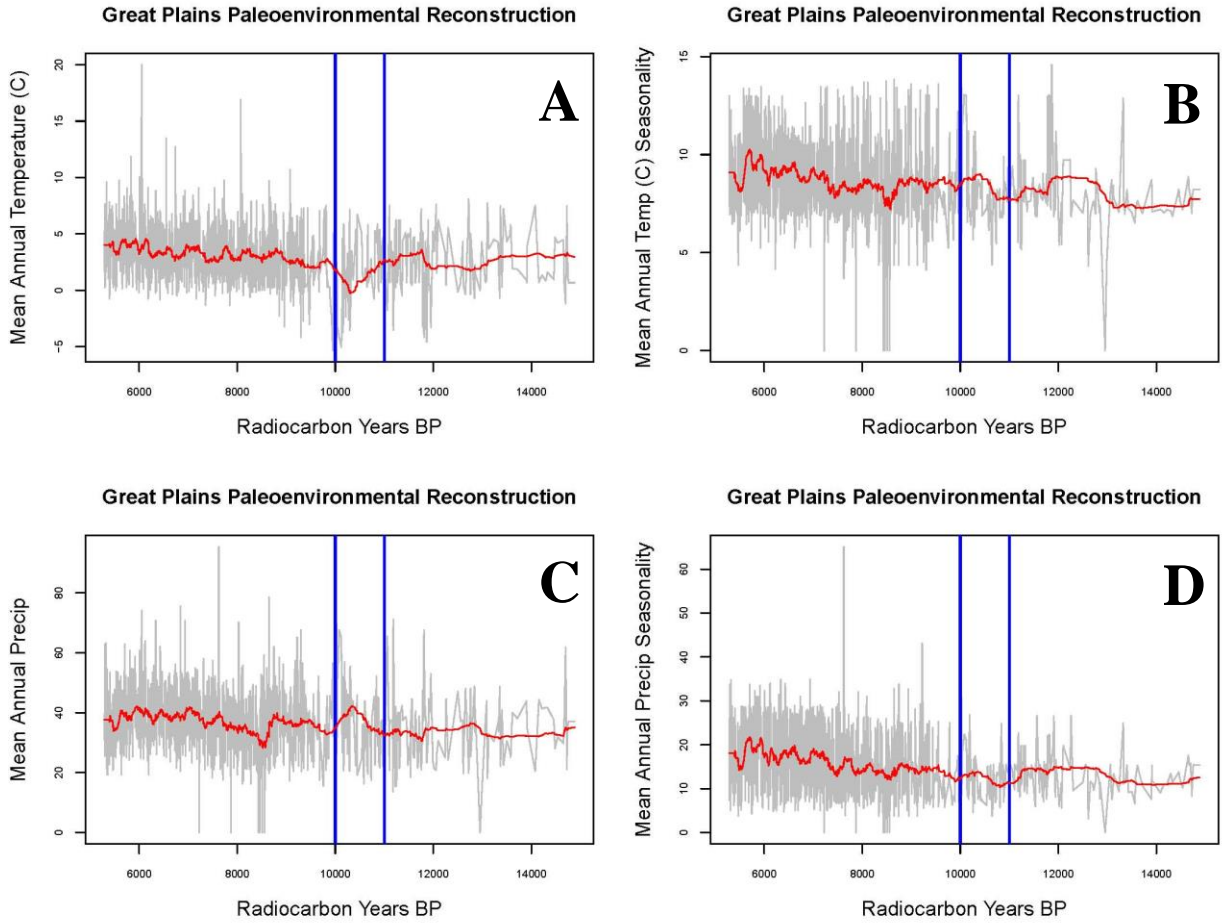


Figure 3.6. Plot of reconstructed Great Plains environmental variables across time between 15,000 and 6,000 years BP. Blue vertical lines denote the span of the Younger Dryas event: A) mean annual temperature, B) standard deviation of mean annual temperature (seasonality), C) mean annual precipitation, and D) standard deviation of mean annual precipitation (seasonality).

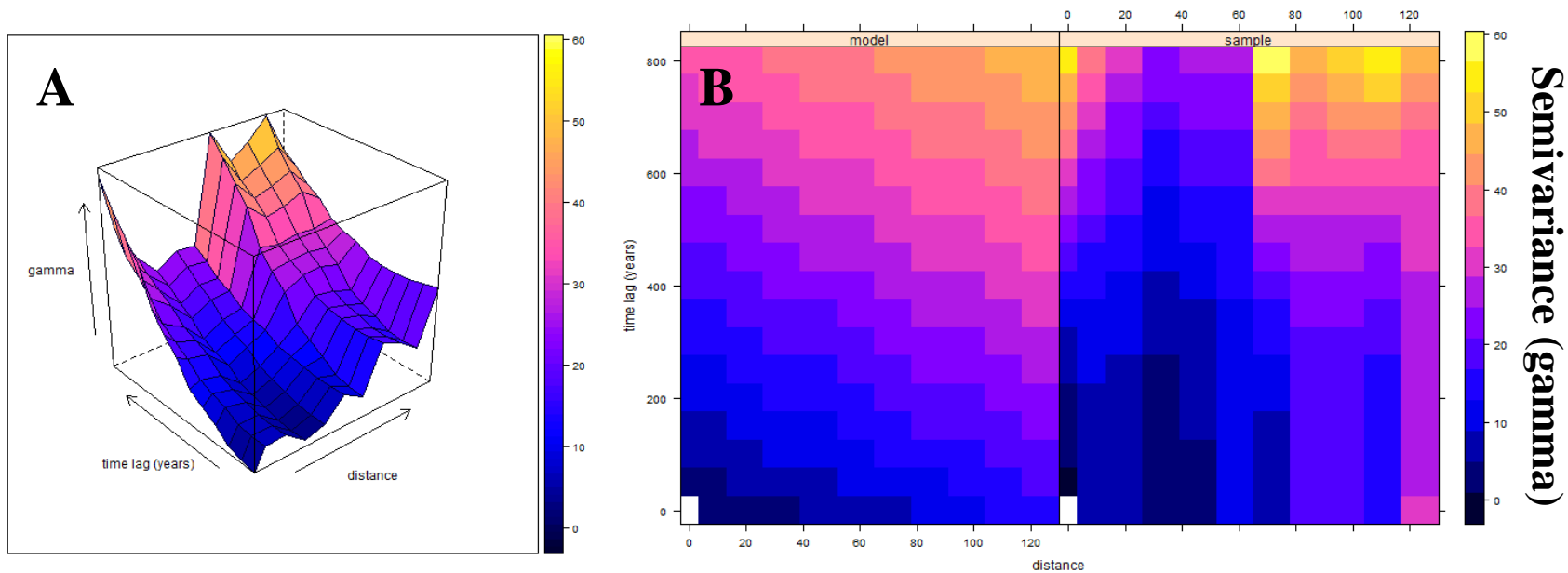


Figure 3.7. Space–time semivariogram: A) 3-dimensional view of empirical semivariogram showing spatial and temporal lags in the x and y axes, while the semivariance (γ) is shown in the z-axis; B) Left: Modeled semivariogram; right: empirical semivariogram; colors illustrate semivariance.

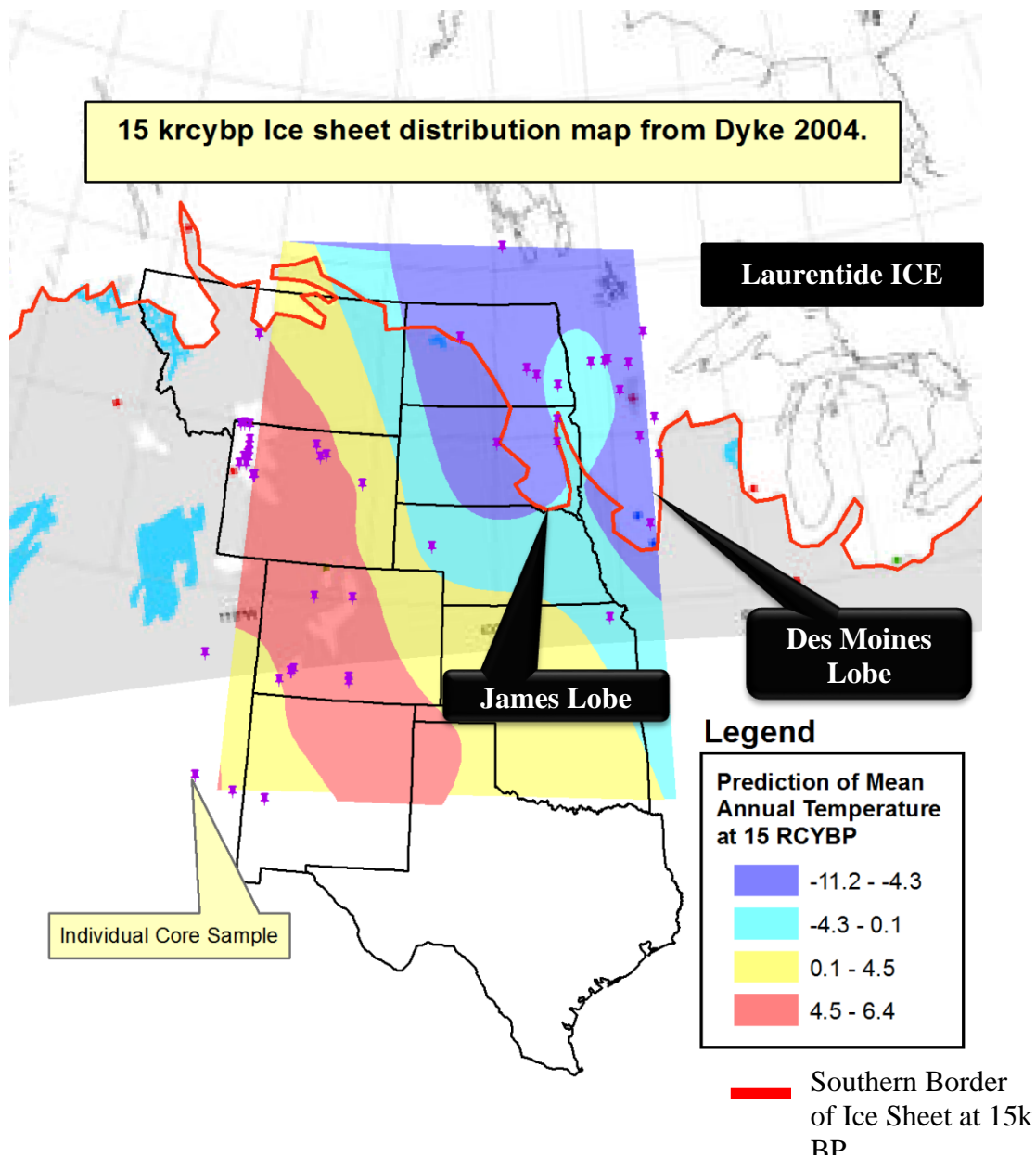


Figure 3.8. Superimposed plots of 1) ice sheet coverage (southern border in red) and 2) a space–time prediction (kriging) map of mean annual temperature, reconstructed from pollen samples. The time period for both maps is 15,000 radiocarbon years before present. The ice sheet distribution map was obtained and digitized from Dyke (2004). The map using primary colors is a prediction map from space-time kriging. Note that the prediction map’s coldest contours correspond to the spatial signal from Dyke’s Des Moines Lobe, James Lobe, and the warm invagination between the two. The two maps were generated using independent sources of information.

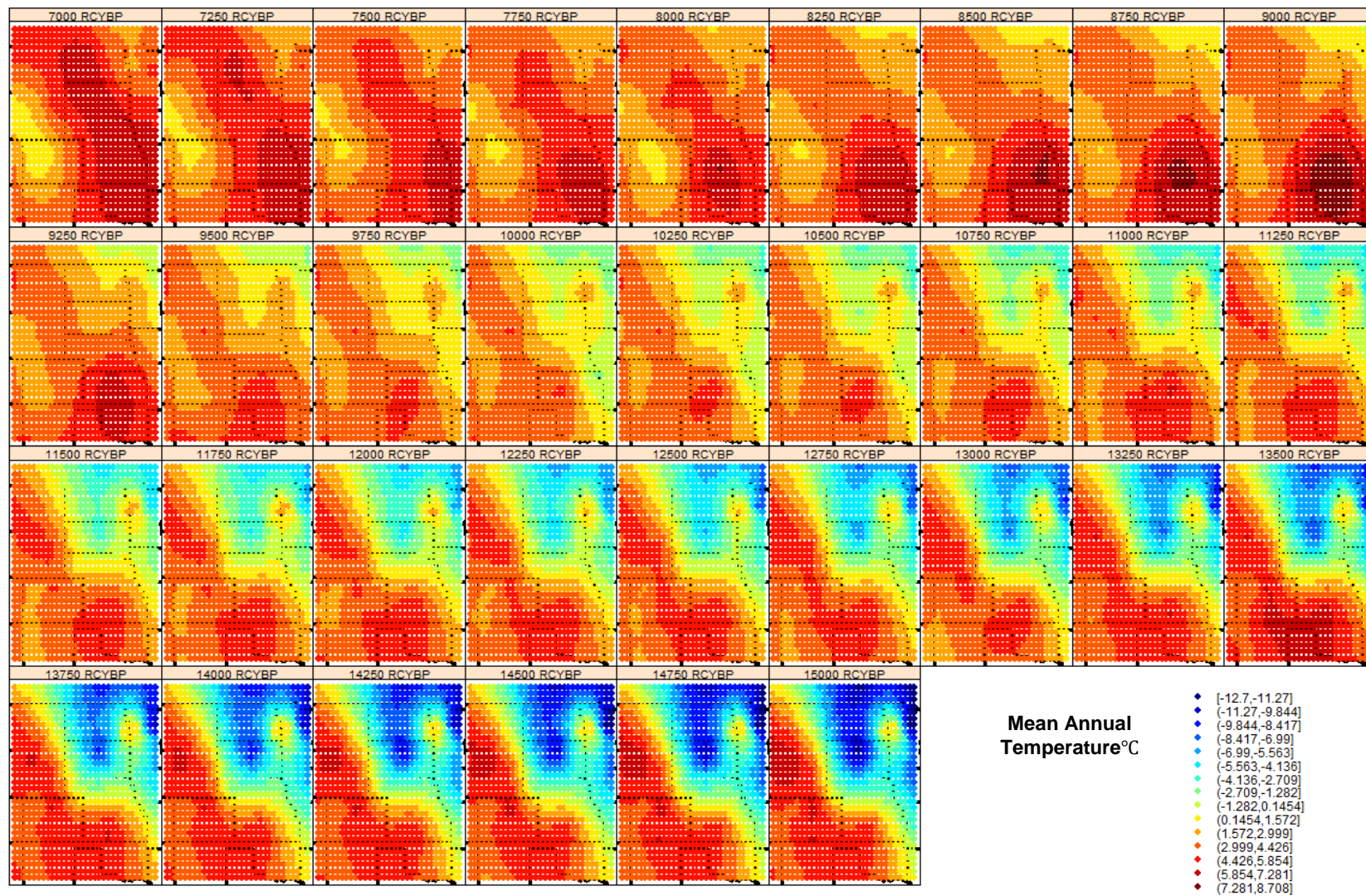


Figure 3.9. Space–time ordinary kriging predictions of mean annual temperatures (degrees centigrade). The temporal range here is between 15 and 7 rcybp (uncalibrated). The outline of the Great Plains states underlies the prediction points.

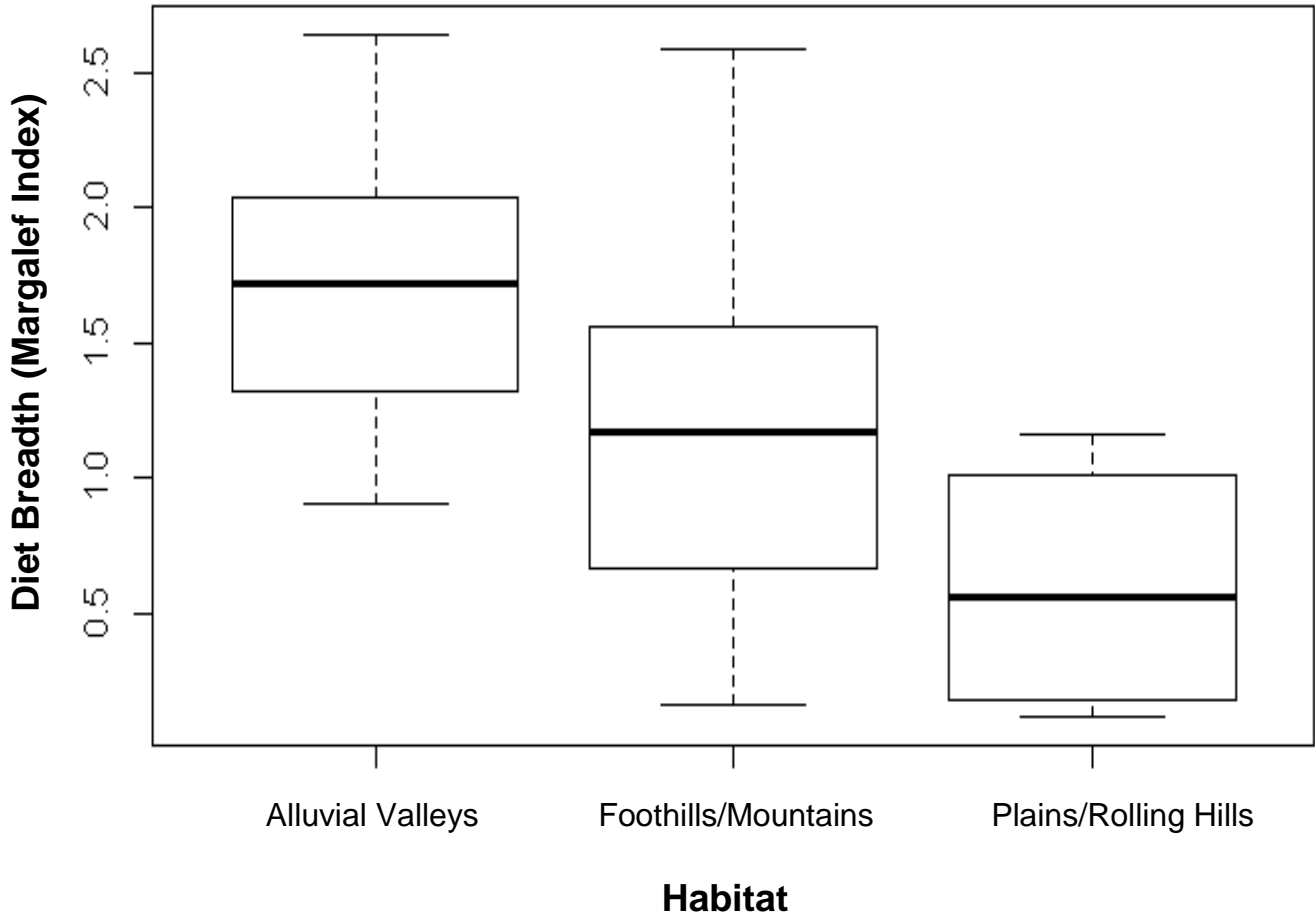


Figure 3.10. Cross-habitat comparison of Paleoindian diet breadth, as measured by the Margalef Index

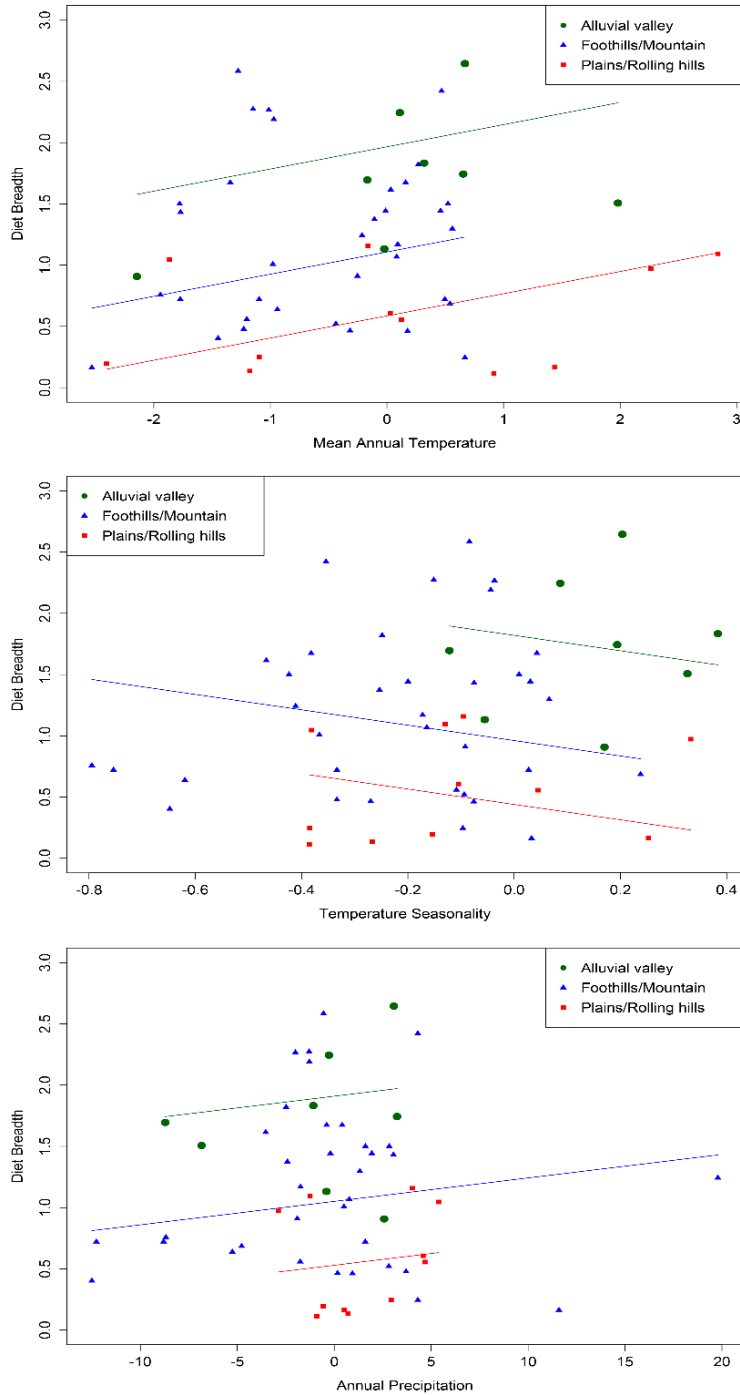


Figure 3.11. Illustration of best model (see Table 3.4 for parameter estimates). Plots show relationships between diet breadth and mean annual temperature (top), temperature seasonality (middle), and annual precipitation (bottom). Legend illustrates the habitat variable. Prediction lines average the diet breadth response to the value of the corresponding predictor variable (labeled on the respective x-axis), while holding all other variables constant at their mean value.

Table 3.1. *Biome-specific threshold values above which 5% or less of distances occur*

Biome	D ≤ 5%
Boreal forest	0.15
Forest-tundra	0.14
Conifer/hardwood	0.25
Deciduous forest	0.33
Prairies	0.23
Arctic	0.21
Coastal	0.29
Mountain vegetation	0.15
Desert	0.18
Mediterranean	0.05
Mean	0.20

Table 3.2. Summary of data from archaeological sites (residential camps) used in this study

<i>SITE</i>	<i>Component</i>	<i>Habitat</i>	<i>State/ Province</i>	<i>Pooled ¹⁴C Date B.P.</i>	<i>Margalef Index</i>	<i>Reference</i>
<i>Bottleneck Cave</i>	III	Foothills/Mountain	WY	8466	1.616	Husted 1969
<i>Sorenson</i>	II	Foothills/Mountain	MT	8525	1.820	Husted 1969
<i>Allen</i>	OL2	Alluvial Valley	NE	8550	2.646	Hudson 2007
<i>Bottleneck Cave</i>	II	Foothills/Mountain	WY	8641	1.170	Husted 1969
<i>48UT375</i>	2	Plains/Rolling Hills	WY	8723	0.607	Smith et al. 2003
<i>Mummy Cave</i>	Layer 13	Foothills/Mountain	WY	8853	0.721	Hughes 2003
<i>Bottleneck Cave</i>	I	Foothills/Mountain	WY	8853	1.674	Husted 1969
<i>Mummy Cave</i>	Layer 14	Foothills/Mountain	WY	8872	1.443	Hughes 2003
<i>Mummy Cave</i>	Layer 12	Foothills/Mountain	WY	9011	1.297	Hughes 2003
<i>Mummy Cave</i>	Layer 11	Foothills/Mountain	WY	9102	0.462	Hughes 2003
<i>Blue Point</i>	2	Plains/Rolling Hills	WY	9106	1.158	Johnson and Pastor 2003
<i>Medicine Lodge Creek</i>	Fire Pit Level	Foothills/Mountain	WY	9181	2.191	Walker 1975
<i>Mummy Cave</i>	Layer 10	Foothills/Mountain	WY	9187	1.068	Hughes 2003
<i>Medicine Lodge Creek</i>	Pryor Stemmed	Foothills/Mountain	WY	9210	2.267	Walker 1975
<i>Mummy Cave</i>	Layer 9	Foothills/Mountain	WY	9294	0.465	Hughes 2003
<i>Medicine Lodge Creek</i>	N. Paleo (6-ft deep)	Foothills/Mountain	WY	9373	2.274	Walker 1975
<i>48SW8842</i>	5	Plains/Rolling Hills	WY	9380	0.135	Byers et al. 2005
<i>48UT375</i>	1	Plains/Rolling Hills	WY	9444	0.248	Smith et al. 2003
<i>Mummy Cave</i>	Layer 8	Foothills/Mountain	WY	9450	1.007	Hughes 2003
<i>Mummy Cave</i>	Layer 6	Foothills/Mountain	WY	9481	1.674	Hughes 2003
<i>Medicine Lodge Creek</i>	Fish Fauna	Foothills/Mountain	WY	9520	0.558	Walker 1975
<i>Medicine Lodge Creek</i>	N. Paleo	Foothills/Mountain	WY	9632	2.585	Walker 1975
<i>Mangus</i>	I	Foothills/Mountain	MT	9692	0.910	Husted 1969
<i>Helen Lookingbill</i>	Layer 7/9	Foothills/Mountain	WY	9707	0.478	Larson et al. 1995
<i>Mummy Cave</i>	Layer 7	Foothills/Mountain	WY	9747	1.443	Hughes 2003
<i>48sw13156</i>	I	Plains/Rolling Hills	WY	9780	0.195	Byers et al. 2005

Table 3.2. Summary of data from archaeological sites (residential camps) used in this study

<i>SITE</i>	<i>Component</i>	<i>Habitat</i>	<i>State/ Province</i>	<i>Pooled ¹⁴C Date B.P.</i>	<i>Margalef Index</i>	<i>Reference</i>
<i>Hell Gap</i>	IIIs/V-Cody	Foothills/Mountain	WY	9820	0.685	Knell et al. 2009
<i>Horner</i>	I	Foothills/Mountain	WY	9871	0.521	Hill Jr. and Knell 2013
<i>Medicine Lodge Creek</i>	Cody	Foothills/Mountain	WY	9912	1.501	Walker 1975
<i>Myers-Hindman</i>	Unit 1	Foothills/Mountain	MT	10005	1.375	Cannon and Cannon 2004
<i>Lime Creek</i>	Zone I	Alluvial Valley	NE	10329	1.744	Jones 1999
<i>O.V. Clary</i>	Middle	Plains/Rolling Hills	NE	10333	0.556	Hill et al. 2008, 2011
<i>Mummy Cave</i>	Layer 4	Foothills/Mountain	WY	10421	2.422	Hughes 2003
<i>Wilson Leonard</i>	Unit II	Alluvial Valley	TX	10493	1.507	Baker 1998
<i>Allen</i>	IZ	Alluvial Valley	NE	10850	2.245	Hudson 2007
<i>Mummy Cave</i>	Layer 1	Foothills/Mountain	WY	10850	1.501	Hughes 2003
<i>Blue Point (32sw5734)</i>	1	Plains/Rolling Hills	WY	10904	1.046	Johnson and Pastor 2003
<i>Vermilion Lakes</i>	6a	Foothills/Mountain	Alberta	10979	0.721	Fedje et al. 1995
<i>Medicine Lodge Creek</i>	23 ft-deep deer	Foothills/Mountain	WY	11025	1.432	Walker 1975
<i>Wilson Leonard</i>	Upper Unit I	Alluvial Valley	TX	11042	1.695	Baker 1998
<i>Vermilion Lakes</i>	8	Foothills/Mountain	Alberta	11497	0.638	Fedje et al. 1995
<i>Vermilion Lakes</i>	6b	Foothills/Mountain	Alberta	11950	0.721	Fedje et al. 1995
<i>Vermilion Lakes</i>	9a	Foothills/Mountain	Alberta	12174	0.758	Fedje et al. 1995
<i>Waugh</i>	ALL	Plains/Rolling Hills	OK	12301	0.166	Hill and Hofman 1997
<i>Helen Lookingbill</i>	Layer 2/4	Foothills/Mountain	WY	12314	1.243	Larson et al. 1995
<i>Allen</i>	OL1	Alluvial Valley	NE	12400	1.833	Hudson 2007
<i>Lake Theo</i>	Folsom	Plains/Rolling Hills	TX	12412	0.113	Baxevanis 1997
<i>Lindenmeier</i>	Folsom	Plains/Rolling Hills	CO	12469	1.093	Wilmsen and Roberts 1978
<i>Vermilion Lakes</i>	9b	Foothills/Mountain	Alberta	12729	0.402	Fedje et al. 1995
<i>Agate Basin</i>	Area 2-Folsom	Plains/Rolling Hills	WY	12764	0.972	Hill 2001
<i>Cattle Guard</i>	ALL	Foothills/Mountain	CO	12792	0.245	Jodry 1999
<i>Colby</i>	ALL	Foothills/Mountain	WY	12903	0.163	Frison and Todd 1986

Table 3.2. *Summary of data from archaeological sites (residential camps) used in this study*

SITE	Component	Habitat	State/ Province	Pooled ¹⁴C Date B.P.	Margalef Index	Reference
<i>Wilson Leonard</i>	EP Bonebed	Alluvial Valley	TX	13097	0.908	Baker 1998
<i>Aubrey</i>	Camp A and B	Alluvial Valley	TX	13477	1.132	Ferring 2001

Table 3.4. List of the 24 regression models evaluated in this study and their AIC values. Model 24 is best model

ID	AIC	Model and Parameters
1	208.20	Diet Diversity = AnnTempMu + AnnPrecip + Date + AnnTempMu-x-AnnPrecip + AnnTempMu-x-Date + AnnPrecip-x-Date + AnnTempMu-x-AnnPrecip-x-Date
7	173.15	Diet Diversity = AnnTempMu + AnnPrecip + AnnTempSD + AnnPrecipSD + AnnTempMu-x-AnnPrecip + AnnTempMu-x-AnnTempSD + AnnPrecip-x-AnnTempSD + AnnTempMu-x-AnnPrecipSD + AnnPrecip-x-AnnPrecipSD + AnnTempSD-x-AnnPrecipSD + AnnTempMu-x-AnnPrecip-x-AnnTempSD + AnnTempMu-x-AnnPrecip-x-AnnPrecipSD + AnnTempMu-x-AnnTempSD-x-AnnPrecipSD + AnnPrecip-x-AnnTempSD-x-AnnPrecipSD + AnnTempMu-x-AnnPrecip-x-AnnTempSD-x-AnnPrecipSD
8	115.94	Diet Diversity = AnnTempMu + AnnPrecip + AnnTempSD + AnnPrecipSD + Date + AnnTempMu-x-AnnPrecip + AnnTempMu-x-AnnTempSD + AnnPrecip-x-AnnTempSD + AnnTempMu-x-AnnPrecipSD + AnnPrecip-x-AnnPrecipSD + AnnTempSD-x-AnnPrecipSD + AnnTempMu-x-AnnPrecip-x-AnnTempSD + AnnTempMu-x-AnnPrecip-x-AnnPrecipSD + AnnTempMu-x-AnnTempSD-x-AnnPrecipSD + AnnPrecip-x-AnnTempSD-x-AnnPrecipSD + AnnTempMu-x-AnnPrecip-x-AnnTempSD-x-AnnPrecipSD
11	115.06	Diet Diversity = AnnTempMu + AnnPrecip + AnnTempSD + AnnPrecipSD + AnnTempMu-x-AnnPrecip + AnnPrecip-x-AnnTempSD + AnnTempMu-x-AnnPrecipSD
12	114.91	Diet Diversity = AnnTempMu + AnnPrecip + AnnTempSD + AnnPrecipSD + AnnPrecip-x-AnnTempSD + AnnTempMu-x-AnnPrecipSD
14	114.19	Diet Diversity = AnnTempMu + AnnPrecip + AnnTempSD + AnnPrecipSD + Date + AnnPrecip-x-AnnTempSD
13	113.25	Diet Diversity = AnnTempMu + AnnPrecip + AnnTempSD + AnnPrecipSD + AnnPrecip-x-AnnTempSD
10	113.16	Diet Diversity = AnnTempMu + AnnPrecip + AnnPrecipSD + AnnTempMu-x-AnnPrecip + AnnTempMu-x-AnnPrecipSD
15	112.87	Diet Diversity = AnnTempMu + AnnPrecip + AnnTempSD + AnnPrecipSD + Date
2	111.89	Diet Diversity = AnnTempMu + AnnPrecip + Date + AnnTempMu-x-AnnPrecip + AnnTempMu-x-Date
9	111.80	Diet Diversity = AnnTempMu + AnnPrecip + AnnTempSD + AnnTempMu-x-AnnPrecip + AnnPrecip-x-AnnTempSD
4	110.59	Diet Diversity = AnnTempMu + AnnPrecip + Date + AnnTempMu-x-AnnPrecip
19	110.59	Diet Diversity = AnnPrecip
20	110.58	Diet Diversity = AnnTempSD
3	110.19	Diet Diversity = AnnTempMu + AnnPrecip + Date + AnnTempMu-x-AnnPrecip + AnnPrecip-x-Date

Table 3.4. List of the 24 regression models evaluated in this study and their AIC values. Model 24 is best model

ID	AIC	Model and Parameters
6	110.08	Diet Diversity = AnnTempMu + AnnPrecip + Date
5	109.97	Diet Diversity = AnnTempMu + AnnPrecip + AnnTempMu-x-AnnPrecip
18	109.48	Diet Diversity = AnnPrecipSD
16	108.97	Diet Diversity = Date
17	107.77	Diet Diversity = AnnTempMu
21	100.10	Diet Diversity = Habitat
23	99.30	Diet Diversity = AnnTempMu + Date + Habitat + AnnTempMu-x-Habitat + AnnTempMu-x-Habitat
22	97.15	Diet Diversity = Date + Habitat
24	96.42	Diet Diversity = AnnTempMu + AnnTempSD + AnnPrecip + Date + Habitat

Table 3.5. *Parameter estimates of best model*

Effect	Estimate (β)	SE
Intercept	3.27	0.737
Mean Annual Temperature	0.191	0.080
Annual Precipitation	0.017	0.017
S.D. of Mean Annual Temperature (Seasonality)	-0.677	0.395
Time	-0.00014	0.00006
Plains/Rolling hills	-1.33	0.321
Foothills/Mountains	-0.83	0.313

**CHAPTER 4. HOW DID SPATIO-TEMPORAL BISON
ABUNDANCE AND DISTRIBUTION AFFECT THE HUNTING
STRATEGIES OF PALEOINDIAN FORAGERS?**

A Model of Grass Biomass Concentration as a Proxy Measure for Bison
Carrying Capacity across the North American Great Plains during the
Modern and Paleoindian Periods

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~6,966 words, 2 tables, 9 figures

Chapter Overview

Chapter 3 presented a study using pollen assemblages from across the North American Great Plains to reconstruct multiple paleoenvironmental variables in order to test current hypotheses regarding the climatic influence on Paleoindian dietary strategies. In reconciling such hypotheses, the results of the study enrich the understanding of Paleoindian foraging and subsistence within the context of paleoenvironmental and nutritional resource reconstruction. This chapter applies those paleoenvironmental reconstructions along with estimates of bison carrying capacity to further test hypotheses related to Paleoindian foraging behavior in the context of explaining the variability of bison killsites across the Great Plains.

In North America, the foraging behavior of Paleoindian hunters and gatherers, particularly big-game hunters across the Great Plains grasslands, has been a topic of study for well over a century. Researchers have investigated several predator responses to prey abundance; however, quantitative studies linking Paleoindian predator responses to bison prey abundance have been nonexistent. This study bridges this knowledge gap by using several quantitative methods to reconstruct a baseline of Paleoindian bison prey availability and to test hypotheses related to the relationship between Paleoindian predators and bison as their prey. The study focuses on hypotheses generated from traditional research on Paleoindian hunting and derived from foraging theory; in particular, it addresses those hypotheses explaining the well-known latitudinal pattern of increasing bison abundance that has been observed in Great Plains bison kills of Paleoindian age. Paleoenvironmental reconstructions and carrying capacity estimates challenge the assumption that, during the Paleoindian period, bison were more abundant in the northern Great Plains than in the

southern Great Plains. Rather, in accordance with foraging theory, the observed latitudinal abundance pattern was more likely the result of variations in Paleoindian foraging behavior in response to the time between bison herd encounters.

Introduction

Homo sapiens occupy a general and flexible foraging niche. The ability to successfully obtain nutritional resources has undoubtedly enabled our species to disperse and thrive in a diverse range of habitats. Natural selection and other evolutionary forces (e.g., sexual selection, genetic drift, gene flow, and cultural selection) have likely shaped the observed diversity and plasticity of human foraging. Therefore, the study of human foraging, in its many expressions, is pivotal to our understanding of the proximate (mechanistic) and ultimate (evolutionary) causes that have shaped human evolutionary history.

In North America, the foraging behavior of Paleoindian hunters and gatherers has been a topic of study for close to a century. Researchers initially focused on finding a connection between “early man” weaponry and North American Pleistocene fauna (see Meltzer 2006, 2009). The discovery of the Folsom site in New Mexico revealed such a connection and answered the question of whether people lived in North America during the Pleistocene; it also likely encouraged archaeologists to start thinking about the foraging and subsistence activities of Paleoindians.

Kelly and Todd’s (1988) model of Paleoindian settlement and subsistence has been the principal explanatory framework for Paleoindian foraging behavior (KT model from here on). Over the past 20 years, there has been general agreement, however, that the predictions drawn from the KT model offer a better depiction of the initial colonization of North America and the early Paleoindian period than of later Paleoindian times (e.g., Bamforth 2002b, 2011). Many of the KT model’s predictions have been explored, and many aspects have been supported. For example, more recent research on the regional

variability of early Paleoindian projectile point technology (Buchanan and Collard 2007; Buchanan and Hamilton 2009) has continued to support the hypothesis of the frequent shifts in range of Paleoindian groups (Kelly and Todd 1988: 234). Additionally, evidence of increasingly future-oriented subsistence behavior in the face of increased seasonality, as proposed by the KT model (Kelly and Todd 1988: 240), has emerged from several Late Paleoindian sites (Hill 2001, 2008).

At the same time, several of the KT model's predictions appear to have been refuted. For example, more recent investigations (Bamforth 2002b) have found that the characterization of Paleoindians' heavy reliance on "high-tech" bifacial lithic technology (Kelly and Todd 1988: 237) is inaccurate for later Paleoindian groups. Furthermore, whereas the KT model described Paleoindian groups as having "little emphasis on place" (Kelly and Todd 1988: 239), more contemporary research has begun to demonstrate that, in some contexts, Paleoindians seemed to follow a more "place-oriented" subsistence strategy than previously hypothesized (Bamforth et al. 2005; LaBelle 2005; Hill Jr. 2007, 2008). The KT model also emphasized the use of terrestrial animal prey as the focus of Paleoindian subsistence (Kelly and Todd 1988: 234), yet whether Paleoindian hunters were megafauna specialists (e.g., Hofman and Todd 2001) and even the extent to which they hunted megafauna remain debatable questions (Grayson and Meltzer 2003, 2004; Surovell and Waguespack 2008; Faith and Surovell 2009).

Although current research on Paleoindian subsistence behavior, particularly their hunting strategies, is yielding new, more nuanced hypotheses on this topic, these hypotheses are not necessarily in agreement with one another. For example, some researchers argue that, despite the abundant evidence for bison hunting, this large herbivore

was probably not an important part of the Paleoindian diet (Kornfeld 2007; Kornfeld and Larson 2008); rather, smaller game was the emphasis of the Great Plains Paleoindian foragers' diet. Researchers tend to agree that an emphasis on smaller game as part of the Paleoindian diet existed and increased over time. Some have proposed that this increasing consumption of small game was these people's response to the climatic changes and environmental reorganization observed across the Late-Pleistocene–Holocene transition (Hill Jr. 2007, 2008). Meanwhile, others have argued that the apparent emphasis on smaller game is merely perceived (Bamforth et al. 2005; LaBelle 2005); instead, the variability in the abundance of smaller game in the Paleoindian diet has been explained according to the location of Paleoindian camps relative to landscape productivity. In other words, in highly diverse environments, the Paleoindian diet became more diversified accordingly. Although these hypotheses are not necessarily mutually exclusive, they explain an observed phenomenon through fundamentally different mechanisms.

The variability and potentially conflicting nature of these conclusions likely stems from the broad variability of the available data. Paleoindian foraging strategies were most likely neither static nor monolithic across the geographic extent of the North American Great Plains. Over time, these strategies were probably expressed somewhat like a “reaction norm” according to variations in seasonal and long-term climatic contexts across a broad spatial and temporal ecological gradient. In other words, the factors that affected the abundance and distribution of key resources shaped the organization of hunter-gatherer subsistence and settlement strategies.

Unfortunately, there is a lack of quantitative and spatially explicit knowledge regarding the abundance and distribution of food resources, particularly bison, during the

Paleoindian period. Current knowledge of prehistoric bison abundance in the Great Plains is generally based on historical and ethnographic descriptions, rather than on measurable and testable hypotheses (e.g., Roe 1951; Lott 2002). This is particularly problematic in the context of making inferences regarding Great Plains Paleoindian foraging behavior. Even though bison was a staple food source for historical foragers (Roe 1951) and it is a ubiquitous prey animal across Paleoindian archaeofaunal assemblages (Figure 4.1), model-based inferences of bison paleo-distribution and abundance have been lacking. This dearth of knowledge has hindered researchers' ability to test hypotheses regarding Paleoindian bison hunting.

The purpose of this study is to fill this knowledge gap by quantitatively modeling a proxy measure for bison carrying capacity across the North American Great Plains during the Paleoindian period in order to test various hypotheses related to Paleoindian bison predation. In particular, this analysis tests the hypothesis that the greater archaeological abundance of bison observed in the northern Great Plains compared to the southern Plains (Figure 4.2) is a function of the greater emphasis on bison hunting in the north due to more favorable ecological conditions to sustain bison (Bamforth 1988, 2011).

Studies have shown that it is possible to reliably and verifiably estimate bison abundance at small scales across the Great Plains (e.g., Flores 1991). Researchers can derive biologically informed estimates of prehistoric bison distribution by employing a combination of models related to bison's evolutionary history in North America (e.g., Mack and Thompson 1982; Axelrod 1985; Anderson 2006), theoretical models, and empirical results related to ungulate foraging preferences in terms of forage quality and

quantity (e.g., McNaughton 1984, 1988; Fryxell 1991; Wallis De Vries 1996; Fortin et al. 2002; Fortin et al. 2003; Fryxell et al. 2004).

These ungulate foraging and distribution models suggest that it can be misleading to use only total forage production as a proxy for carrying capacity, as Great Plains Paleoindian research has assumed (e.g., Bamforth 1988: 61). This is because if the physiological characteristics and evolutionary history of grass species (e.g., defense mechanisms, compensation, and herbivore coevolution) are not considered, total forage production might not track the net amount of edible quantities available. Therefore, this study integrates theoretical and experimental studies of herbivore/plant dynamics and grazing optimization to develop a general, biologically informed model of potential forage production and bison carrying capacity.

Background

Great Plains, grasslands productivity studies, and grazing optimization

The expansion of the North American Great Plains grasslands occurred approximately 5–7 million years ago. This shift was occasioned by an increase in climatic aridity during the Miocene–Pliocene transition, an increased abundance of grasses using the C₄ photosynthetic pathway, a decline in woodlands, and the coevolution of mammals adapted to grazing and open habitats (Mack and Thompson 1982; Axelrod 1985; Anderson 2006). These factors shaped the composition of the Great Plains grasslands' biological communities and their individual organismal characteristics. In particular, the coevolution of large mammal grazers and primary producers (grasses) appears to have resulted in benefits to both.

Among the most obvious benefits of this grazer–grass coevolution are that grazers gain necessary energy and nutrients, while grass productivity increases through the constant clipping of older, less productive tissue, thereby improving light, moisture, and photosynthetic activity (Grime 1973; McNaughton 1979, 1984). Moreover, large mammal grazing has positive effects on grass seedling survival (Lawson et al. 2004), seed dispersal (Ellison 1960), the ability to compete against dominant tall grasses (Knapp et al. 1999), and the acquisition of nutrients such as nitrogen (McNaughton 1984; Knapp et al. 1999).

In his studies of African Savanna herbivore/plant dynamics and grazing optimization, McNaughton (1976) reported an inverse relationship between grass heights and total edible portions. During controlled field experiments, McNaughton observed that while grazed grasses appeared to be reduced in height by grazing, this process resulted in higher biomass concentrations and thus higher food yields per mouthful for herbivores. McNaughton (1984: 872) further observed and estimated biomass concentration or density as a function of grass height (cm), measured in terms of milligrams divided by cubic centimeters. This model establishes a relationship between grass height and its biomass concentration (Figure 4.3). According to this model, habitats with shorter grasses and higher grass biomass concentration (GBC), which have evolved alongside herbivory, should support a greater number of herbivores than their taller ungrazed counterparts.

As McNaughton observed (1976, 1984: 868–870, Figure 2 therein), habitats with shorter grass canopy height (~5cm tall on average) and greater GBC are indeed more capable of supporting higher herbivore population densities. This finding suggests that GBC is a very useful indicator of herbivore carrying capacity, as increases in GBC also improve the per capita forage mass yield per bite within a range of herbivore population

densities (e.g., Ludlow et al. 1982: 197) and the grasses' quick recovery due to grass grazing response (McNaughton 1976). Grasses compensate for the removal of tissue under intermediate grazing regimes by producing optimum yields of above-ground net primary productivity (ANPP) and biomass concentration (mg/cc; e.g., Dyer 1975; Grime 1973; McNaughton 1979, 1983, 1984; Hilbert et al. 1981; McNaughton and Georgiadis 1986). In turn, the increase in above-ground biomass concentration after clipping encourages grazing herds to continually return to feed in such patches. The higher GBC increases the herd's instantaneous intake rate (Bergman et al. 2000) and reduces the time spent grazing. For this model to be supported, this phenomenon should be independently observed in other grassland landscapes that have similarly coevolved with herbivory.

Researchers have also observed increased grass productivity under bison grazing under experimental conditions in the grasslands of the North American Great Plains (Bouteloua province), which have a deep evolutionary history of large grazers (e.g., Frank and McNaughton 1993; Frank et al. 1998; Frank et al. 2002; Schoenecker 2012). Field experiments have found that grazed grasslands yield greater above-ground productivity than ungrazed controls (~50%, see Frank and McNaughton 1993), suggesting that there is active selection for functional and morphological traits associated with grazing by modern, large herbivores. Bison, for example, maximize their instantaneous intake rate (Bergman et al. 2000; Babin et al. 2011) through their preference for shorter grasses with higher biomass yields. Foraging on these types of grasses accounts for approximately 90% of their foraging time (Bergman et al. 2000). In the grasslands of Yellowstone Park, endemic ungulate migration patterns reveal herds engaging in short periods of intense grazing before moving on to graze higher quality forage (Frank and McNaughton 1992). This behavior

appears to follow the logic of grazing optimization whereby short-duration feeding prevents overgrazing, while herd migration allows a time lag for the grazed grasses to recover (Frank et al. 1998). These patterns indicate that the morphological attributes of such grasses, coupled with experimental results, can be used to track GBC and thus grazing potential (absolute and/or relative) across the Great Plains.

Current hypotheses of Paleoindian foraging

In this study, GBC is used as a proxy for bison carrying capacity to test various hypotheses regarding Paleoindian hunter-gatherer foraging behavior, mainly in terms of the predator-prey relationship with bison. Bamforth (1988: 65) linked bison abundance to a northeast-to-southwest decreasing-gradient model of forage production (grass lbs./acre), proposing that bison would have been more abundant in the north than in the south. Using archaeological evidence, Bamforth found that the southern Great Plains' archaeological bison kill sites contained fewer numbers of bison killed than their counterparts to the north. He hypothesized that this was a direct result of differences in bison carrying capacities between the southern and northern Great Plains. This hypothesis can be independently evaluated using the proxy for bison carrying capacity proposed in this study. Bamforth's hypothesis can be partitioned into two derived null hypotheses, as correlates of this model:

Ho1: Due to higher carrying capacity, Paleoindian hunters encountered bison herds more frequently in the northern Great Plains than in the southern Great Plains.

Ho2: The greater frequency of bison herd encounters in the northern Great Plains facilitated larger scale bison hunting compared to the southern Great Plains.

Expectations from foraging theory

To provide alternative explanatory hypotheses, this study turns to predictions from behavioral ecology and foraging theory. Optimal Foraging Theory is a body of models developed to generate optimal expectations of organisms faced with energetic cost/benefit tradeoffs when searching for, selecting, and consuming prey. The logic behind these models is centered on the increase of an individual forager's fitness when foraging, as it maximizes the net rate of energy intake over the long-term time average (e.g., Charnov and Orians 1973; Stephens and Krebs 1986). There are two major types of foraging models: prey models and patch models (e.g., MacArthur and Pianka 1966). Prey models focus on the predator's decision to either attack a given prey or continue to search in order to maximize the long-term average. On the other hand, patch models are concerned with the forager's decision of when it is most profitable to stop foraging a given resource patch and leave in search of another.

In habitats where foods might be distributed as discrete clumps or patches (akin to bison herds), the Marginal Value Theorem (MVT; Charnov 1976) provides an optimal solution for the length of time after which a forager should leave a patch in favor of another. Here, again, the assumption is that a forager increases its fitness during a foraging event (or foraging bout) by maximizing the net rate of energy intake over the long-term time average. The net rate of energy intake is defined as the amount of energy a forager gains per unit of time when harvesting a patch, accounting for the amount of energy spent and the average time between patch encounters in the habitat. An additional assumption is that the predator depresses the patch-specific intake rate as a function of the time spent foraging (Charnov et al. 1976). The optimal time to leave the patch, and thus the expected time a

forager should stop harvesting, is the point at which the patch-specific net intake rate drops to the average intake rate for the habitat. This occurs when the net rate of energy intake, R , is maximized with respect to the time spent in the patch.

The net energy intake rate (R) is given by:

$$R = \frac{\sum P_i \times g_i(T_i) - t \times E_t}{t + \sum P_i \times T_i} \quad (1)$$

Where,

P_i = the proportion of foraged patches of type i ($i = 1, 2... k$).

t = the interpatch travel time (a measure of patch density)

E_t = the energy cost per unit time spent when traveling between patches

E_{si} = the energy cost per unit time spent when searching in patch type i

T_i = time in patch

$h_i(T_i)$ = the cumulative energy gained from foraging for a time length T , within the i^{th} patch type, subtracting all foraging energetic costs except for the search cost

$g_i(T_i) = h_i(T_i) - E_{si} \times T_i$ = the cumulative energy corrected for the cost of searching

Here, the gross average cumulative caloric intake rate $\sum P_i \times g_i(T_i)$ is discounted by $t \times E_t$ (the amount of calories spent traveling between patches) and divided by the average interpatch travel time t plus the cumulative average time spent in the patch, $\sum P_i \times T_i$. Analytically, the predator should leave the patch in which it is presently foraging when the marginal capture rate in the patch ($g_i(T_i) / T_i$) drops to the average capture rate for all patches. This occurs when the net rate of energy intake R is maximized with respect to the time spent in the patch (T_i). This can be solved by setting the partial derivative $\frac{\delta R}{\delta T_i} = 0$.

A model parameter directly linked to the “stop harvest time” is t , the inter-patch travel time parameter (a measure of patch density). This parameter is quite important, as it represents the average amount of time it takes for a forager to encounter another patch. Holding energetic gain constant, if the average distance between patches, t , increases, as would be the case when the patch encounter rate decreases, equation 1 shows that the value of the numerator decreases while the denominator increases. This results in a lower net energy intake rate. In this case, to maintain an optimal payoff, the forager needs to stay in the patch longer in order to maximize R. Conversely, if the average distance between patches decreases, as for example when patch encounter rates increase, the habitat’s intake rate increases; the forager can maximize R sooner and, thus, quits harvesting sooner.

Herds as foraging patches

This study makes the simple assumption that a group of bison functioned as a foraging patch from which Paleoindian hunters harvested energy. This model assumes that Paleoindians probably did not kill individual bison sequentially, one after the other. Rather, once these foragers encountered a bison herd, they could kill multiple bison instantaneously (average number of bison killed per site: lognormal mean and SD = 8.9 and 3.7; data from sites in Table 4.2). However, this study also assumes that due to logistical constraints (e.g., number of available hunters, butchers, distance to camp, etc.), Paleoindians decided on the most profitable number of bison to harvest prior to the kill. This decision influenced approximately when to stop harvesting. It should be clear that although the decision to kill was a decision about the living herd, the actual harvesting of nutrients was done on the animal carcasses. Here, assumptions from the MVT (largely, herd encounter rate) can inform the decision of *how many individual animals to kill* and, therefore, the time when

Paleoindian foragers should quit harvesting individual bison carcasses. As noted above, by determining the number of bison to harvest in this manner, Paleoindians would have already made the decision of when to leave the patch prior to the action of killing the prey.

Following this decision, Paleoindian hunter(s) killed their prey likely using one of several ethnographically documented methods (e.g., Verbicky-Todd 1984). In this model, the necessary patch depression is caused during butchery, a reductive process. When butchering, the density of carcasses available for harvest (individuals or mass per unit area) decreases, while handling time increases. In this process, by butchering, hunters lower the net rate of energetic intake (R) in the current patch as they harvest. The stopping point is highly dependent on the number of herds, and thus the probability of encountering one, as well as the number of individuals in a bison herd.

Bison herd dynamics

In the context of Great Plains Paleoindian foraging, forage quality in a given habitat was probably an influential factor underlying the number of individual bison in a given herd and the rate at which bison herds would have been encountered across space or time. Bison herds are known to intensely feed in one area before moving to adjacent localities where they can find better forage (Frank et al. 2002). In habitats with higher quality forage, herds are assumed to migrate shorter distances to find more suitable forage.

Herd dynamics also affect the size and number of bison herds. In general, living in herds can provide benefits to individual organisms. These include defense from predation, dilution from predation, and ease of finding mates, among others (Wrona and Dixon 1992; Krause and Ruxton 2002). These benefits, however, are also associated with some costs. In groups, competition for food and mates increases, as does the probability of contracting

disease. If groups become overly large, they can also more easily attract the attention of predators. In most situations, an optimal herd size, in which these tradeoffs are balanced, should be preferable. Nevertheless, some have argued that group sizes greater than optimal, i.e., Sibly sizes (Sibly 1983), should be the most frequent because individuals still reap greater benefits in a group than when living alone. Regardless, there should be a maximum group size among organisms living in herds.

In the case of bison, herd sizes tend to be much smaller (e.g., Lott and Minta 1983) than those of African ungulate herds such as buffalo (Sinclair 1977). This discrepancy might be a consequence of population density, as bison population densities per km² are smaller than those of African buffalo (Krause and Ruxton 2002). Nevertheless, ungulate group dynamics predict that as population density increases, as it should in higher quality habitats, group sizes should increase initially until a preferred median group size is reached. After this critical point, however, as population density continues to increase, the number of groups should increase (Krause and Ruxton 2002: 149).

Empirically, Jolly and Messier (2004) compiled historic records of bison group sizes and number of groups as a function of bison population density in the Delta population of Wood Buffalo National Park between 1981 and 1999. Their results showed that, as population density increased, the number of bison groups increased at a much higher rate than the typical bison group size (Jolly and Messier 2004). Their model of this relationship indicated that at population densities of 50 bison, the expected group size was 13, while the expected number of groups was 12 (Figure 4.4). On the other hand, when bison population density increased to 1,000 bison, the expected average group size increased to 42 and the expected number of groups increased to 158. Hypothesis testing

showed these differences to be significant ($X^2 = 11.56$, $p = 0.000673$), indicating that bison group sizes are relatively stable, while the number of bison groups shows a high association with population density and grazing quality. For this study, this finding means that the number of patches (bison herds) in a habitat and, consequently, the patch encounter rate fluctuate in positive association with habitat quality, and that patch size (i.e., the number of bison in a herd) can be held relatively constant.

Qualitative predictions using the MVT help to generate testable hypotheses. For example, as predicted by the MVT, in “poor quality” habitats where Paleoindians would not have encountered bison herds frequently, foragers are expected to have harvested more individual bison prey, staying in the patches for longer periods of time. On the other hand, in “good” habitats where Paleoindians would have encountered bison herds more frequently, human predators are expected to have spent less time in a foraging patch, thus harvesting fewer bison than in a poor habitat.

Archaeologically, this translates into a gradient of a higher number of individual bison procured in poor habitats per foraging trip. This number decreases as herd encounters increase and foragers need not harvest for as long. In addition, if Paleoindian hunter-gatherers’ bison procurement was proportionate to bison natural abundance, the negative relationship between the number of bison harvested and their natural abundance would be linear. Relatively “good” or “bad” habitats for the herds can be proxied by a measure of grazing potential. This rationale can be summarized by the following hypotheses:

H₁: In general, as bison potential carrying capacity and the probability of encountering a herd increase, foragers will leave bison herd patches earlier, resulting in a negative

trend between the probability of encountering a bison herd and the number of individual bison harvested, represented archaeologically.

Ha2: When bison are hunted in proportion to their natural abundance, the above relationship will be positive and linear.

To evaluate the above hypotheses, this study models a proxy for potential bison carrying capacity across the North American Great Plains during modern times and during the time period between 15,000 and 7000 years before present. This study employs total GBC (as formulated by McNaughton 1984) as a quantitative proxy for bison carrying capacity and uses it to infer where populations of this large ungulate might have thrived. In order to accomplish this, the GBCs of several species of grasses native to the Great Plains are calculated and summed, weighted by their probability of occurrence across the Great Plains and in the adjacent landscape. Following model construction, the estimated model parameters are used in conjunction with reconstructed paleoenvironmental variables (see Chapter 3) to estimate the grazing potential (a proxy for bison abundance) of archaeological locations showing evidence of bison predation during the Paleoindian period.

Methods

In order to estimate grazing potential across the Great Plains, this study required the sampling of native grass species along their distributions.

Grass sampling

The Global Biodiversity Information Facility provided observations of species presence/absence (<http://data.gbif.org/>; Figure 4.5). In order to predict to prehistoric time

periods, the study only drew on data from species defined as “Native” to the Great Plains by the USDA Plants Database (<http://plants.usda.gov>). In order to estimate the complete range of each species, all observations of the species were used. The complete sample size used contained a total of 48,531 individual observations with longitude and latitude coordinates, representing 116 grass species (see Table 4.1 for list of species and their common names).

Modern species distribution model

The next step was to model the probability of each individual species’ occurrence as a function of its current distribution and climatic attributes (bioclimatic niche). Climatic attributes included *mean annual temperature*, *annual precipitation*, *annual temperature seasonality*, and *annual precipitation seasonality*. These data were obtained as raster spatial data arrays from the bioclim database (<http://www.worldclim.org/>) and modeled using generalized linear models (GLMs) for binomial response, using a logit link (logistic regression). Each species was dually modeled in the following manner: The first model was entirely additive for quadratic main effects (temperature, precipitation, and their respective seasonalities); in effect, no interaction (multiplicative) effects were assumed. The second model assumed interactions between temperature and temperature seasonality, and between precipitation and precipitation seasonality. The best models were arbitrated by Akaike’s Information Criterion (AIC; Akaike 1974; Burnham and Anderson 2002), and then probability of occurrence grids (and maps) were generated for each species.

Modern GBC

The modern individual GBC of a single species i (mg/cc) was computed using the equation formulated by McNaughton (1984: 872):

$$\text{GBC}_i \text{ (mg/cc)} = e^{3.99 - 0.95 \cdot \log(\text{height}_i)} \quad (2)$$

Grass heights were obtained from descriptions in the literature, for example, in botany handbooks (e.g., McGregor et al. 1991) and Herbarium databases, such as Grassbase: Online World Grass Flora (<http://www.kew.org/data/grasses-db/sppindex.htm>) and the Manual of Grasses for North America (<http://herbarium.usu.edu/grassmanual/>). In order to obtain the total GBC of a map location (represented by a pixel), a weighted sum was used, for which each individual (the i^{th}) species-specific GBC (see equation 2) was weighted according to its respective estimated probability of occurrence P_i across all N species. Therefore,

$$\text{Total Biomass Concentration} = \sum_{i=1}^N P_i \cdot e^{3.99 - 0.95 \cdot \log(\text{height}_i)} \quad (3)$$

Here, the notation follows equation (2), but in addition, N is the number of species sampled (116).

Prehistoric GBC

Once species-specific environmental parameters were estimated, the grass species' distributions were modeled using the parameter estimates, and the “paleo” counterparts to the modern environmental variables (see Chapter 3) were used to create the modern distribution models. Following the estimates of grass species' distributions, the procedure outlined under the “Modern GBC” section was followed to obtain the archaeological “site-specific” GBCs.

Archaeological data and archaeological “site-specific” GBCs

A dataset containing information regarding 84 Great Plains Paleoindian archaeological components was compiled from the published literature (references in Table 4.2; cf. Hill Jr 2007a, b, 2013). The dataset contained subsistence-related information (e.g.,

bison MNI, Table 4.2, Appendix A.4) recorded using the archaeological material recovered at the individual sites, including site location (e.g., state, longitude, latitude) and temporal association (e.g., calendar date, temporal grouping, archaeological culture).

Site-specific environmental variables were estimated through spatio-temporal kriging (see Chapter 3), and the archaeological site-specific temporal and spatial information was obtained from the Paleoindian database. Parameters from the modern 116 grass species distribution models were used to generate the probability of occurrence at each “paleo” location (paleo P_i). Finally, the weighted sum described by equation (3) was again used to obtain the total GBC at each site’s spatio-temporal location.

Hypothesis testing

In order to test the hypotheses presented above, a combination of the archaeological dataset and the paleo GBC was used. The archaeological database provided this study with values for each site’s bison abundance, quantified as the minimum number of individuals (MNI; Grayson 1984; Lyman 1994, 2008), as well as the spatial location and radiocarbon date. The estimated paleo GBC served as a proxy for bison carrying capacity at each site given its location and calendar date.

Results

Grass species distribution models

The full model with interaction terms, for the most part, provided the best fit for the individual species’ distributions. The Akaike Information Criteria were higher than 2 for approximately 80% of the additive-only models; therefore, the models were not considered to be better than those accounting for the interactions between mean annual

temperature and annual temperature seasonality, and annual precipitation and annual precipitation seasonality (Burnham and Anderson 2002). The models with the best AIC values were used to construct the modern GBC model.

Modern, prehistoric, and archaeological “site-specific” GBCs

The results from the modern GBC model are illustrated in Figure 4.6. As an exploratory endeavor, GBC models resulting from completely additive and interactive grass SDMs were also computed and compared. A set of 10,000 randomly distributed spatial locations was generated within the boundaries of the Great Plains (see Figures 4.1 & 4.5). GBC values generated by each model (additive and interactive) were extracted at each of the 10,000 locations. The Pearson’s r correlation coefficient was calculated at 0.98 ($p < 0.001$). Therefore, inference seemed to be similar whether using the additive models or the models with interactions. Here, the best model per species was used to compute GBCs (as arbitrated by AIC).

To illustrate prehistoric values of GBC, 33 maps were generated across the region of interest, at equal temporal intervals between 15,000 and 7000 years before present (Figure 4.7). These maps produce a novel, dynamic view of potential bison carrying capacity across the Great Plains and through time during the Paleoindian period. Total GBC at each site’s spatio-temporal location was calculated for the 84 archaeological sites (Table 4.2).

Hypothesis testing

In order to test the hypotheses presented above, a combination of the archaeological dataset and the paleo GBC was used.

Ho1: Due to higher carrying capacity, Paleoindians encountered bison herds more frequently in the northern Great Plains than in the southern Great Plains. The reconstructed map of potential grazing sites proxied by their GBCs showed a different trend than the hypothesis anticipated. Figure 4.6 illustrates the modern GBC pattern across the Great Plains. The bison abundance potential increases from southern Texas, reaching an apex around the 39–40th parallel in mid to northern Kansas and then decreasing toward the north. By contrast, the prehistoric GBC illustrated in Figure 4.8 shows a negative relationship between GBC and latitude ($R^2 = 0.5$, $p < 0.001$), and therefore this hypothesis was not supported.

Ho2: The greater frequency of bison herd encounters in the northern Great Plains facilitated larger scale bison hunting compared to the southern Great Plains. Reconstructed bison grazing potential did not support this hypothesis, as its fundamental premise of “greater bison abundance in the northern Great Plains” was not supported.

Grazing potential and archaeological bison remains (MNI)

Ha1: In general, as bison potential carrying capacity increases, foragers will leave bison herd patches earlier, resulting in a negative trend between bison herd frequency and the number of individual bison harvested, represented archaeologically. A negative relationship between archaeological bison abundance (Bison MNI) and GBC is illustrated in Figure 4.9 in the form of a Poisson regression fit (parameter estimate fit using Iteratively Reweighted Least Squares, weighted by variance and estimated spatial dependence: $\text{Bison MNI} = e^{14.09 + -1.46 \text{ GBC}}$, $p < 0.001$). This model supported the foraging theory prediction based on the Marginal Value Theorem. Here, as bison carrying capacity and thus herd

encounter rate increase, the average number of individuals harvested from a patch in a single foraging bout decreases.

Ha2: When bison are hunted in proportion to their natural abundance, the above relationship will be positive and linear. The model did not support this hypothesis, suggesting instead that Paleoindian hunter-gatherers hunted bison in inverse proportion to their natural abundance. Moreover, the best model fit was not linear, but negatively exponential ($AIC > 2$; Figure 4.9). This means that the ratio of bison MNI to potential bison abundance is not constant. Rather, it is larger when potential bison abundance is low, and smaller when bison abundance is high. This means that in areas where bison were scarce, Paleoindians harvested them in greater proportion than in areas where bison were more abundant.

Discussion

Combining several analytical concepts has allowed this study to estimate potential bison carrying capacity across the Great Plains during the Paleoindian period, and to quantitatively evaluate several hypotheses with respect to hunter-gatherer foraging across this temporal and spatial scale. These concepts included the coevolutionary history of grass-herbivore interactions, foraging theory, species bioclimatic niche and distribution modeling, and spatio-temporal paleoenvironmental reconstruction. The quantitative nature of this approach is novel, providing insight into the behavioral ecology of Paleoindian hunters and gatherers living in the North American Great Plains.

Model of prehistoric grazing lawns and bison foraging

Considering the evolutionary and ecological mechanisms involved in the creation, productivity, and maintenance of grazing landscapes provides an experimentally supported theoretical backdrop against which to estimate the spatial distribution of herbivore population densities, particularly that of bison. North American Great Plains field experiments have shown that grazed grasslands yield greater above-ground productivity than ungrazed controls (~ 50%, see Frank and McNaughton 1993). Although the grazing effect on grass productivity in this context is high, the response is not as high as in the field experiment results from the Serengeti, in which grazed grasslands yielded greater than 100% above-ground productivity over ungrazed controls (McNaughton et al. 1996; Frank et al. 1998). A possible explanation for the dampened effect observed in the North American experiments is that the experiments took place in geographic locations outside of the peak range of short stature grasses, such as the species in the *Bouteloua* genus. Indeed, greater effects would be expected in areas of the Great Plains grasslands where population densities of grass species such as *Bouteloua gracilis* and *Bouteloua dactyloides* are at their highest, especially given their morphological attributes that appear to have been selected under lawn grazing regimes. Regardless of this discrepancy, the effect of grazing on above-ground productivity remained significantly higher than on ungrazed systems, providing evidence of “grazing lawn” processes, and the coevolution of large grazers, such as bison, and the grass species of the Great Plains.

Arguably, it is possible that not all Great Plains’ grass species are important for the bison diet, including some of the 116 grass species used by this study (see Methods section and Table 4.1). However, the majority of information regarding bison diet composition has not been derived from habitat settings chosen by the “selected for” biological intuition of

bison. Thus, making the assumption that the diet composition observed reflects the most important dietary species for bison seems to be circular reasoning. For example, in parts of the Great Plains, less than 2% of the total bison diet is composed of a few species of grass (e.g., Peden 1976: Table 2). At the same time, bison seem to be general enough feeders, including grass species in their diet in proportion to the species' natural abundance. The latter, of course, fluctuates across space and time. For example, in the short grass steppe of Colorado, bison graze short grasses such as blue grama (*Bouteloua gracilis*) and buffalo grass (*Bouteloua dactyloides*) with great frequency, composing more than 80% of their diet (Peden 1976: 228). However, in the prairies of central Iowa, less than 2% of the bison diet is composed of the *Bouteloua* genus as a whole (Kagima 2008: Appendix B1.a and B1.b, male/female mean). In this region, bison apparently prefer tall grasses such as big bluestem (*Andropogon gerardii*), which is the most abundant species at the research study site, alone making up roughly 20% of the bison diet. Yet, big bluestem is completely absent from the bison feed in the Colorado study (Peden 1976). Therefore, using the information from either example alone would create a bias in the understanding of bison diet composition, as this would omit grass species apparently important to bison yet analytically invisible.

Sampling bias might be further exacerbated by the fact that most information regarding bison diet composition has been derived from less than a handful of discrete stations across the Great Plains, rather than from a randomly distributed sample representative of the total variability. At the spatial scale of the Great Plains, statistical bias may result from excluding endemic grass species potentially selected as feed by bison, but absent from our knowledge of their diet due to a lack of sampling effort. Consequently, the lack of complete information regarding which grass species have been absent or in low

abundance across the full extent of the Great Plains and across time has important implications for understanding the potential dietary items of bison that occurred in the past. At this time, a better strategy seems to involve incorporating all potential sources of food for bison, which researchers can then further test as new knowledge arises. Moreover, this model could be enhanced by making occupancy predictions derived from modeling grass species abundances, while accounting for the sampling biases inherent in the observation data.

Hypothesis testing

The analysis did not support a positive relationship between bison carrying capacity and latitude. First, the results indicated that, on average, the potential abundance of bison was not greater in the northern Great Plains than in the southern Great Plains (Figure 4.8). Today, the range of grass species adapted to bison grazing is found mostly in the central and southern plains, and this range appears to have shifted across the landscape with environmental changes throughout the Paleoindian period (Figure 4.7). In addition, this hypothesis fails to explain the high abundance of bison observed at kill sites in the northern plains. In fact, foraging theory predicts a pattern opposite to that of hypothesis *H₀₁*, wherein the increased harvesting of bison should reflect greater abundance. As in habitats where encounter rates of bison prey are higher, harvesting time should end sooner than in habitats where encounter rates are lower. The expected archaeological pattern would, therefore, be one in which Paleoindians harvested, on average, fewer individual prey per foraging bout in habitats with higher carrying capacity.

Hypothesis testing supported a negative relationship between the reconstructed proxy for bison carrying capacity (GBC) and the number of bison harvested by

Paleoindians (bison MNI). The archaeological data analyzed here supported the MVT hypothesis (Figures 4.8 and 4.9). Bison herd encounter rates in the southern and central plains were higher than in the north. Ample encounters with bison herds would have been conducive to a hunting strategy whereby Paleoindians procured small numbers of animals as needed to either provide or share with conspecifics. As a result, under such conditions (i.e., when encounter rates were high), group hunting and sharing as a hunting-success-variance reduction strategy (e.g., Smith 1991: 287-309) would not have been necessary. However, group foraging and sharing would have increased in contexts where hunting risk was high, and group foraging would have helped to alleviate individual hunting failure (Smith 1980, 1991; Bliege Bird et al. 2002: Table 1). In resource-rich areas, therefore, one might expect conditions to be unsuitable for the emergence of highly organized hunter-gatherer groups. This perspective from foraging theory, thus, contradicts Bamforth's hypothesis of highly organized groups hunting bison in northern Great Plains' latitudes. High variation in annual seasonality might also have increased the variability in prey encounters, resulting in a more intensified seasonal pattern of prey encounter versus no encounter – a pattern expected in habitats with cold winters and warm summers, similar to those of the northern plains.

The northern latitudes of the Great Plains should therefore be expected to have yielded disproportionately larger kills than the southern Great Plains. The already relatively low encounter rates in the north when coupled with a prey-harvesting window narrowed by the length of the colder months predict that once Paleoindians encountered a herd, they would have harvested an even greater yield.

Conclusions

Thirteen years ago Douglas Bamforth considered his hypothesis testing work as a qualitative “first step”, explicitly leaving the quantitative study of Paleoindian hunter-gatherer ecology in the context of bison abundance and distribution as “a second step in future research” (Bamforth 1988: 21). This study takes that second step by using several quantitative methods to reconstruct a baseline of Paleoindian bison prey availability. These results were then used to test several hypotheses related to the relationship between Paleoindian predators and bison as their prey. In particular, this study tested hypotheses explaining the well-known correlation between increases in bison abundance and increases in latitude, observed in hunted assemblages of Paleoindian age. The results challenge the assumption that, during the Paleoindian period, bison were more abundant in the northern Great Plains than in the southern Great Plains. Paleoenvironmental reconstructions and carrying capacity estimates showed that bison natural abundance was likely not greater in the northern Great Plains than in the south and central portions of that region. Rather, in accordance with foraging theory, the observed latitudinal abundance pattern is more likely the result of variations in Paleoindian foraging behavior in response to the time between bison herd encounters.

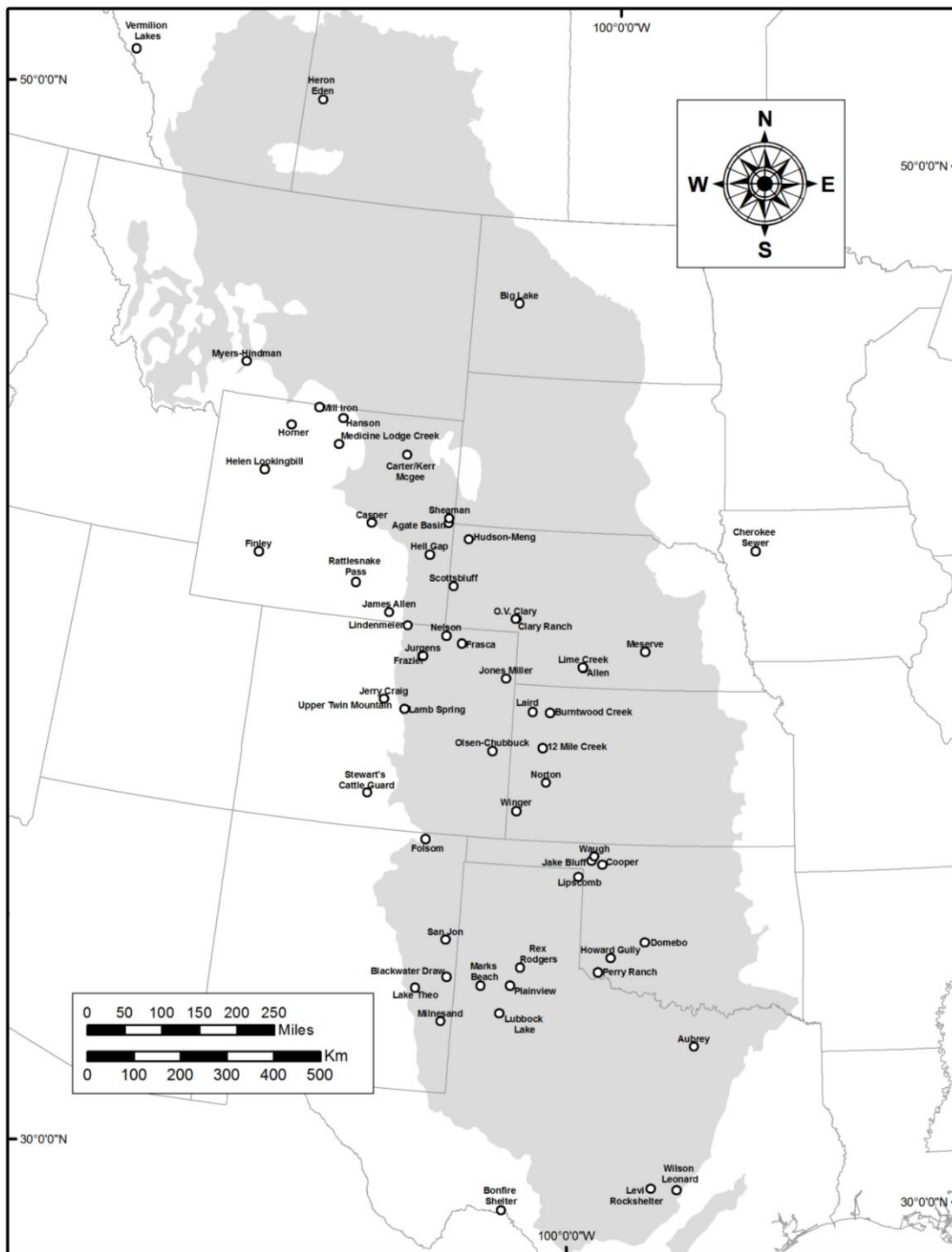


Figure 4.1. Geographic distribution of archaeological sites with Paleoindian components that have yielded bison (see Table 4.2 for related information).

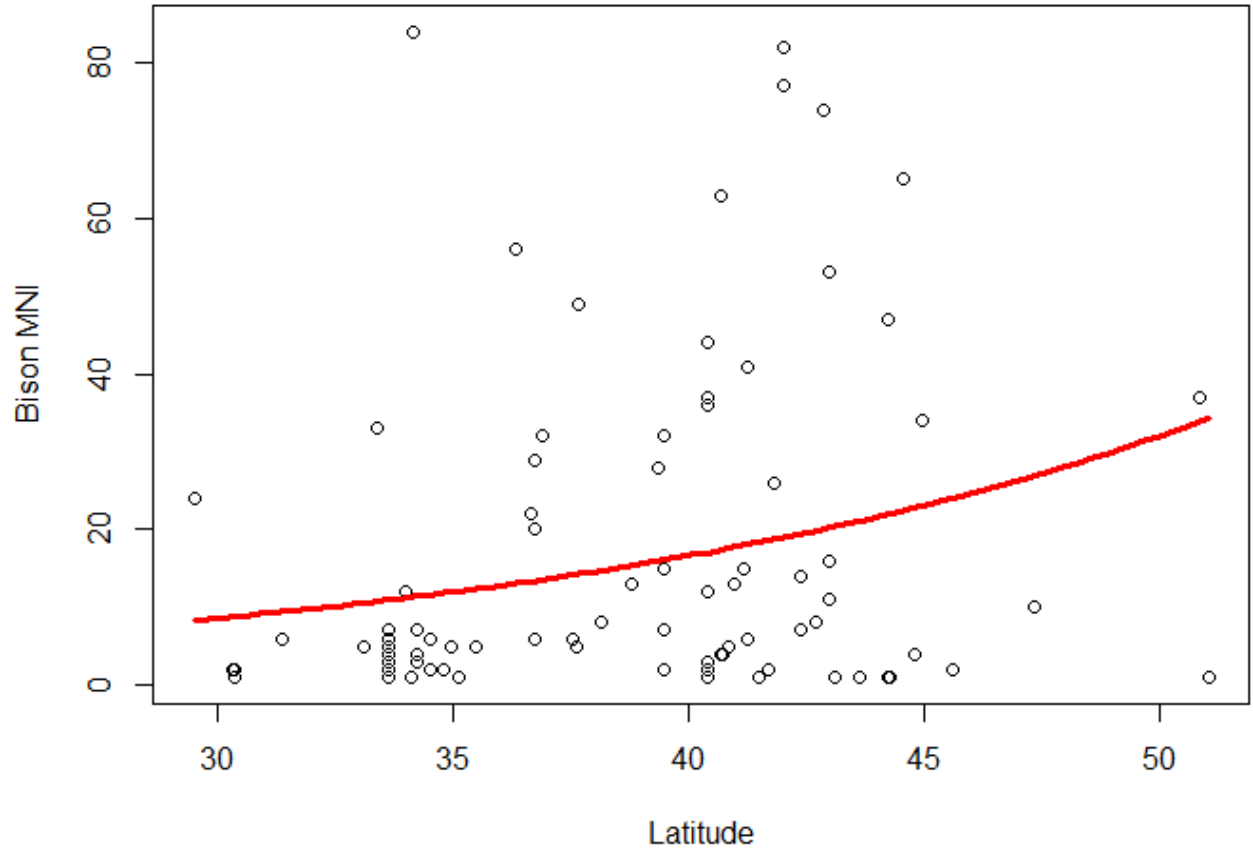


Figure 4.2. Illustration of the relationship between Bison Minimum Number of Individuals from Paleoindian archaeological sites across the Great Plains’ north–south gradient. The pattern in this figure illustrates the Bamforth (1988, 2011) hypotheses showing that as latitude increases so does the potential abundance of bison (MNI data recorded by this study, see Table 4.2 and Appendix A.4).

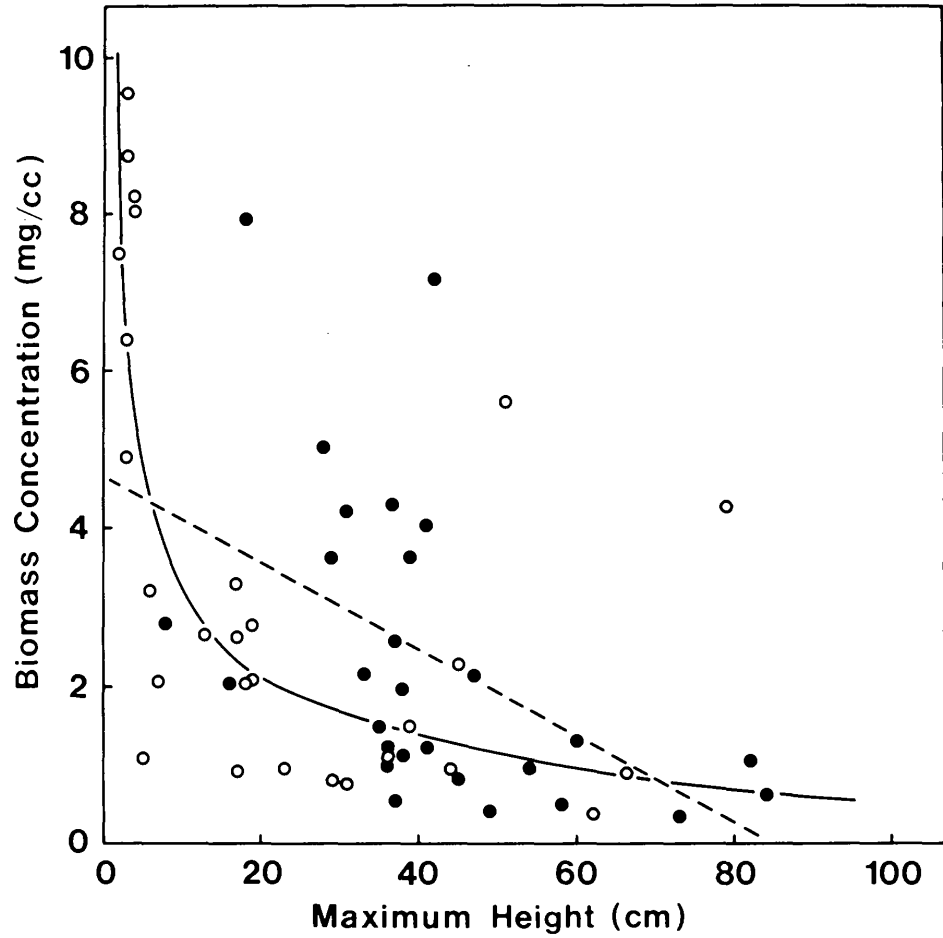


Figure 4.3. Relationship between maximum height and maximum biomass concentration (GBC) of ungrazed (dark circles) and grazed (white circles) grasses. Solid line is nonlinear fit of grazed grasses. Dashed line is fit of ungrazed grasses (illustration adapted from McNaughton 1984: 872).

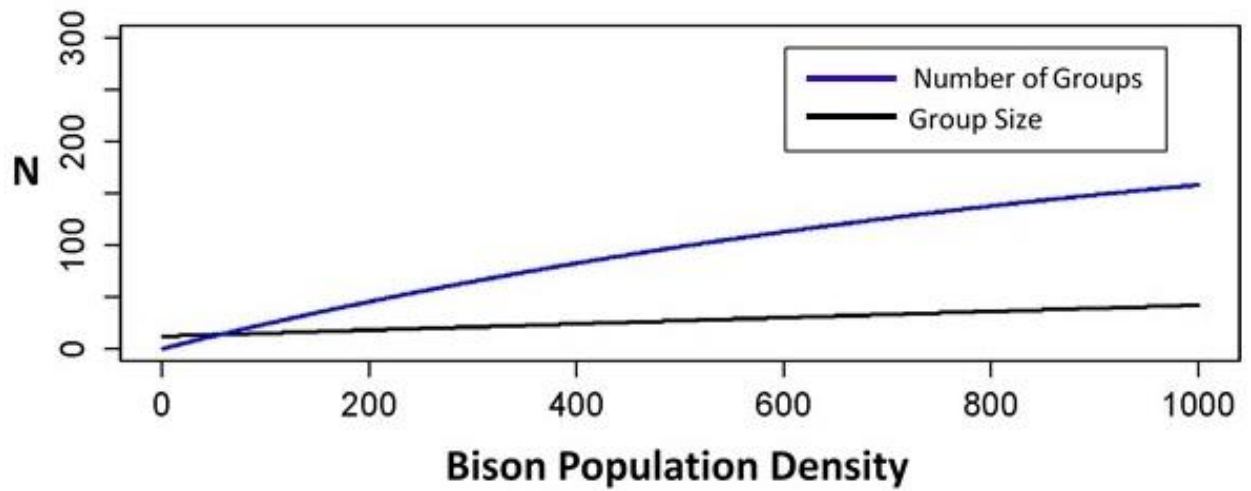


Figure 4.4. Plot of empirical model of the number of bison groups and bison group size as a function of population density in the Delta population of Wood Buffalo National Park between 1981 and 1999. Data show that as population density increases (as it would due to higher grazing quality), the number of bison groups increases at a much higher rate than bison group size. Group size seems constant across increasing population density (illustration adapted from Jolly and Messier 2004).

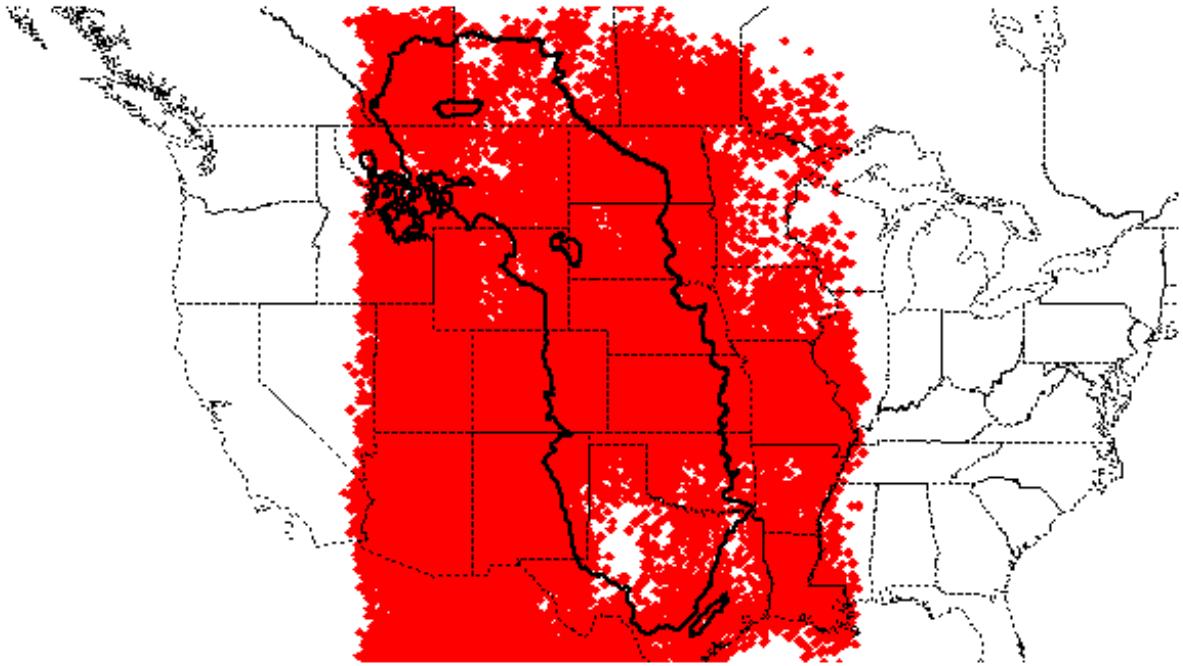


Figure 4.5. Locations of grass distribution sample. Each red dot represents an individual species observed (N = 48,531 individuals representing 116 species).

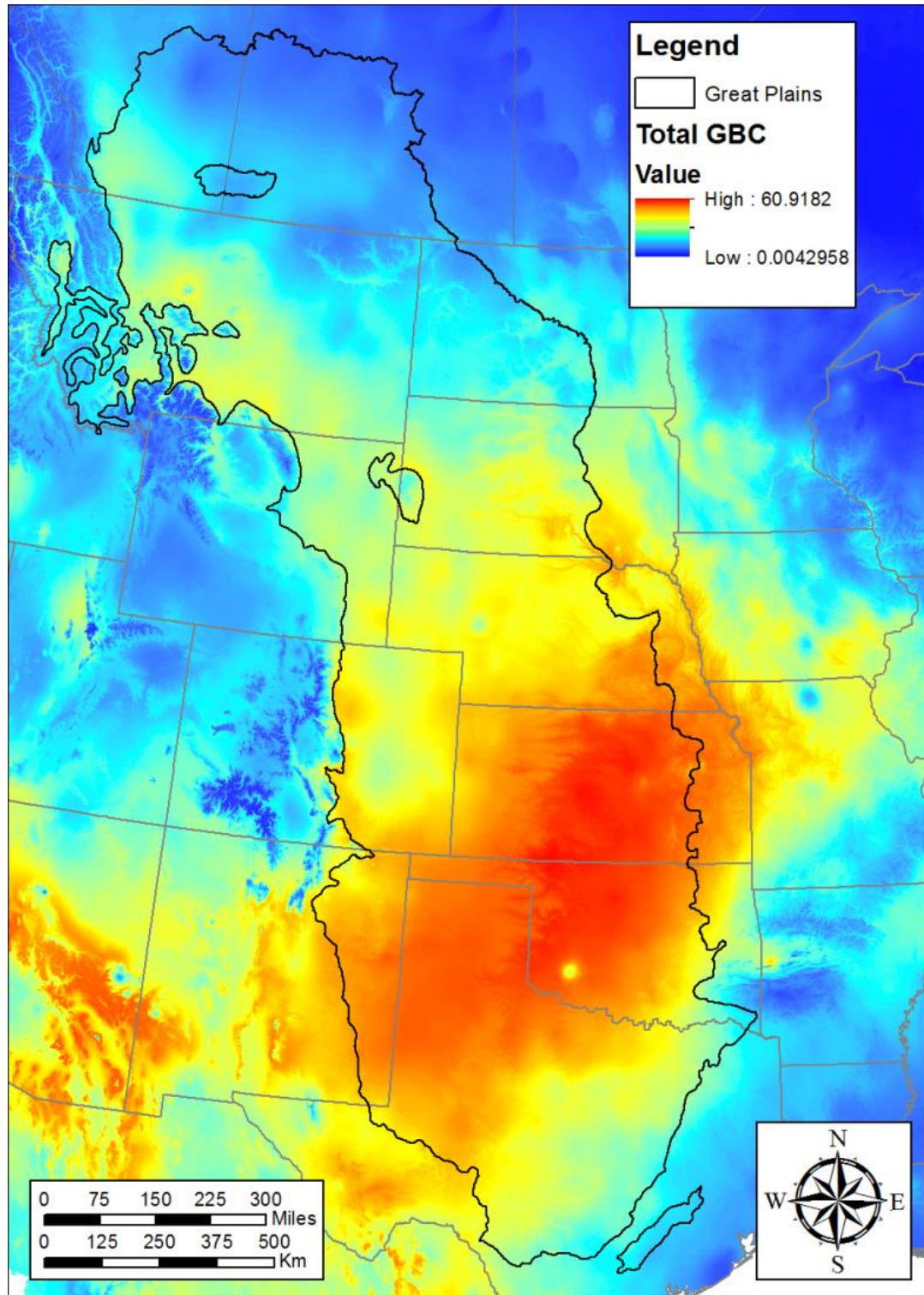


Figure 4.6. Map showing results of the total modern GBC (mg/cc) model, a proxy for bison carrying capacity. Map is the result of the best additive and interactive grass species distribution models.

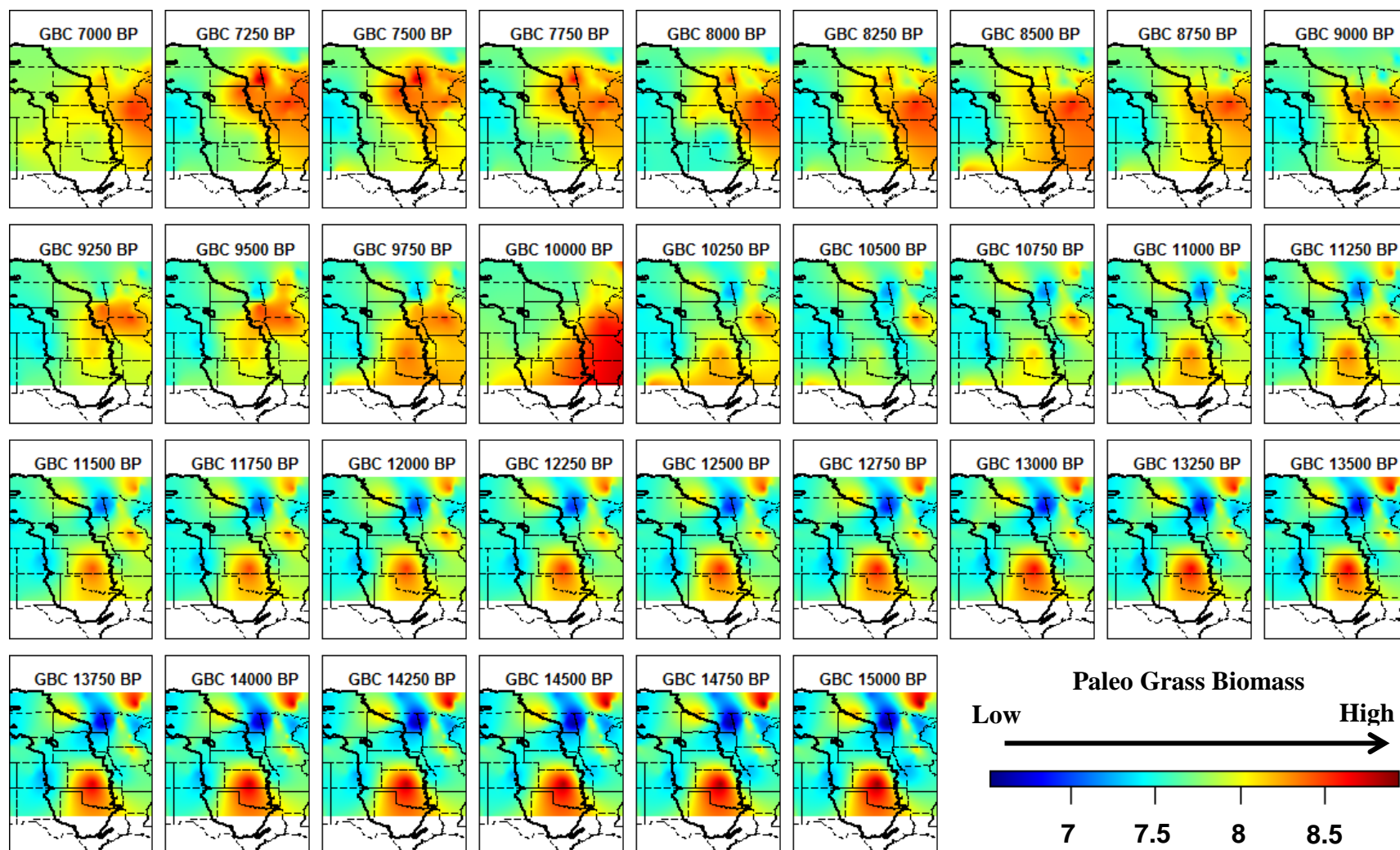


Figure 4.7. Multipanel plot illustrating spatio-temporal kriging estimates of GBC across the North American Great Plains between 15,000 and 7,000 years before present. Several paleoecological events are evident across the panel. For example, the recession of the Des Moines Lobe is illustrated by a gradual increase in GBC; in addition, the effects of onset and exit of the Younger Dryas event is also visible between 11 and 10 KYBP.

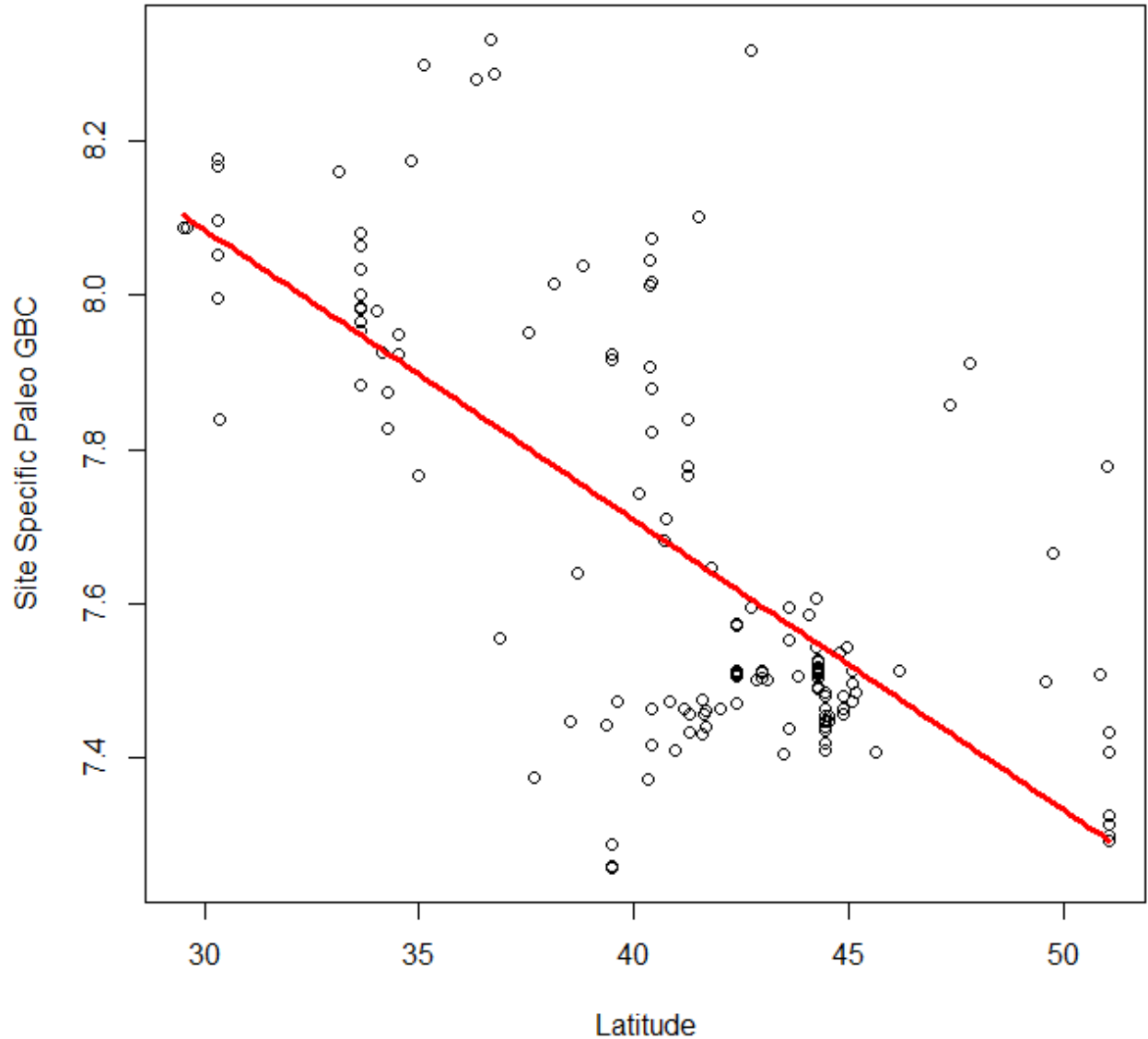


Figure 4.8. Plot illustrating the relationship between Paleo GBC and latitude. Paleo GBC was estimated through spatio-temporal kriging, accounting for each individual site's location in time and space. Latitude is the physical northing location of each archaeological site. The scatter plot and fit model suggest that bison populations would have thrived at lower latitudes than in the northern Great Plains. This relationship between the reconstructed paleoenvironment and site location across the Great Plains does not lend support to the hypothesis that Paleoindians living in the northern Great Plains would have enjoyed better bison hunting grounds (linear model parameter estimates $y = 9.21 + x * -0.03$, $R^2 = 0.50$, $p < 0.001$, $df = 152$).

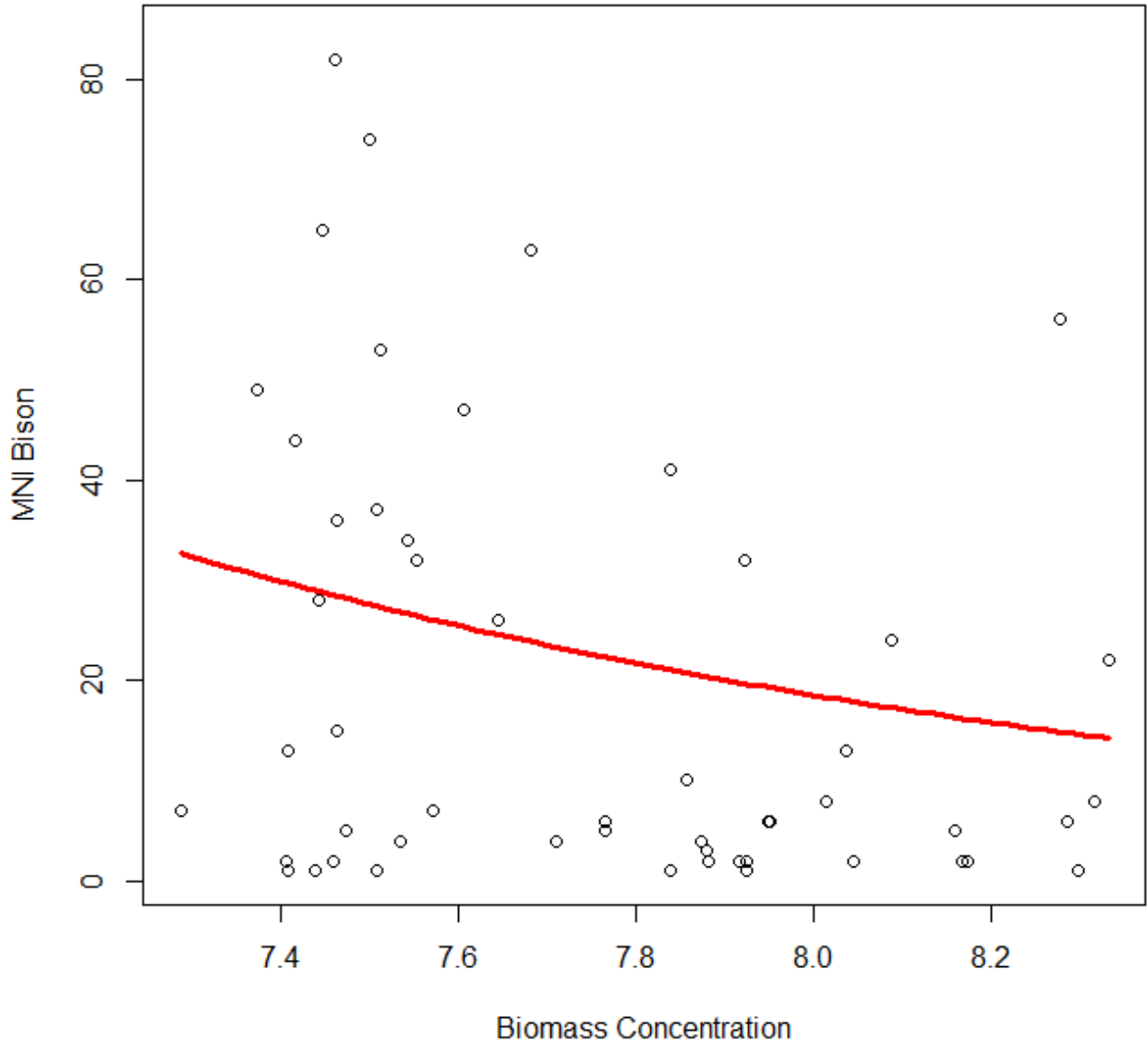


Figure 4.9. Scatterplot of bison MNI as a function of prehistoric GBC (all MNI < 150). The MNI data seem to decrease in a non-linear manner as GBC increases. The relationship is modeled by a Poisson regression, where $y = e^{a+bx}$ (parameter estimates $a = 14.09$, $b = -1.46$, $p < 0.001$). This relationship supports the Marginal Value Theorem hypothesis that when bison encounter rates are higher (in richer areas where GBC is higher), harvesting events are smaller, but greater where encounter rates are low, as in areas with low GBC.

Table 4.1. Grass species used in this study to generate GBC estimates.

	Grass Species	Common Name
1	<i>Achnatherum contractum</i>	Contracted Ricegrass
2	<i>Achnatherum nelsonii</i>	Dore's Needlegrass
3	<i>Achnatherum robustum</i>	Sleepygrass
4	<i>Agropyron albicans</i>	Montana Wheatgrass
5	<i>Agropyron arizonicum</i>	Arizona Wheatgrass
6	<i>Agropyron bakeri</i>	Baker's Wheatgrass
7	<i>Agropyron molle</i>	Western Wheatgrass
8	<i>Agrostis cryptandra</i>	Sand Dropseed
9	<i>Agrostis geminata</i>	Rough Bentgrass
10	<i>Agrostis mexicana</i>	Mexican Lovegrass
11	<i>Agrostis pyramidata</i>	Madagascar Dropseed
12	<i>Agrostis trichopodes</i>	Cutover Muhly
13	<i>Aira caespitosa</i>	Tufted Hairgrass
14	<i>Aira obtusata</i>	Prairie Wedgescale
15	<i>Aira spicata</i>	Spike Trisetum
16	<i>Alopecurus aequalis</i>	Shortawn Foxtail
17	<i>Alopecurus carolinianus</i>	Carolina Foxtail
18	<i>Anatherum virginicum</i>	Mohr's Bluestem
19	<i>Andropogon barbinodis</i>	Cane Bluestem
20	<i>Andropogon chrysocomus</i>	Big Bluestem
21	<i>Andropogon divergens</i>	Little Bluestem
22	<i>Andropogon nutans</i>	Indiangrass
23	<i>Aristida adscensionis</i>	Sixweeks Threeawn
24	<i>Aristida basiramea</i>	Forked Threeawn
25	<i>Aristida brownii</i>	Wright's Threeawn
26	<i>Aristida divaricata</i>	Poverty Threeawn
27	<i>Aristida oligantha</i>	Prairie Threeawn
28	<i>Atheropogon curtispendus</i>	Sideoats Grama
29	<i>Beckmannia eruciformis</i>	American Sloughgrass
30	<i>Blepharoneuron tricholepis</i>	Pine Dropseed
31	<i>Bouteloua arenosa</i>	Sixweeks Grama
32	<i>Bouteloua dactyloides</i>	Buffalograss
33	<i>Bouteloua eriopoda</i>	Black Grama
34	<i>Bouteloua glandulosa</i>	Hairy Grama
35	<i>Bouteloua gracilis</i>	Blue Grama
36	<i>Bromopsis canadensis</i>	Fringed Brome
37	<i>Bromopsis lanatipes</i>	Woolly Brome
38	<i>Bromus breviaristatus</i>	Mountain Brome
39	<i>Calamagrostis ×lactea</i>	Bluejoint
40	<i>Calamovilfa longifolia</i>	Prairie Sandreed

Table 4.1. Grass species used in this study to generate GBC estimates.

	Grass Species	Common Name
41	<i>Cenchrus incertus</i>	Coastal Sandbur
42	<i>Chaetochloa geniculata</i>	Marsh Bristlegrass
43	<i>Chloris cucullata</i>	Hooded Windmill Grass
44	<i>Chloris verticillata</i>	Tumble Windmill Grass
45	<i>Chloris virgata</i>	Feather Fingergrass
46	<i>Cinna arundinacea</i>	Sweet Woodreed
47	<i>Coix dactyloides</i>	Eastern Gamagrass
48	<i>Critesion brachyantherum</i>	Meadow Barley
49	<i>Danthonia spicata</i>	Poverty Oatgrass
50	<i>Dasyochloa pulchella</i>	Low Woollygrass
51	<i>Dichanthelium acuminatum</i>	Tapered Rosette Grass
52	<i>Dichanthelium depauperatum</i>	Starved Panicgrass
53	<i>Dichanthelium leibergii</i>	Leiberg's Panicum
54	<i>Dichanthelium polyanthes</i>	Roundseed Panicgrass
55	<i>Digitaria adscendens</i>	Southern Crabgrass
56	<i>Digitaria arenicola</i>	Sand Crabgrass
57	<i>Digitaria californica</i>	Arizona Cottontop
58	<i>Diplachne uninervia</i>	Mexican Sprangletop
59	<i>Distichlis spicata</i>	Saltgrass
60	<i>Elymus arkansanus</i>	Hairy Wildrye
61	<i>Elymus australis</i>	Virginia Wildrye
62	<i>Eragrostis caroliniana</i>	Tufted Lovegrass
63	<i>Eragrostis hypnoides</i>	Teal Lovegrass
64	<i>Eragrostis intermedia</i>	Plains Lovegrass
65	<i>Eragrostis pilifera</i>	Sand Lovegrass
66	<i>Eragrostis reptans</i>	Creeping Lovegrass
67	<i>Eragrostis spectabilis</i>	Purple Lovegrass
68	<i>Eriochloa contracta</i>	Prairie Cupgrass
69	<i>Erioneuron pilosum</i>	Hairy Woollygrass
70	<i>Festuca gracilentia</i>	Sixweeks Fescue
71	<i>Festuca oregona</i>	Sandberg Bluegrass
72	<i>Glyceria elata</i>	Fowl Mannagrass
73	<i>Glyceria grandis</i>	American Mannagrass
74	<i>Hesperostipa comata</i>	Needle And Thread
75	<i>Hesperostipa curtisetia</i>	Shortbristle Needle And Thread
76	<i>Hesperostipa neomexicana</i>	New Mexico Feathergrass
77	<i>Hilaria jamesii</i>	James' Galleta
78	<i>Koeleria albescens</i>	Prairie Junegrass
79	<i>Lycurus setosus</i>	Bristly Wolfstail
80	<i>Melica nitens</i>	Threeflower Melicgrass

Table 4.1. Grass species used in this study to generate GBC estimates.

	Grass Species	Common Name
81	<i>Monroa squarrosa</i>	False Buffalograss
82	<i>Muhlenbergia ×curtisetosa</i>	NANA
83	<i>Muhlenbergia asperifolia</i>	Scratchgrass
84	<i>Muhlenbergia glomerata</i>	Spiked Muhly
85	<i>Muhlenbergia montana</i>	Mountain Muhly
86	<i>Muhlenbergia pauciflora</i>	New Mexico Muhly
87	<i>Muhlenbergia porteri</i>	Bush Muhly
88	<i>Muhlenbergia pungens</i>	Sandhill Muhly
89	<i>Muhlenbergia wrightii</i>	Spike Muhly
90	<i>Nassella leucotricha</i>	Texas Wintergrass
91	<i>Oryzopsis micrantha</i>	Littleseed Ricegrass
92	<i>Panicum alatum</i>	Winged Panicgrass
93	<i>Panicum anceps</i>	Beaked Panicgrass
94	<i>Panicum barbipulvinatum</i>	Witchgrass
95	<i>Panicum bulbosum</i>	Bulb Panicgrass
96	<i>Panicum obtusum</i>	Vine Mesquite
97	<i>Panicum virgatum</i>	Switchgrass
98	<i>Paspalum bushii</i>	Thin Paspalum
99	<i>Paspalum difforme</i>	Florida Paspalum
100	<i>Paspalum geminum</i>	Hairyseed Paspalum
101	<i>Phalaris arundinacea</i>	Reed Canarygrass
102	<i>Phalaris caroliniana</i>	Carolina Canarygrass
103	<i>Phragmites australis</i>	Common Reed
104	<i>Poa agassizensis</i>	Kentucky Bluegrass
105	<i>Poa arida</i>	Plains Bluegrass
106	<i>Poa interior</i>	Inland Bluegrass
107	<i>Redfieldia flexuosa</i>	Blowout Grass
108	<i>Schedonnardus paniculatus</i>	Tumblegrass
109	<i>Scleropogon brevifolius</i>	Burrograss
110	<i>Spartina gracilis</i>	Alkali Cordgrass
111	<i>Spartina michauxiana</i>	Prairie Cordgrass
112	<i>Sporobolus flexuosus</i>	Mesa Dropseed
113	<i>Sporobolus giganteus</i>	Giant Dropseed
114	<i>Sporobolus heterolepis</i>	Prairie Dropseed
115	<i>Sporobolus neglectus</i>	Puffsheath Dropseed
116	<i>Tridens strictus</i>	Longspike Tridens

Table 4.2. Great Plains Paleoindian archaeological sites containing bison remains and radiometric dates.

State	Site	Component	Function	Date ¹	Bison MNI
Wyoming	Carter/Kerr-Mcgee	Cody	K/P ²	7800	47
Iowa	Cherokee Sewer	IIIA	K/P	8024	8
Texas	Lubbock Lake	FA5-8/10	K/P	8301	2
Nebraska	Allen	OL2	C	8550	2
Texas	Big Lake	Site	K/P	8788	10
Texas	Levi Rockshelter	Zone IV	C	9249	1
Texas	San Jon	Area 2	NA	9333	5
Oklahoma	Perry Ranch	Site	K/P	9431	2
Wyoming	James Allen	Site	K/P	9455	15
Kansas	Laird	Site	K/P	9471	2
Texas	Lubbock Lake	FA6-3	C	9578	7
Texas	Lubbock Lake	GA5-2	K/P	9632	1
Wyoming	Helen Lookingbill	Layer 7/9	C	9707	1
Wyoming	Hell Gap	IIIs/V-Cody	C	9820	7
Wyoming	Horner	I	C	9871	158
Nebraska	Scottsbluff	Site	NA	9893	26
Colorado	Frasca	Area 1	K/P	9987	63
Colorado	Lamb Spring	Cody-1980/1981	K/P	10000	28
New Mexico	Milnesand	Site	K/P	10000	33
Montana	Myers-Hindman	Unit 1	C	10005	2
Saskatchewan, Ca.	Heron Eden	Site	K/P	10148	37
Nebraska	Clary Ranch	Site	K/P	10154	41
Colorado	Jurgens	Area 3	K/P	10217	36
Kansas	Norton	Site	K/P	10251	8
Kansas	Winger	Site	K/P	10251	6
Kansas	Burntwood Creek	Site	K/P	10269	32
Nebraska	Lime Creek	Zone I	C	10329	3
Nebraska	O.V. Clary	Middle	C	10333	6
Wyoming	Finley	WYO Station B	K/P	10341	82
Colorado	Nelson	Site	NA	10460	5
Texas	Lubbock Lake	FA5-7/GA5-3	K/P	10514	6
Nebraska	Meserve	Site	NA	10612	4
Colorado	Jerry Craig	Site	K/P	10639	7
Texas	Rex Rodgers	Site	K/P	10642	6
Colorado	Olsen-Chubbuck	Site	K/P	10656	190
Nebraska	Allen	IZ	C	10850	3
		Bone midden-22.2-23.3			1
Wyoming	Medicine Lodge Creek	ft	NA	10939	
Colorado	Frazier	Site	K/P	10987	44

Table 4.2. Great Plains Paleoindian archaeological sites containing bison remains and radiometric dates.

State	Site	Component	Function	Date ¹	Bison MNI
Texas	Lubbock Lake	FA5-12	K/P	11126	4
Nebraska	Hudson-Meng	All	K/P	11266	474
Wyoming	Rattlesnake Pass	All	K/P	11373	2
Texas	Bonfire Shelter	Strat. A and B/C	K/P	11390	24
Texas	Lubbock Lake	FA6-11	K/P	11422	6
Texas	Lubbock Lake	FA9-1	K/P	11422	5
Alberta, Ca.	Vermilion Lakes	Component 8	C	11497	1
Texas	Lubbock Lake	FA5-17	K/P	11498	4
Oklahoma	Cooper	Upper Kill	K/P	11508	29
Texas	Lubbock Lake	FA6-15	K/P	11549	1
Texas	Lubbock Lake	GA12-5	K/P	11549	3
Colorado	Jones Miller	All	K/P	11576	250
Wyoming	Casper	All	K/P	11583	74
Oklahoma	Cooper	Middle Kill	K/P	11598	29
Oklahoma	Cooper	Lower Kill	K/P	11622	20
Wyoming	Horner	II	K/P	11721	65
Oklahoma	Howard Gully	All	K/P	11917	2
		HPP 1961-Loc	3		3
New Mexico	Black Water Draw	Bonebed	K/P	11975	
		HPP 1962-Loc	5		3
New Mexico	Black Water Draw	Bonebed	K/P	11975	
Texas	Plainview	All	K/P	11975	84
Wyoming	Hanson	All	C	12040	4
Texas	Lubbock Lake	FA2-2	K/P	12137	3
Texas	Lubbock Lake	FA6-8	K/P	12137	3
Texas	Marks Beach	All	K/P	12139	1
Colorado	Upper Twin Mountain	All	K/P	12300	15
Oklahoma	Waugh	All	C	12301	6
Wyoming	Carter/Kerr-Mcgee	Folsom	NA	12308	1
Wyoming	Helen Lookingbill	Layer 2/4	C	12314	1
Wyoming	Agate Basin	Agate Basin	K/P	12341	53
Wyoming	Agate Basin	Hell Gap	K/P	12356	16
Nebraska	Allen	OL1	C	12400	12
Kansas	12 Mile Creek	All	K/P	12409	13
Texas	Lake Theo	Folsom	C	12412	12
Colorado	Lindenmeier	Folsom	C	12469	13
Wyoming	Sheaman	All	C	12614	1
		Sellards Clovis Bison			7
New Mexico	Black Water Draw	Kill	K/P	12700	
Wyoming	Agate Basin	Folsom	C	12764	11

Table 4.2. Great Plains Paleoindian archaeological sites containing bison remains and radiometric dates.

State	Site	Component	Function	Date¹	Bison MNI
New Mexico	Black Water Draw	Jelinek Bonebed	K/P	12766	4
Colorado	Stewart's Cattle Guard	All	C	12792	49
Oklahoma	Jake Bluff	Unit I	K/P	12798	22
Texas	Lipscomb	All	K/P	12799	56
New Mexico	Folsom	All	K/P	12859	32
Wyoming	Mill Iron	All	K/P	12893	34
Oklahoma	Domebo	All	K/P	12995	1
Texas	Wilson Leonard	EP Bonebed	C	13097	2
Texas	Aubrey	Camp A and B	C	13477	5

¹Date in Calibrated Years B.P.

²K/P; Kill/Processing; C: Camp; NA: Designation not available.

**CHAPTER 5: CREAM SKIMMERS AND CRUMB PICKERS: HOW
DID ENCOUNTER RATES OF BISON AFFECT THE FORAGING
BEHAVIOR OF PALEOINDIAN FORAGERS?**

An Experimental Approach

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Chapter Overview

In Chapter 3, the study reconstructed paleoenvironmental variables to test various hypotheses regarding Paleoindian foraging behavior. The results showed the magnitude and direction of the effect of climatic variables on Paleoindian diet diversity, supporting current knowledge of these processes. Chapter 4 offered a next step in the evaluation of current hypotheses regarding Paleoindian foraging, presenting a quantitative reconstruction of bison availability across the Great Plains. Specifically, the study used grass biomass concentration (GBC) as a proxy for bison carrying capacity in order to evaluate hypotheses related to the predator–prey relationship between Paleoindian hunters and bison. This chapter examines Paleoindian foraging behavior in terms of the decision-making dynamics involved in the transport of bison skeletal elements.

Foraging theory provides a framework with which to understand human subsistence behaviors in terms of the energetic tradeoffs between caloric and time costs and benefits. Researchers have increasingly applied this framework to the foraging behavior of Paleoindian hunter-gatherers, who were notable predators of big game. In the North American Great Plains, bison remains are among the most prevalent evidence of Paleoindian big-game hunting. However, there has been a lack of information regarding the energetic tradeoffs involved in foragers extracting nutrients from bison. As a result, our ability to make inferences about Paleoindian foraging in an evolutionary context has been limited. This study addresses this gap in knowledge by conducting experiments designed to yield this necessary information. The experiments provide data related to the caloric benefits and time costs of bison butchery. These data are used to test existing hypotheses about Paleoindian foraging behavior.

Professional, modern butchers conducted disarticulation and defleshing on one male and one female bison individual, using stone tools. I measured the caloric gains of meat and marrow and the time taken to extract them per bison anatomical part. To demonstrate the usefulness of these data, I collected information on the Minimum Number of Skeletal Elements (MNE) from published manuscripts on Paleoindian bison kills. I used this information in conjunction with the bison butchery cost and benefit data to generate assemblage-wide return rates. I then modeled these return rates as a function of several variables, including bison encounter rates, in order to test hypotheses derived from the Marginal Value Theorem. Results showed that Paleoindian foragers, like other foraging organisms, behaved according to the predictions generated from foraging theory.

Introduction

Understanding the decision-making dynamics of prey-part transport by hunter-gatherers is fundamental to inferences on prehistoric subsistence behavior. White's (1952, 1953, 1954, 1955), and later Perkins and Daily's (1968), pioneering work on skeletal element patterning provided a context within which zooarchaeological patterning could be used to understand the transport practices of prehistoric hunters. Binford's (1978) studies of the anatomical patterning of Nunamiut prey and its relationship to economic use through utility models show a sophisticated attempt to understand zooarchaeological remains. Following these groundbreaking studies, other researchers have attempted not only to refine the prey-part economic utility approaches (e.g., Metcalf and Jones 1988), but also to replicate and apply them to a wide array of contexts and animal types (e.g., Borrero 1990; Lyman et al. 1992; Mengoni-Gonalons 1991; O'Connell et al. 1990; Will 1985).

Skeletal part economic indices have played a key role in understanding the dynamics of hunters and gatherers with respect to the origins of hominin hunting versus scavenging during the Plio-Pleistocene; the contribution of scavenging to Neanderthal diets and the effectiveness of Neanderthal hunters; the signature of human versus carnivore faunal accumulation; the importance of meat in hominid evolution; the development of urban complexity and subsistence specialization; and the evaluation of hypotheses regarding resource over-exploitation and societal collapses (Binford 1984; Blumenschine 1991; Bunn 1986a, b; Emery 1997; Gaudzinski and Roebroeks 2000; Grayson 1989, 2001; Isaac and Crader 1981; Klein 1999; Marean and Frey 1997; Marean and Kim 1998; Mellars 1996; Monahan 1996; Munson and Marean 2003; Potts et al. 1983; Speth and Tchernov 1998; Stiner 1994, 1998; Zeder 1988).

Human behavioral ecology and foraging theory have emerged as some of the leading theoretical concepts explaining the tradeoff between the net energetic gains and time costs involved in human subsistence activities (e.g., Bird and O'Connell 2006; Burger et al. 2005; Hawkes et al. 1982; Hill 1982; Hill and Hawkes 1983; Metcalfe and Barlow 1992). Through optimality models, foraging theory has generated expectations of organisms' behaviors when faced with the energetic cost and benefit tradeoffs involved in searching for, selecting, and consuming prey (e.g., Burger et al. 2005; Kaplan and Hill 1992; Stephens and Krebs 1986). There are two major types of foraging models: prey and patch models. While prey models ask questions of which prey to include in the diet (MacArthur and Pianka 1966), patch models are concerned with the forager's decision as to when it is most profitable to stop foraging and leave a given resource patch in search of another (Charnov 1976).

The Marginal Value Theorem (MVT) patch model, for example, has been used to generate archaeological expectations regarding Paleoindian bison foraging across the North American Great Plains. Studies of Paleoindian bison carrying capacity and herd encounter rates over space and time have shown that empirical trends fit the expectations derived from the MVT. The quantitative analyses presented in Chapter 4 showed that in habitats where herd encounter rates were higher, foragers left the foraging patch (the bison herd) earlier and harvested fewer bison than in habitats where herd encounter rates were lower. In such locations, as expected, Paleoindian foragers harvested patches for longer periods of time and procured a greater number of bison prey.

In addition to generating foraging expectations related to herd scale, the MVT is useful for interpreting archaeological remains at the level of individual animal butchery.

Burger and colleagues (2005) developed the “prey-as-patch” model, applying the MVT foraging principles to individual prey carcasses (usually ungulates) used as analogies for structured patches. Faced with a killed prey, human foragers harvest carcasses for the calories contained in the meat and marrow (and sometimes grease) encapsulated within individual anatomical parts (Burger et al. 2005). A cost–benefit tradeoff is inherent in how the individual anatomical parts from each captured prey animal are handled. The expectation is that the forager spends time and energy preparing the carcass for transport to a central residential location (cf. Orians and Pearson 1979). To do so, the forager begins by harvesting the prey parts with the highest gain-to-cost ratio and then continues by harvesting anatomical parts sequentially “down rank.” In effect, the caloric returns from meat butchered diminish until the forager reaches a stopping point at which the payoffs of encountering, handling, and processing another prey for transport outweigh the payoffs to be gained from continued butchery. Therefore, the probability of encountering prey (prey encounter rate) directly affects the critical point at which to stop butchering an animal.

Thus, as prey encounter rates increase, the time spent harvesting energy from the prey decreases. In other words, the higher the probability of encountering another prey animal, the sooner the stopping point is reached in the butchery process. As a result, high prey encounter rates may result in foragers “skimming the cream” by minimally butchering carcasses. When prey encounters are low on the other hand, foragers may take all they can get by “picking the crumbs” of their captured prey, resulting in more intensively butchered carcasses. Historical accounts provide examples of such cream-skimming and crumb-picking behaviors.

For example, in the face of overwhelming numbers of bison at the end of the nineteenth century, there are abundant stories recounting massive numbers of bison being killed and only their tongues extracted (Roe 1951). By contrast, interviews with Alaskan Nunamiut informants revealed more intense butchery behaviors due to the uncertainty of caribou encounters (Binford 1978; Burger et al. 2005). The older Nunamiut individuals interviewed by Binford (1978) recalled how, in the face of food shortages caused by rare encounters with caribou (a staple in their diet), caribou carcasses were processed intensely for food products. Despite the presence of these historical accounts, more comprehensive information regarding the caloric gains and time costs of carcass butchery is needed in order to evaluate the extent to which such hypotheses are consistent with the behaviors of Paleoindian hunter-gatherers (e.g., Burger et al. 2005).

Energetic returns can be operationalized as the rate of caloric gain (E) over time (T). Over the past two decades, data have emerged on hunting and butchery E/T, linking zooarchaeological remains to foraging theory (e.g., Egeland and Byerly 2005; Jones and Metcalfe 1988; Lupo 2006; Madrigal and Holt 2002; Stiner et al. 2000). Given the broad range of species humans prey upon, however, the list of prey for which these data are available is far from complete. Such is the case with archaeological studies of the North American Great Plains, in which bison (*Bison bison*) appears to be the dominant prey species throughout the prehistoric record.

Research on the properties of bison anatomical parts in the context of archaeological transport inference throughout the North American Great Plains has included skeletal element fluvial transport potential (Frison and Todd 1986:61-68), differential bone preservation (Kreutzer 1992), and variability in bulk economic utility

(Brink 1997; Emerson 1990). Increasingly, Great Plains hunter-gatherer subsistence studies have been using optimal foraging theory as their theoretical point of departure (e.g., Hill Jr. 2007, 2008; Hill et al. 2008; Knell 2007). However, there has been a notable lack of studies exploring butchery return rates, while simultaneously accounting for the processing costs of food extraction and the transport of bison parts (Cannon 2003; Burger et al. 2005). This study presents experimentally derived data on meat and marrow return rates from two bison carcasses (one male and one female) processed by professional, modern butchers using stone tools. I use these data to make inferences about the foraging behavior of Paleoindian bison hunters dispersed across a landscape with variable bison encounter rates. I apply foraging theory to provide explicit theoretical hypotheses regarding hunter-gatherers preying on large game. Finally, these hypotheses are tested using zooarchaeological data on the frequencies of bison skeletal parts dated to the Paleoindian period in the Great Plains of North America.

Background

History of anatomical part (skeletal elements) studies in the context of subsistence inference

Studies of anatomical part consumption and use by groups of North American natives arguably began with the observations of European colonial explorers following the re-discovery of the American continent (Winship et al. 1896) and by incipient ethnologists toward the end of the nineteenth century (e.g., Dodge 1882; Coues, ed. 1897; Wissler 1910; Fletcher and La Flesche 1911; Densmore 1918; Wilson 1924; Turney-High 1937, 1941; Tixier 1949; Ewers 1958; Morgan 1959). These endeavors gathered critical cultural

information, including details of the practices related to the hunting and butchering of North American bison. However, such observations were descriptive in nature, more aimed at relating a narrative to the general public, rather than geared toward confronting and answering specific scientific questions. The result was a set of disparate narratives in which the observers did not record similar phenomena using comparable methods (e.g., sampling effort, quality, etc.). For example, during their time spent with the Omaha tribe, Fletcher and La Flesche (1911: 273) provided detailed information regarding hunters' meat preferences; 'side meat' was ranked highest by butchers, while meat from the forequarters was ranked lowest. At the same time, Ewers (1958: 80-81) coined the terms and described the processes of 'light butchery' and 'heavy butchery'. Through his observations of the Blackfeet tribe, Ewers provided very little detail beyond noting his study subjects' preferences for hindquarter and forequarter meat units. Although these anecdotal accounts are useful for familiarizing readers with the diversity of butchery practices among Native American tribes, they do not offer any explanations as to *why* the hunters chose to butcher and transport the anatomical parts they did.

Faced with this inferential problem, White (1952, 1953, 1954, 1955) developed a theoretical butchery ranking system based on the amount of meat associated with individual skeletal elements. He then compared the ranked values to the ethnographic butchery observations made by Wilson (1924) and Wissler (1910) in order to explain the respective hunters' transport decisions. A little over a decade later, archaeologists excavating Neolithic sites in Turkey (Daly 1969; Perkins Jr. and Daly 1968) adopted White's approach. These researchers wanted to explain the anatomical part patterning they observed on the excavated faunal assemblages. Perkins Jr. and Daly (1968: 104) coined the

term ‘schlepp effect’, derived from the German verb ‘to drag’, to describe differences in the observed patterning of cattle foot and leg bones.

These works were followed by Binford’s (1978) renowned work among Nunamiut hunter-gatherers in Alaska. In order to understand the patterns he observed in archaeological assemblages, Binford (1978: 451), like White, ranked anatomical parts based on their food value, which he referred to as their “utility”. Binford’s goal was to create a reference model with which to interpret the patterning observed in archaeological faunal assemblages (1978: 81). He proposed a collection of patterns characterized by the utility of the part as a function of the abundance of bone. Binford proposed that each type of utility pattern could indicate different hunter-gatherer economic behaviors observed in the zooarchaeological assemblages. He named these patterns of utility strategies (or curves when graphed) “unbiased,” “gourmet,” and “bulk.” In Binford’s view, an “unbiased” strategy occurs when hunters transport skeletal elements to a residential site in direct proportion to their nutritional yield or utility. The “gourmet” pattern reflects the transport of only those anatomical parts with the highest utility. The “bulk” strategy occurs when hunters supply residential sites with high quantities of transportable parts. These strategies have formed the basis of zooarchaeological skeletal pattern comparisons and inference for the past 36 years. To these strategies, Faith and Gordon (2007) subsequently added an “unconstrained” transport strategy in which all elements are transported in equal frequencies.

Foraging return rates and subsistence

Despite the influence of Binford's work, there are several problems with expecting the archaeological frequencies of skeletal elements to reflect his proposed utility strategies. Binford developed these hypothetical models based on patterns he observed in the Arctic. Predictions derived from these observations may not be generalizable to other hunter-gatherer populations outside of Arctic conditions (Binford 1978: 87). Moreover, not accounting for the taphonomic history of hunter-gatherer faunal return data may also obfuscate the true net returns of the Nunamiut faunal transport documented by Binford (Marean and Cleghorn 2003). Most importantly, Binford's utility curves only consider the energetic gains of the foraging process and not the cost portion of the tradeoff. The latter point is significant in an evolutionary context, since foragers must maximize their rate of net energetic return over time (see subsequent section).

In a recent study, Schoville and Otárola-Castillo (2014) demonstrated how including skeletal element processing and transport costs in the calculation of relative ranks causes a notable shift in rankings based solely on utility. Figure 5.1 illustrates Metcalf and Jones's (1988) standardized Food Utility Index S(FUI) ranking of high-survival elements of zebra. These rankings are compared to their respective rankings based on estimates of Energy/Time (Lupo 2006). In many cases, the meat yield rankings of individual skeletal elements differ greatly because the S(FUI) does not account for the costs of meat removal. Although the S(FUI) provides a gross measure of an element's nutritional concentration relative to its mass, the net energetic gains can be very different. Even if processing costs are considered, transport costs ensure that the ranks can never remain static. Indeed, Schoville and Otárola-Castillo (2014) showed that the rankings of zebra skeletal elements shift at different distances from a home base, indicating that anatomical part return rate

ranks (and utility ranks) are contingent upon the return-trip travel distance and the weights of individual parts.

Human behavioral ecology (or OFT) and subsistence inference

Human foragers, whether prehistoric or modern, must make decisions regarding the quality and quantity of resources they need to transport. Researchers have hypothesized these foraging decisions to be largely driven by natural selection and based on biological principles related to individual fitness, whereby individual foragers maximize their net rate of energy intake over the long-term average (e.g., Charnov and Orians 1973; Stephens and Krebs 1986: 16).

When making inferences about the evolution of human subsistence and prey-part transport strategies, researchers have generally observed faunal assemblages and documented changes in the relative abundance of skeletal parts (e.g., Binford 1978; Faith 2008). Given that taphonomic factors are accounted for, evolutionary models of foraging behavior can help to explain the processes and mechanisms behind these changes. Such evolutionary models focus on the energetic tradeoffs involved in acquiring and transporting resources for consumption. Briefly, in an evolutionary context, a forager's fitness (G) is a tradeoff between his/her reproductive output (F) at time t , and the probability of surviving (p) until that time ($G(t) = pF$) (e.g., Brown 1988; Houston and McNamara 1989; Ludwig and Rowe 1990). Both reproductive potential and survivorship depend on the forager's energetic reserves. Energy reserves are generally dictated by the amount of energy a forager obtains during a foraging bout at a given patch (cf, Brown 1988; Burger et al. 2005; Metcalfe and Barlow 1992) minus the energy costs of harvesting the patch, traveling to the patch, and transporting the prey from the exploited patch to a central place. These travel,

harvest, and transport costs negatively affect both the forager's harvesting gains and his/her potential fitness. Therefore, in order to increase the probability of survival until reproductive events, individual foragers must maximize their energetic returns over the long-term average.

Current empirical and theoretical research has attempted to better understand the energetic tradeoffs involved in human foragers' fitness levels. These efforts have largely focused on explicating the human foraging decisions made at the time of harvesting anatomical parts from a prey item (e.g., Burger et al. 2005; Lupo 2006; Madrigal and Holt 2002). However, the impacts of travel time between patches, load yield, and the energetic costs to transport a load on skeletal element patterning are not yet fully understood. Considering that zooarchaeological patterning has provided evidence of transport decisions that optimize energetic tradeoffs between the costs and benefits of obtaining and transporting resources, incorporating the costs of resource transport is essential for constructing a more comprehensive theoretical model with which to predict and test skeletal element transport strategies (skeletal element frequencies) related to prehistoric and modern hunter-gatherer faunal assemblages. Furthermore, although foraging mechanisms and the underlying energetic tradeoffs of skeletal element transport have often been described (e.g., Cannon 2003; Metcalfe and Barlow 1992), much remains unknown about the range of expected variability with respect to foraging. Over time, models should become better informed, increasing the match between theoretical prediction and observed ethological or archaeofaunal evidence of foraging (e.g., Bamforth 2002c; Egeland and Byerly 2005; Hill and Kintigh 2009; Lupo 2006).

Modeling Paleoindian foraging

In the Paleoindian context, the Marginal Value Theorem (MVT) can be used to predict the degree of effort put forth by Paleoindian hunter-gatherers as they foraged individual bison prey. Burger et al. (2005) adapted the prey-as-patch model and MVT foraging rationale to conceive of individual ungulate prey as a structured patch. They detailed the mechanisms by which a cost and benefit tradeoff is inherent in the handling of each captured prey animal's individual anatomical parts. In effect, a forager spends time and energy preparing a carcass to be transported to a central residential location. The forager gains energetic returns from this endeavor. According to the MVT, the decision as to when to stop butchering an individual carcass depends largely on the rate at which a forager encounters this prey. As Burger et al. (2005) predicted, during "good times," when the frequency of prey encounters is high, foragers leave the foraging patch relatively early, whereas during "bad times," when the frequency of prey encounters is low, foragers stay in the foraging patch for longer periods of time.

These predictions are in line with Brown's (1988) widely applied operationalization of the MVT concept, which he terms the "giving-up density" (GUD). The GUD is a methodological extension of the MVT, representing the food density at which a forager decides to stop harvesting and leave one food patch for another. GUDs measure several key effects on the forager, including the rate of encounter with foraging patches, predation risk when foraging, and any cost incurred due to loss of other fitness-enhancing opportunities while foraging (missed opportunity cost). GUDs can be used to monitor foraging behavior akin to Burger et al.'s (2005) treatment of the MVT. Rather than observing the optimal load returned to the residential hub, however, GUDs measure the amount of food foragers leave behind once they have decided to stop harvesting a patch.

The inference is therefore the inverse: When the encounter rate with food patches is high, more food is likely to be left behind, resulting in the high GUD of the forager; when the encounter rate with food patches is low, the forager must harvest the patch for a longer period of time, resulting in a lower GUD.

The scale of Paleoindian hunter-gatherer bison harvesting is tied closely to bison carrying capacity and herd encounter rates across the North American Great Plains (Otárola-Castillo 2015). As such, Paleoindian foragers should be expected to follow predictions from the MVT and GUD in the context of bison hunting. In terms of the MVT, the frequency of foragers' encounters with bison prey should dictate the degree of bison butchery, carcass processing, and anatomical part removal. In terms of the GUD, since Paleoindian bison kill sites are located across the landscape in areas thought to be unfavorable for residential camps (LaBelle 2005; Hill Jr. 2007; Bamforth 2007; Hill Jr. 2008), researchers have inferred their functionality as places where hunters killed relatively large numbers of individual prey (average ~16, see Chapter 4) and harvested their nutrients to supply residential camps (e.g., Binford 1978). The remains at any kill site, therefore, are comprised of nutritional products not harvested, which can indicate the point at which the foragers made the decision to stop harvesting the patch. Accordingly, these archaeological remains can be considered Paleoindian GUDs. Paleoindian GUD values are thus expected to increase with higher bison herd encounter rates and decrease with lower bison herd encounter rates. These predictions from foraging theory can be evaluated using experimental data, archaeological remains, and appropriate statistical analyses.

Methods

I obtained male and female bison carcass specimens of the same age from a local ranch in Iowa (n=2, each 3 years old). The specimens were completely eviscerated, skinned, disarticulated, and defleshed at a local meat locker in Edgewood, Iowa. The animals' live weights were 760 lbs for the male specimen and 640 lbs for the female specimen. The carcasses were hung for evisceration, but placed on a butcher table for butchery, including skinning, disarticulation, and defleshing. Professional butchers conducted all butchery activities, using stone tools. The butchers selected had several years of animal butchery experience, but lacked experience in stone tool usage. However, I believe that the knowledge of efficient anatomical dismemberment is more vital to butchery than the use of a stone's sharp edge. The stone tools were simple chert flakes struck from Midwestern raw materials. The butchers selected the particular flakes used for butchery after initial cutting trials.

I instructed the butchers to disarticulate and deflesh the anatomical parts under our supervision. In consultation with the butchers, I decided on the sequence of butchery, taking advantage of the butchers' dismemberment experience. Our goal was to proceed in the most efficient manner. I obtained the weights of the meat, marrow, "wet" bone (defleshed bone with remnant meat still attached), and "dry" bone (inedible bone) separately for each individual part (in grams) (Lupo 2006). The marrow extraction was conducted in a laboratory setting at the Iowa State University Kinesiology Laboratory. In the laboratory, a butcher experienced at this task (Boehm) breached the marrow bones and extracted the marrow. I videorecorded the complete butchery process in order to later quantify the butchery efforts (time in seconds).

Disarticulation

Following evisceration, the head and all limb quarters (left + right fore and hind limbs) were disarticulated and weighed, each as a single complete package. The ribcage was then disarticulated, followed by the vertebrae. The latter was removed in anatomical sections (cervical, thoracic, and lumbar). Following this initial disarticulation, all individual skeletal elements were also disarticulated and weighed (Table 5.1).

Defleshing

Following disarticulation, each skeletal element was defleshed, and the respective meat yields were weighed. Although most meat can easily be attributed to its respective skeletal element (e.g., humerus, femur, etc.), yields from the ribcage and vertebrae are not as discrete. I attributed the meat yields from these sections by demarcating the approximate area where the head of the proximal ribs articulated with the costal pit on the lumbar vertebrae. Meat above this point (from an anatomically correct perspective) was considered to be part of the lumbar vertebrae, while meat below this point was attributed to the ribs.

Marrow extraction

Marrow was extracted from 28 long bones using hammerstone-to-anvil technology. In addition to the long bones, 10 phalanges, 9 first phalanx, and 1 second phalanx were broken by an experienced marrow extraction butcher (Boehm) using the same hammerstone-to-anvil technology. All skeletal elements to be processed were already disarticulated and defleshed at the time of breakage. I did not remove the periosteum layer from the specimens prior to breakage. Each element was placed on an anvil stone (0.6 kg) and struck with a hammerstone (2.8 kg) until the marrow was accessible with “minimal pulling apart” (Bunn 1983: 303).

I used two methods to break the bison phalanges and extract marrow from them: 1) breaking individual phalanges, and 2) breaking articulated phalanges. Initially, an individual first phalanx was broken by balancing a single phalange on the anvil stone. This method proved to be unsuccessful, as the slippery, thick toe not only failed to break, but was also propelled in unpredictable directions. I then held the phalange specimen on the anvil stone with pliers. This method, however, not only presented an unrealistic comparison to a prehistoric analog, but was also unsuccessful. I then attempted to break the first phalanx while it was still attached to the rest of the phalanges. This method was successful, as the still articulated hoof (third and second phalanx) provided a ‘handle’ for the butcher to hold, reducing the chance of accidental impacts to the butcher’s fingers and danger to lab equipment due to “stray” toe projectiles.

Upon breakage, marrow was extracted using a wooden spatula, metal butter knife, metal spatula, or a combination of these tools. No heat was applied to the bone to assist in marrow removal. I weighed the extracted marrow to the nearest hundredth of a gram. I captured the complete breakage process on video in order to later quantify our efforts (time in seconds). The effort (time) was recorded for each skeletal element, beginning at the point prior to first impact and ending at the point when marrow extraction stopped.

This study converted weight measures into calories. To accomplish this, I consulted the USDA National Nutrient Database for its information on bison meat. The search provided us with nutrient values for the raw ground meat of grass-fed bison and yielded a conversion factor of 1.49 Kcals per gram of meat. I also used the USDA Nutrient Database to estimate the caloric returns of marrow, which yielded a conversion factor for marrow of 7.86 per gram.

Archaeological data: Testing foraging theory

The information recorded in these experiments enabled us to then assess the various expectations of Paleoindian foraging behaviors derived from foraging theory, the MVT, and GUDs. I measured the amount of caloric gain from each individual anatomical part according to the total amount of meat and marrow it contained. I measured the handling expense according to the time cost of removing each part from the individual animal (Table 5.1).

I compiled the data with which to analyze assemblage-level E/T from the published literature. I aggregated information from archaeological sites located on the Great Plains and nearby regions that had a radiometric date, geographic coordinates, and detailed bison data. Since I wanted to focus on skeletal elements, I only used published manuscripts reporting the frequencies of Minimum Number of Skeletal Elements (MNE; Binford 1984: 50-51; Marean et al. 2001; Otárola-Castillo 2010). I further refined the data to contain MNE information from those sites designated as bison kills, narrowing this list to 27 sites (Table 5.2). Although I have adopted the functional designations of site types, I stress that the assignment of site function typologies to archaeological sites (e.g., residential camps or kill sites) should be approached with caution. As some researchers have argued, archaeological sites might not reflect discrete typologies; instead, they could be part of an occupation continuum (Binford 1982; Shott 2010). Nevertheless, the site function designations used here are generally accepted and have been operationalized as such by previous research (e.g., Hill Jr. 2007, 2008).

Modeling prehistoric GBC

I modeled the potential for encountering prey at each of the 27 sites using Grass Biomass Concentration (GBC; see Chapter 4). Experimental and observational studies conducted in African and North American grasslands have demonstrated that GBC is a good proxy for potential ungulate carrying capacity, particularly that of bison. For the Paleoindian period, I reconstructed GBC following the methods developed in Chapter 4. GBC was then used to test the foraging hypothesis that Paleoindian bison GUD increases as the rate of bison encounter potential increases.

Calculating assemblage E/T

I quantified the rate of energetic return over time for each skeletal element using the experimental bison butchery data (Table 5.1). The E/T value for each faunal assemblage was computed by first multiplying each identified skeletal element by its respective value of energetic gain. Likewise, skeletal elements were multiplied by their respective cost. These quantities were subsequently summed and the ratio of the sums computed. Although the resultant value is the assemblage-wide E/T, it is referred to simply as E/T from here on. The following expression summarizes the E/T algorithm:

$$\frac{E}{T_j} = \frac{\sum_{i=1}^N MNE_i \cdot Gain_i}{\sum_{i=1}^N MNE_i \cdot Cost_i} \quad (1)$$

where j represents the j th bison skeletal element assemblage, i denotes each type of skeletal element within assemblage j , and N is the total number of type i skeletal elements used in this study. The term E is the caloric gain (in Kcals), and T is the handling time cost (in seconds) associated with assemblage j . MNE_i estimates the minimum number of skeletal element of type i within assemblage j . $Gain_i$ and $Cost_i$ refer to the caloric gain and handling time cost, respectively, of skeletal element type i within the j th assemblage. The numerator

denotes the product of each MNE_i with respect to its associated caloric gain ($Gain_i$), summed across all N categories. The denominator, in turn, describes the product of each MNE_i with respect to its associated handling time cost ($Cost_i$), also summed across all N categories. The quotient of these two product sums measures each assemblage's E/T.

Analyses: GLS model of E/T as a response to GBC

I used regression modeling to test the hypothesis of a positive association between E/T and GBC. Regression could also provide estimates of the magnitude and direction of the effect of GBC on E/T, while accounting for other variables (e.g., size of the kill). I took several preparatory steps prior to the regression modeling of E/T as a response to GBC. Once the GBC and E/T had been calculated, I inspected both variables for outliers. I removed any outliers using the z-score method (Freedman et al. 2007). Since temporal and spatial autocorrelation can result from closely positioned spatial locations in similar time periods and cause residuals to violate the statistical assumption of independence (Cressie 1993; Hulbert 1984), I modeled the effects of temporal autocorrelation using methods developed to analyze time-series data (Box and Jenkins 1976; Box et al. 1994). I used residuals from an Auto-Regressive Integrated Moving Average (ARIMA) model on the E/T variable. The E/T ARIMA residuals were adjusted to account for temporal autocorrelation. The ARIMA residuals were computed in the R programming environment v. 3.3.1 (R Core Team 2016). I accounted for spatial autocorrelation through Generalized Least Squares (GLS), which introduces a distance covariance matrix created from a model of spatial dependence (Anselin and Griffith 1988; Cressie 1993). This procedure was able to account for the effect of locations being in close proximity when computing the

parameter estimates of the regression model. In order to assess the significance of the parameter estimates, p-values were computed through permutation (Manly 2006).

Results

Bison anatomical part nutritional values (flesh and marrow in grams) and removal costs (in seconds).

Table 5.1 shows the results of the experimental butchery in terms of the amount of edible products (meat and marrow) and handling times for the skeletal elements used in this study: cervical, thoracic, and lumbar vertebrae; ribs, scapulae, humeri, radius/ulnae, innominate, femora, and tibiae. Figure 5.2 illustrates the gain curve calculated using the bison caloric and cost data.

Archaeological data: Testing theory

Table 5.2 shows the GBC and standardized assemblage E/T values (ARIMA residuals). Several outliers were removed from the sample using the z-score method; these outliers included the Cherokee Sewer, Milnesand, and San Jon sites. Table 5.3 provides the parameters used to model the data (including spatial and temporal autocorrelation). The results of a model accounting for overall faunal assemblage size, represented by the Minimum Number of Individual bison (MNI), have not been included. MNI was not a significant covariate ($p > 0.05$). The GLS results showed that GBC had a positive ($\beta=0.924$) and significant ($p < 0.0001$) effect on E/T (Figure 5.3). The effect of GBC on E/T was considered to be large (Cohen's $d > 0.8$); for every unit increase in GBC, E/T increased by 92%.

Discussion

This study evaluated hypotheses regarding Paleoindian foraging behavior that are grounded in foraging theory, particularly those related to bison hunting. Foraging theory, specifically the MVT operationalized as GUD, predicts that mean energetic return rates should vary according to the probability of encountering a given foraging patch. When the patch is a prey animal to be processed for transport, the probability of encounter may be directly related to the carrying capacity specific to the prey's habitat. In general, when the probability of encountering bison is high, the GUD associated with bison butchery should be high. Under these conditions, the forager is expected to "give up" and quit harvesting nutrients from a prey animal relatively early in the butchery process, leaving behind high-return parts. Conversely, when the probability of encounter is low, foragers are expected to quit harvesting at a lower GUD. For our study, I used Paleoindian bison kills as samples of patch GUDs and calculated the rate of caloric return per unit of time spent butchering each anatomical part of bison through our experimental methods. I subsequently computed GBC as a proxy for bison carrying capacity designed to reflect the probability of encounter.

In order to interpret the results from the experimental butchery, I plotted the butchered and quantified anatomical parts by E/T rank to create a patch gains curve (Figure 5.2). This bison gains curve differs somewhat from the results of Burger et al. (2005); this discrepancy, however, is to be expected, given that Burger et al. used Madrigal and Holt's (2002) data based on deer caloric values. The respective curves indicate that the muscle distribution of the two animal species is quite different. For the bison, the highest ranked part was the ribs, whereas the thoracic vertebrae were ranked highest in Burger et al.'s study. During our butchery, the butchers extracted the meat on the ribs as a complete "meat

sheet” that was almost peeled off the animals, from ventral to dorsal sections, when they were laid on their side.

The GLS modeling procedure accounted for spatial and temporal autocorrelation in the data in order to avoid sampling bias over space or time. When modeled, the effect of GBC on assemblage E/T was quite high and significant ($p < 0.05$; Table 5.3, Figure 5.2). A slope of 0.92 represents a large, positive magnitude. These data show that as encounter rates with bison increased, Paleoindian foragers only harvested the most profitable parts, thus yielding higher GUDs. By contrast, when encounter rates were low, Paleoindian foragers harvested carcasses more intensely, generating lower GUDs represented by a low average E/T.

Conclusions

In this study, I conducted butchery experiments to generate the data necessary to test foraging hypotheses regarding Paleoindian hunter-gatherers. Our experiments provided data related to the caloric benefits and time costs of bison butchery. Professional, modern butchers conducted the bison disarticulation and defleshing, using stone tools. The caloric gains of meat and marrow and the time costs to extract them were quantified per bison anatomical part. I also collected data from published manuscripts on Paleoindian bison kills reporting the Minimum Number of Skeletal Elements. The latter were coupled with the bison butchery cost and benefit data generated by this study to calculate assemblage-wide return rates. I modeled return rates as a function of several variables, including bison encounter rates and assemblage size (MNI), in order to test foraging hypotheses derived from the Marginal Value Theorem operationalized as giving-up

densities. I used Generalized Least Squares for the hypothesis testing in order to account for sampling bias in space and time. The results showed that Paleoindian foragers, like other foraging organisms, followed the behavioral predictions drawn from foraging theory.

In particular, the archaeological record of foragers should be expected to match the predictions of the MVT and GUD in the context of bison hunting. Considering the archaeological remains of bison kills as Paleoindian GUDs, Paleoindian GUD values are expected to increase with higher bison herd encounter rates, and decrease with lower bison herd encounter rates. The results showed that bison carrying capacity (and thus potential encounter rates) had a large, positive effect of 0.92 on assemblage return rate. Moreover, the results supported the hypothesis, showing that Paleoindian foragers harvested only the most profitable parts when encounter rates (proxied by GBC) were high, and harvested carcasses more intensely when encounter rates were low.

The results of this study also present avenues for future research. Since, up to this point, data on bison butchery costs and benefits have been non-existent, I hope that these data will motivate those interested in this topic to use this new information to test other hypotheses related to Paleoindian foraging energetics.

Table 5.1. Average caloric returns and time butchery costs from this study.

Anatomical Part	Average Edible Weight (g)	Average Disarticulation Cost (s)
Cervical	4980.08	63.78
Thoracic	6844.3	279.745
Lumbar	7566.15	160.415
Ribs	36156.9	258.6913
Scapula	10220	159.8613
Humerus	7735.12	326
Radius/Ulna	3381.55	249.18
Metacarpal	23.4	240.625
Pelvis	8548.3	235.5375
Femur	29956.17	298.9375
Tibia	5091.45	183.5
Metatarsal	46.14	229.75
Phalanges	1.62	1105

Site	Component	Label	Reference	MNI	CRN	MR	CE	TH	LM	SAC	RB	SC	HM	RD	UL	MC	IM	FM	TA	MT	PH
12 Mile Creek	All	12MC	Hill Jr. 2002	13	2	5	25	53	18	3	34	6	8	10	8	16	3	10	14	10	165
Blackwater Draw	Sellards Clovis Bison Kill	BWD7	Hester 1972	4	4	5	0	0	0	0	0	3	0	0	0	0	0	0	1	0	4
Blackwater Draw	HPP 1961, Locality 3 Bonebed	BWD12	Hester 1972	3	3	1	0	0	0	0	16	1	2	0	1	0	1	1	2	0	20
Blackwater Draw	HPP 1962, Locality 5 Bonebed	BWD15	Hester 1972	7	0	0	0	0	0	0	3	1	2	2	0	0	2	0	1	0	0
Blackwater Draw	Jelinek Bonebed	BWD1	Johnson and Holliday 1997	4	0	2	5	1	2	0	12	0	1	2	0	1	2	3	4	5	6
Bonfire Shelter	Strat A & B/C	BFS	Byerly et al. 2005	24	5	26	57	65	42	13	43	13	30	26	18	18	16	33	26	14	171
Burntwood Creek	All	BRC	Hill Jr., et al. 1992	32	3	55	25	13	0	0	9	0	5	5	2	23	0	1	3	12	577
Cherokee Sewer	IIIa	CS	Pyle 1980	8	0	6	0	0	0	2	0	9	3	11	12	7	5	3	14	0	0
Clary Ranch	All	CR	Hill 2001	41	13	20	48	34	20	8	82	18	42	25	21	21	26	18	29	19	157
Cooper	Lower Kill	CPRL	Bement 1999	20	14	0	10	15	13	6	16	23	21	24	21	18	13	21	17	15	149
Cooper	Middle Kill	CPRM	Bement 1999	29	16	0	15	17	15	10	29	29	30	33	27	29	0	32	32	29	242
Cooper	Upper Kill	CPRU	Bement 1999	29	19	0	32	55	18	15	65	34	34	31	33	32	20	36	40	42	312
Folsom	All	FOL	Meltzer 2006	32	11	57	126	187	93	15	280	26	30	39	32	43	29	28	32	49	507
Frazier	All	FRAZ	Borresen 2002	44	5	27	24	33	12	14	16	41	29	36	0	41	0	23	37	44	341
Horner	I	HORN1	Frison and Todd 1987	158	7	29	14	20	15	7	257	25	41	36	23	35	29	39	40	44	82
Jake Bluff	All	JB	Bement and Carter 2003	15	0	0	0	0	0	0	0	0	25	23	12	20	0	30	25	16	0
Jerry Craig	All	JC	Hill and Kornfeld 1999	7	1	14	3	2	4	0	1	1	2	3	2	3	1	0	0	0	4
Jurgens	Area 3	JURG3	Wheat 1979	36	32	61	0	0	0	0	0	66	42	53	32	69	34	60	74	62	0
Lake Theo	Folsom	LKTH	Baxevanis 1997	12	2	8	10	5	5	1	0	3	8	4	5	11	1	1	6	4	56
Lamb Spring	All	LMBSP	McCartney 1983	28	8	13	50	53	26	3	69	12	15	14	15	9	15	14	17	13	89
Lipscomb	All	LIPS	Todd et al. 1992	56	0	47	39	0	0	14	0	34	49	56	43	96	0	36	37	67	153
Milnesand	All	MILSN	Hill Jr. 2002	33	1	6	1	1	0	0	1	2	6	6	2	8	1	1	0	2	38
Norton	All	NORT	Hofman et al. 1995	8	8	6	3	14	7	3	31	11	5	6	2	2	5	7	8	6	41
Olsen-Chubbuck	All	OLCH	Wheat 1972	190	64	102	313	865	320	64	1120	99	95	86	69	0	64	85	92	0	875
Plainview	All	PLAIN	Guffee 1979	2	0	0	0	0	0	0	192	16	27	17	5	23	4	18	19	27	30
Rex Rodgers	All	RXROD	Hill Jr. 2010	6	6	9	13	9	9	0	10	3	2	5	4	7	0	2	2	4	42
San Jon	All	SNJN	Hill et al. 1995	5	5	5	1	0	1	0	0	1	2	3	3	6	1	0	2	6	79

CRN = Cranium; MR = Mandible; CE = Cervical 1-7; TH = Thoracic 1-14; LM = Lumbar 1-5; SAC = Sacrum; RB = Rib; SC = Scapulae; HM = Humerus; RD = Radius; UL = Ulna; MC = Metacarpal; IM = Innominate; FM = Femur; TA = Tibia; MT = Metacarpal; PH = Phalange

Table 5.2. Paleoindian anatomical part data reported from bison kills used in this study.

Table 5.3. Model of assemblage E/T as a function of GBC. Parameters include ARIMA residuals and GLS regression coefficients, which account for spatio-temporal dependence.

ARIMA	p=0, d=1, q=1			
MA1	S.E.	AICc		
-1	0.118	220.76		
GLS Model (accounting for spatial auto correlation)				
<i>Spatial Dependence Model: Exponential</i>				
Range	Nugget			
0.000000003	0.11			
<i>Regression Model</i>				
	Estimate	S.E.	t	p value
Intercept	-510.35	203.090	-2.51293	<0.0001
GBC	0.924	0.3673	2.51648	<0.0001

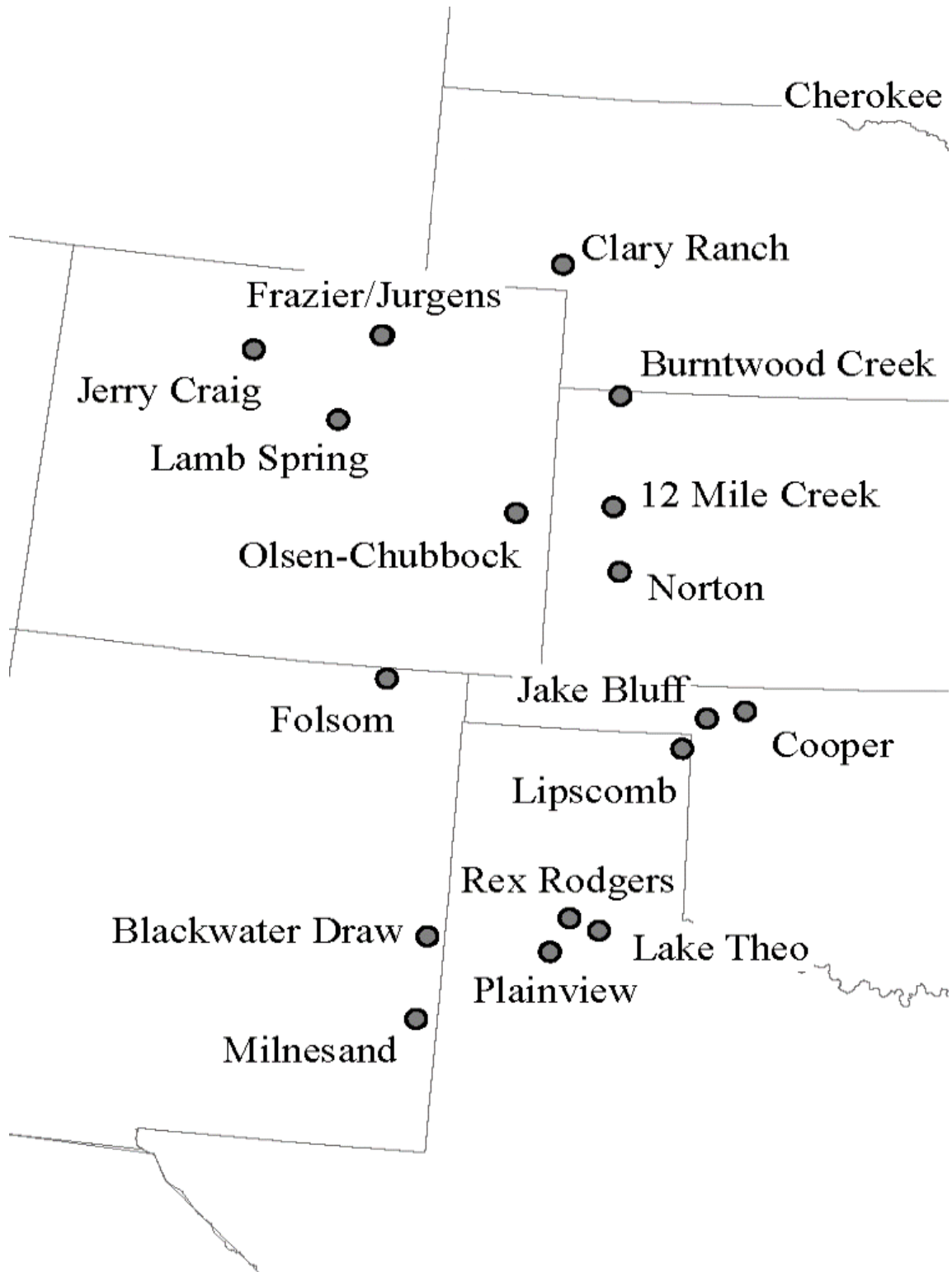


Figure 5.1. Map showing locations of kill sites used in this study.

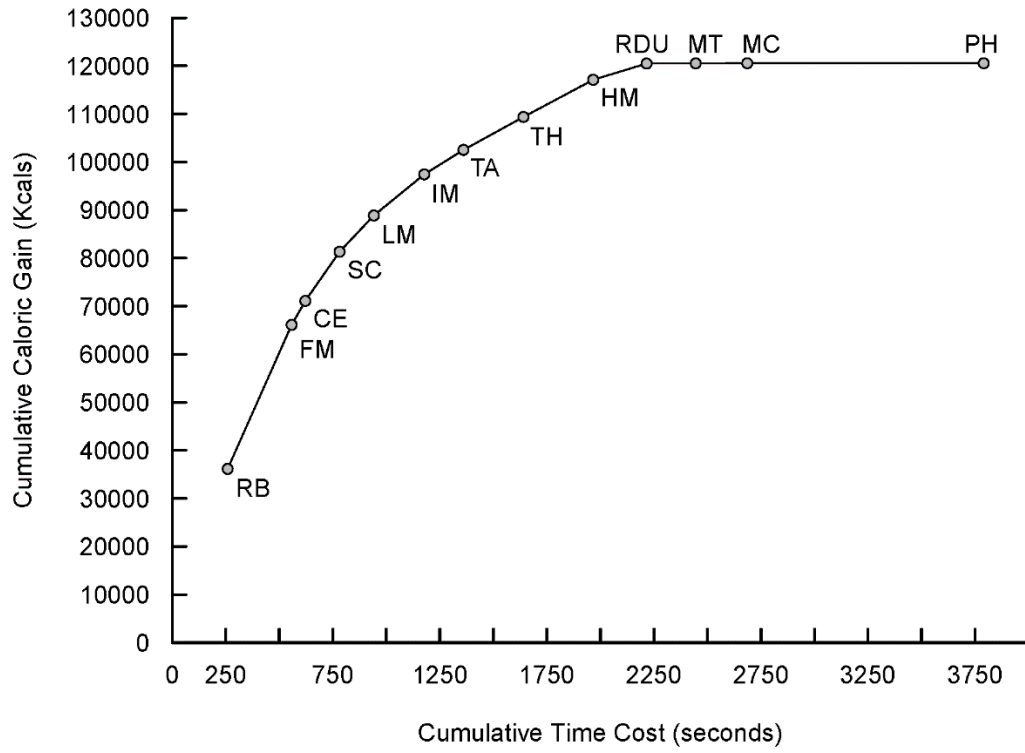


Figure 5.2. Bison gains curve derived from experiments.

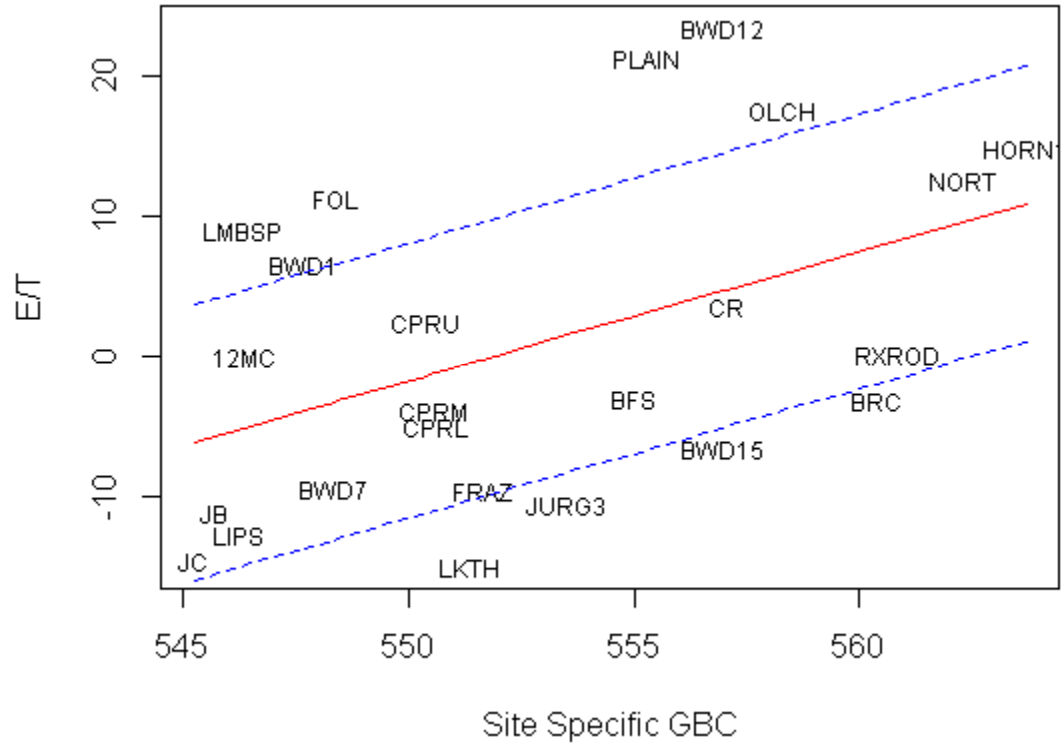


Figure 5.3. Model of assemblage-wide GUDs as a function of bison encounter rates

CHAPTER 6: SUMMARY AND CONCLUSIONS

Chapter Overview

This dissertation is an exploration of the use of predictive modeling to answer archaeological questions, particularly those related to the effects of climate on Paleoindian foragers' dietary diversity and bison hunting behavior. This study statistically modeled the distribution of paleoclimatic variables and bison abundance during the Paleoindian Period throughout the North American Great Plains, and then evaluated the effects of those variables on the diversity and spatial distribution of archaeofaunal remains composing the diet of these prehistoric hunter-gatherer populations. Through a series of quantitative investigations, the study generated the following key findings:

1. Chapter 3's reconstruction of paleoenvironmental variables showed that mean annual temperature, temperature seasonality, and annual precipitation had a great influence on Paleoindian foragers' dietary choices. Temperature seasonality had the greatest effect on Paleoindian diet diversity.
2. In modeling bison abundance in relation to grazing quality, Chapter 4 showed support for the hypothesis (derived from foraging theory) that the number of bison killed would decrease as grazing quality and the frequency of bison encounters increased. Evidence of Paleoindian foraging is consistent with the inference that these populations killed and harvested fewer bison when herd encounter rates were high, and more bison when encounter rates were low.
3. The bison butchery experiments presented in Chapter 5 indicated that Paleoindian foragers behaved as "cream-skimmers", harvesting only the most profitable skeletal

elements when bison herd encounter rates were high. On the other hand, they behaved like “crumb-pickers”, harvesting carcasses more intensely and removing more skeletal elements from kill sites when bison encounter rates were low.

As I will expand below, these findings and the statistical techniques used have important theoretical and practical implications.

Importance of Research on Paleoindians

The archaeological evidence of Paleoindians continues to be the most robust signal of the first colonizers of the North American continent. The colonization of the Americas is an exceptional context of relatively recent human forager dispersal. These foragers appear to have adapted well to their new environment, seemingly developing new technology (fluted points) to procure game to survive. The speed at which these early Paleoindians traversed the continent (500-300 years, Waters and Stafford 2007) suggests that these foragers developed a dispersal adaptation coupled with social network scales not observed in modern foragers. Thus modern models of forager behavioral variability currently used to interpret the Paleoindian archaeological record likely require additional information. To this end, this dissertation provides fresh view on the causal relationships between climatic and forager behavioral variability as observed in the zooarchaeological record.

In this context, Paleoindians left a rich and variable zooarchaeological record across the Great Plains and surrounding areas. However, these foragers have been normatively depicted as technologically savvy big-game hunters who, moving from kill to kill, settled the North American continent in record time. This stereotypical view of Paleoindians arose as the result of prominent Paleoindian megafauna kill sites associated with high frequencies

of good-quality, exotic tool-stone and proficient bifacial thinning and fluting technology. Granted, archaeological evidence of Paleoindian hunting patterns is noisy and far from a clear signal. Nonetheless, in the past few decades, archaeologists have learned that Paleoindian foragers were more complex than this traditional view, and new archaeological studies have continued to expand what is known about the Paleoindian lifeway and its variability.

The archaeological record of North American Paleoindians presents several advantages for testing hypotheses about hunter-gatherer foraging ecology. The infrastructure in Great Plains states (U.S.) and provinces (CAN) is stable and conducive to research. Archaeological databases are available from government agencies, for example, in addition to published literature. These data stem from nearly a century of public and private archaeological investigations in the region. Moreover, these prehistoric foragers lived within a relatively narrow period of time (~5,000 years). The resulting archaeological record for this time period is of relatively high quality, compared to the record of the deeper past in other parts of the world. The high resolution of this record facilitates the detection of changes in foraging behavior at small spatial and temporal scales.

Several mechanisms have been proposed to account for the observed variation in archaeofaunal diversity and abundance during the Paleoindian period throughout the Great Plains. For example, research has linked the climatic changes accompanying the onset of the Holocene epoch to changes in Paleoindians' diet diversity. However, researchers have rarely identified the climatic variables involved or conducted statistical evaluations of their relationship with patterns of diet diversity. Likewise, the bison abundance observed at Paleoindian-age kill sites has varied drastically across latitude throughout this region, with

more bison individuals recovered from northern Great Plains kill sites than from their southern counterparts. This zooarchaeological pattern has been hypothesized to reflect grazing quality and bison carrying capacity.

To test such hypotheses of hunter-gatherer foraging ecology and behavior, information about the foragers' abiotic (effects of non-living factors such as geography, climate, etc.) and biotic (effects of living factors, e.g., predators, prey, social context) environment is needed. This information provides ecological context to foraging observations – in this case, faunal remains recovered from archaeological sites. To this end, this study reconstructed key paleoclimatic variables and bison distribution during the Paleoindian period using pollen records as paleoenvironmental proxies and introducing new statistical modeling techniques.

Key Findings

First, this study modeled quantitative paleoenvironmental variables to evaluate hypotheses about the effects of climate change on Paleoindian foraging behavior across the Great Plains. For example, researchers have often causally linked the zooarchaeological record of Paleoindians to increases in seasonal variation and temperature, and to a decrease in precipitation brought on by the Holocene climate regime. Using archaeological evidence to measure diet breadth, results showed that several climatic variables had an effect on the Paleoindian diet. Mean annual temperature, temperature seasonality, and annual precipitation had a strong impact on Paleoindian diet diversity, while temperature seasonality had the greatest effect.

Subsequently, this study evaluated the hypothesis that the number of bison recovered from Paleoindian kill sites (MNI) should be positively correlated with higher bison carrying capacity. Foraging theory, however, predicts that in better grazing habitats where Paleoindian hunters would have encountered bison herds more often, they would have harvested fewer animals. Given that an encounter with another herd was expected soon, there would have been little need to procure a lot of bison in a short amount of time. In this context, Paleoindian foragers probably behaved like “cream-skimmers”, on average procuring fewer bison. By contrast, in habitats where hunters expected to encounter herds less frequently, they would have harvested more animals in order to ensure greater nutritional security. In this case, Paleoindian foragers behaved as “crumb-pickers”, harvesting as much as possible. As shown in Figure 4.8, assessing the zooarchaeological record of Paleoindians in light of the reconstructed bison carrying capacity supports the predictions of the Marginal Value Theorem (MVT); when bison carrying capacity estimates were low, kill sites indicate that more bison were hunted and killed on average than when carrying capacity estimates were high.

Testing foraging hypotheses also requires information about a forager’s behavior and decision-making goals. Researchers have tried to understand human foragers’ energetic and economic goals through the lens of Optimal Foraging Theory (OFT), which predicts behavioral decisions based on the energetic outcomes of foraging events. OFT draws on economic theory to predict the foods organisms should include in their diet (MacArthur and Pianka 1966; Emlen 1966) through the optimal or most economical allocation of time and energy to their foraging behavior. One of the utilities of OFT is that

foragers' deviations from this baseline can be measured, thereby generating further prediction and investigation.

This study modeled Paleoindian prey transport decision-making within an OFT framework using experimental bison butchery. The experiments were designed to quantify the time costs and energetic benefits of bison butchery per skeletal element, providing essential data with which to test hypotheses regarding Paleoindians' foraging decisions. To characterize foraging behavior, data on Minimum Number of Skeletal Elements (MNE) were collected from published manuscripts on a robust sample of Paleoindian bison kills. These and the bison butchery data were used to calculate assemblage-wide return rates for each Paleoindian kill site. Assemblage return rates were analyzed as responses to several variables, including bison encounter rate and assemblage size (bison MNI), in order to test hypotheses from the Marginal Value Theorem (MVT) operationalized through giving-up densities (GUDs, i.e., the density of food left in the foraging patch at the point when a forager decides to stop harvesting and move to another patch). The MVT predicts that Paleoindian GUD values should increase with increasing bison herd encounter rates, and decrease in association with decreased bison herd encounter rates.

The results of the modeling showed that bison carrying capacity (and thus potential encounter rates) had a very large effect on assemblage return rate. These data showed that as encounter rates with bison increased, Paleoindian foragers again behaved as "cream-skimmers", harvesting only the most profitable parts and thus leaving higher GUDs. On the other hand, when encounter rates were low, Paleoindian foragers became "crumb-pickers"; they more intensely harvested carcasses, leaving lower GUDs, as represented by assemblages with low average E/T.

Theoretical and Methodological Contributions

Inferences about the foraging behavior of Paleoindians using the zooarchaeological record have become increasingly nuanced. Researchers continue to discover or re-analyze archaeological sites containing faunal remains. This has resulted in new interpretations about the variation of Paleoindian foraging behavior across the Great Plains (e.g., Knell 2002, Widga, 2007, Hill Jr. 2008). However, current frames of reference through which to interpret the zooarchaeological record have important limitations. For example, Frison (1982: 200) commented that it is difficult to interpret the Paleoindian zooarchaeological record through the lens of ethnographic analogy or recent prehistory, and such an approach has not been fruitful. Todd (1987, 1991) concurred, arguing that Paleoindian foragers faced drastically different environmental contexts compared to foragers documented ethnographically or later Prehistoric foragers (e.g., dampened seasonal extremes, lower temperatures, and greater precipitation during Paleoindian times). Accordingly, these environmental conditions likely affected Paleoindians' ecological relationships, including their foraging behavior. Unfortunately, many interpretations of the zooarchaeological record have not been derived from quantitatively reconstructed environmental contexts. Although investigations of Great Plains Paleoindian foraging have frequently speculated that climate might have caused shifts in these people's diet, they have not tested the association between the zooarchaeological record and paleoclimate. To address this gap, this dissertation quantitatively reconstructed the climatic environment during the Paleoindian period. This is a novel contribution, employing new statistical techniques, including spatio-temporal statistical methods and model selection techniques grounded in information theory.

Paleoindians' dietary patterns evidenced by the zooarchaeological record vary widely across space and time, likely as a response to their biotic and abiotic environment. This study revealed several causes of this variation, including associations between reconstructed paleoclimatic variables and Paleoindian diet diversity. Whereas temperature and precipitation increased diet diversity, temperature seasonality caused it to decrease. The positive effect of temperature on the diet diversity of Paleoindian camps could be related to the increasing aridity of the grasslands and evapotranspiration accompanying warming. Increasingly arid grasslands might not have supported enough bison to secure this prey as a dietary staple; expanding dietary diversity would have been a sensible foraging response to lower bison encounter rates. Increased precipitation also led to greater camp diet diversity, with occupied habitats showing greater species richness. Paleoindians could have easily taken advantage of this increased diversity and incorporated the higher faunal richness into their diet.

By contrast, temperature seasonality negatively affected the dietary diversity of Paleoindian camps. Camps in highly seasonal environments, such as Hell Gap III/V, Waugh, and Agate Basin – Folsom, were probably reoccupied multiple times, serving as short-term base camps to which logistical groups were deployed to perform specific tasks. This type of usage (e.g., specific food procurement, tool-stone gear up) would have generated a low diversity of artifacts, especially with seasonally specific tasks. Camps such as Lindenmeier, located in less seasonal habitats, probably served as more stable residences. In such camps, greater faunal diversity is to be expected, representing a more complete range of the Paleoindian diet.

The paleoenvironmental variables reconstructed by this study were also used to model bison grazing quality and carrying capacity. This model was crucial for testing hypotheses about the predator–prey relationship between Paleoindians and bison. The results did not support the traditional view that higher prehistoric grazing quality was responsible for a greater number of bison being recovered from a Paleoindian kill site. Rather, following the predictions generated by OFT, hunters should harvest more animals in habitats with lower bison encounter rates than in habitats with higher encounter probabilities. In the poor habitat, there is uncertainty over when the next prey encounter will be, whereas in better habitats, this uncertainty is reduced and thus the hunter does not need to expend more energy to ensure greater food security.

Paleoindians were mindful of their energetic budget. Through experimental bison butchery, this study also tested novel hypotheses about the energetics related to skeletal element patterns at bison kills. Results suggested that when bison encounters were high, Paleoindians acted as “cream-skimmers” of killed bison carcasses; skeletal element patterns showed that Paleoindians’ rates of energetic intake over time spent butchering (E/T) were kept high by only removing the highest ranked parts. By contrast, when encounters with bison were low, Paleoindians acted as “crumb-pickers”, expending more effort to remove lower ranked bison skeletal elements. Although this behavior provided marginal energetic gains, it decreased the energetic rate of intake, E/T.

The Paleoindian energy budget needs detailed examination in the context of human evolutionary ecology and biology. For example, individuals in a given habitat are required to capture enough energy to be able to carry out basic biological functions such as basal metabolic rate, cellular repair, organ and immune function, growth, and reproduction. In

several habitats, however, the energy available for human harvest might be lower than the expected amount of energy required to meet the individual's biological requirements. Yet, akin to sharing, human energy transfers (Jaeggi and Gurven 2013) are thought to function as part of a budget of pooled energy investment from many individuals (e.g., Kramer et al. 2009; Kramer and Ellison 2010). Pooled labor as an energetic investment can result in higher expected per capita payoffs than payoffs from individuals working alone.

In the context of Paleoindian behavior in the Great Plains, communal hunts might have been an important manifestation of the pooled energy budgets observed in modern hunter-gatherer and horticultural societies. Many Great Plains habitats had low bison herd encounter rates, consequently decreasing the expected amount of energy individual Paleoindians could harvest. Given that an individual forager's energetic investment in harvesting large numbers of bison is high, presumably the probability of injury or death would also be high, while hunting success rates seem like they would be low. In light of this, energy investment pooling among several individuals might have provided higher per capita energetic returns, while reducing individual energy investment and rates of injury and death. Moreover, such behavior might have turned otherwise energetically unfavorable habitats into habitable environments, increasing the growth rate of these early American populations.

Broader Implications

The implications of this dissertation reach beyond the archaeological contexts of Paleoindian foragers and their diet. Questions about the effects of paleoclimate and paleoenvironments on human and other organismal populations are abundant. Without rigorous scientific hypothesis testing, however, these questions are unanswerable. Sound

statistical evaluations of scientific hypotheses result in stronger statements of the hypotheses' magnitudes and directionality. Continued quantitative studies of the paleoenvironmental context and statistical evaluation of observed archaeological human foraging behaviors will enable archaeologists to provide stronger statements about the human past.

Identifying ecologically sensitive behavioral variability as done in this study is not normative and reflects a major transformation in the way I reconstruct early societies. Examples where pollen can be used to estimate the effects of climate occur in North America, beyond the Great Plains, but also across continents as in the Northern Aegean (Gogou et al. 2016) and Southern Africa (Carrión et al. 2001). Analyzing multiple pollen spectra representing sites across the Northern Aegean from the European Pollen Database, Gogou et al. (2016) showed that cultivation practices seem to have been dependent on climatic fluctuations. As this dissertation demonstrated, other paleoenvironmental data can be extracted from these pollen data using the MAT. This approach might provide insight into more nuanced dynamics between climate and subsistence practices during the time period in question. Contexts where pollen databases might not be as extensive as in North America or Europe, pooling the existing data to create a working model might be an option. The covariation between fluctuations in behavioral variability and climate might be useful hypotheses in such contexts as in the transition from middle to later Stone Age in southern Africa (e.g., Shea 2011) or the mid-Holocene period in Australia (e.g., Hiscock 2008). In this context Spatio-temporal models of the paleoenvironments can be continuously updated as new proxy data are recovered.

Reconstructing herbivore ecological dynamics, as done in Chapter 4, would aid range management practices and repopulation efforts. Understanding how ecological dynamics played out in the past can serve as an effective model to guide modern re-introduction, preservation, and conservation projects, for example, in the reintroduction of wolves in Yellowstone National Park, where their population density can be predicted by the density of elk, their prey (Mech and Barber-Meyer 2015). This is a case where knowledge of the paleo environmental and ecological conditions under which elk and wolf populations thrived (Lyman 2004) might help their management.

Future Research

There are several lines of research yet to pursue. Further conceptual development is required to better understand prehistoric foraging in light of the archaeological record. There is a need for continued studies linking archaeological statics (the artifacts) to behavioral dynamics, and the development of novel analytical tools to make these links. Solid linkages between bones from archaeological contexts to people in foraging contexts will undoubtedly render stronger, more reliable inferences about prehistoric hunter-gatherers.

An obvious area of further research is with regard to the predator–prey dynamic between Paleoindian hunter-gatherers and bison. This dynamic can be modeled using several approaches common in the biological literature (e.g., Rockwood 2006: 207-251). Determining the potential amount of energy that was available and accessible to Paleoindians provides another line of research. Energetically based models of Paleoindian population dynamics, using energy derived from bison availability, are now possible (e.g., Belovsky 1987). Such models might provide insight into the potential life history tradeoffs

faced by North American Paleoindians, and generate hypotheses testable among modern native populations.

Lastly, carrying capacity models are based on sound assumptions and previously well documented experimental evidence (e.g., McNaughton 1984), particularly in the North American Great Plains (Frank et al. 1998). By definition, however, models are simplifications of reality. As such, models do not reflect the complex realities inherent in a system, and predictions of the modeled carrying capacities should be tested, empirically on the ground, using two types of data: 1) prehistoric and 2) modern. The first might help scientists to find more Paleoindian sites, while the second might assist range managers in the current ecologically oriented management of bison and grasslands.

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APPENDIX A: MATERIALS: PALEOINDIAN ARCHAEOLOGICAL DATA

12 Mile Creek (Hill Jr. 2006)

The 12 Mile Creek site is located in the western part of Kansas. Three radiocarbon dates have been averaged to give an expected date of 10,504 BP. These dates are associated with a Clovis or Folsom component and at least 13 bison individuals (MNI), seemingly killed and partially butchered at the site. This site has been classified as a mass bison kill site.

48SW13156 (Byers, et al. 2005)

The 48SW13156 site is located in southwestern Wyoming. Archaeologists have identified 172 faunal remains that have been radiocarbon dated to 8725 BP. The faunal remains found at this site indicate that the main prey type was small, difficult to catch animals. This site was inferred to be a campsite after further investigation.

48SW8842 (Byers et al. 2005)

The 48SW8842 site is a multicomponent site located in southwestern Wyoming. Radiocarbon dating has placed this site at 8490 BP. Similar to the 48SW13156 site, this site contains only small animal remains. Based on the 147 specimens identified, archaeologists declared the 48SW8842 site to be a campsite.

48UT375 (Smith et al. 2003)

The 48UT375 site is located in the southwestern corner of Wyoming. This site consists of two levels; Level 1 was dated to 8479 BP and yielded 926 identified faunal specimens,

while Level 2 was dated to 7890 BP and yielded 3,190 identified specimens. All faunal remains belong to small animals. Archaeologists believe that both Levels functioned as campsites, where Paleoindians regularly targeted small animals for dietary consumption.

Agate Basin (Frison and Stanford 2014)

The Agate Basin site (48N0201) is located in eastern Wyoming. Multiple Paleoindian components of varying ages have been observed at this site ranging between $10,780 \pm 120$ to $10,430 \pm 570$ BP. Cultural components at this site include Folsom, Agate Basin, Hell Gap, and potentially Alberta components. Bison (and pronghorn) kill-butchery bonebeds are common features across these components, with bison and pronghorn among the dietary archaeofaunal remains found. Paleoindians occupied the multiple Agate Basin components and conducted tasks expected at kills, camps, and kill/processing areas.

Allen (Bamforth 2007)

Allen is one of the Medicine Creek sites, located in Frontier County, southwestern Nebraska in the Medicine Creek drainage area. Paleoindians from the Great Plains set up repeat camps at this location, temporally clustered around the Early and Late Paleoindian periods. Faunal remains include a large number of processed species, and particularly high numbers of bison, deer, and pronghorn. Archaeologists have found that the faunal remains at each level of occupation have a different composition, likely indicating changes in environment. Faunal composition and patterning suggest that Allen repeatedly functioned as a Paleoindian camp.

Aubrey (Ferring 2001)

The Aubrey site is located at Lake Ray Roberts, Denton County, Texas. This multi-cluster complex contains Clovis-age materials. Archaeologists have examined and recorded a total of 22,617 animal bones. The presence of bison bones and associated artifacts indicates that there was a butchering site on the pond shore. The faunal remains further indicate that Paleoindians at Aubrey exploited a wide array of animals.

Big Lake (Turpin et al. 1997)

The Big Lake site (41RG13) is located in Reagan County, Texas. It has been dated to 8,000 radiocarbon years ago. At this site, at least 10 female and sub-adult bison appear to have been stuck in mud, and then dispatched and butchered by Paleoindian foragers. The remains were covered by a sand dune. Two fragments of a single projectile point are the only associated lithic artifacts. The site is inferred to have functioned as a kill site.

Blackwater Draw (Hester 1972)

Blackwater Draw is a multicomponent site located in eastern New Mexico, approximately 18 miles west of the New Mexico–Texas border and 13 miles south of the town of Clovis, New Mexico. Blackwater Draw locality 1 represents the type site for the Clovis culture. If Folsom confirmed the presence of humans in the New World during the Pleistocene epoch, Blackwater Draw confirmed that those early humans hunted mammoth. In the 1920s, artifact collectors documented evidence of bifacially reduced stone tools. In 1932, E.B. Howard conducted the first large-scale excavation at BWD. He named these lanceolate projectile points “Clovis” after the nearby town. Archaeologists have recovered faunal

remains of Pleistocene mammoth and bison from several levels associated with Clovis, Folsom, and later Paleoindian occupations.

Blue Point (Johnson and Pastor 2003)

The Blue Point site is located within the Green River Basin, northwest of Green River, Wyoming. It is a multicomponent site reflecting a Late Paleoindian Alberta occupation (9540 BP) and a Terminal Paleoindian/Early Archaic occupation (8200–8300 BP). Blue Point has two Paleoindian components: Component 1 dates to the Late Paleoindian period and Component 2 marks the transition between the Terminal Paleoindian and the Early Archaic periods. The occupation contains the remains of fire-cracked rock and a hearth. This evidence has suggested that Paleoindians used this site as a camp.

Bonfire Shelter (Byerly et al. 2005)

The Bonfire Shelter site is a multicomponent archaeological site located in the southwestern part of Texas near the town of Langtry. The site was excavated in 1963 and re-excavated 20 years later in 1983. Archaeologists have found two distinct bison bone deposits associated with Folsom-aged lithic artifacts dating to 9871 BP. The Bonfire Shelter site was originally believed to be a bison jump site, but was later found to be a secondary processing site, with at least 24 bison being transported there and processed.

Bottleneck Cave (Husted 1969)

Bottleneck Cave (48BH206) is a site located in Bighorn Canyon on the bank of the Bighorn River in northern Bighorn County, Wyoming. This cave was formed by the river, and

between and after habitation, the cave was filled with wind-blown sand. Excavation began in 1962, ultimately revealing five occupation levels. The lower three were within the lower 2.5 feet of sand, the fourth level was separated by 1.5 to 3 feet of sand, and the fifth level was another foot above. The preferred mammals of Occupation 3 were determined to be deer/antelope, bighorn sheep, and assorted small species. The few mammal bones present in Occupation 2 indicate a preference for species of deer/antelope and bighorn sheep. Mammal bones were rare in Occupation 1, with only four bones and some teeth indicating three or four different species (deer/antelope, bison, and bighorn sheep).

Burntwood Creek (Hill Jr. et al. 1992)

The Burntwood Creek site is located in Rawlins County, western Kansas, along a tributary of the Republican River. It is a Late Paleoindian locality where 32 bison were killed and processed approximately 9085 radiocarbon years BP. H.T Martin initially reported the site in 1921. Hill Jr. et al. later conducted a re-examination of the site to evaluate taphonomic effects on the site. Evidence of fluvial activity and carnivore modifications were observed on the assemblage. These factors likely removed an unknown number of skeletal elements from the assemblage, although evidence of carnivore scavenging was minimal. The evidence seems consistent with the interpretation of this site as a bison kill, where the hunters partially butchered and removed parts of these bison for later consumption.

Carter-Kerr-McGee (Frison 1984)

The Carter-Kerr-McGee site is located in the Powder River basin in northeastern Wyoming. The site was discovered during strip mining operations in 1975 and excavated

in 1977. It is a stratified site containing Paleoindian deposits. The Alberta/Cody Paleoindian component is a bison bonebed composed of at least 47 bison individuals. Investigators have inferred that the bison remains are the result of kill/processing activities, including bone breakage to extract marrow.

Casper (Todd et al. 1997)

The Casper site is located in eastern Wyoming and represents a classic multi-animal archaeological bison kill of Paleoindian age (Hell-Gap ~ 10KBP). Casper is thought to have been a sand dune trap where Paleoindian hunters hunted, killed, and butchered 75–100 *Bison antiquus* individuals. Archaeologists have documented extensive marrow breakage and over 80 Hell Gap projectile points, among other tools.

Cherokee Sewer (Pyle 1980)

Cherokee Sewer is a multicomponent site (Late Paleoindian and Archaic) located on the eastern plains of northwest Iowa. Paleoindian bison remains along with an Agate Basin point were discovered during salvage operations in 1973. Several individual bison skeletal elements were still semi-articulated, and archaeologists have inferred that the site served as a kill site.

Clary Ranch (Hill 2001)

The Clary Ranch site is a Late Paleoindian (Allen/Frederick Complex) locality on the central Great Plains in western Nebraska. It is located along the base of a cut bank in Ash Hollow Draw, a tributary of the north Platte River. Archaeologists have found the remains

of at least 41 bison in the form of complete and articulated bison limbs. The assumption is that the site functioned as a secondary processing area; bison were removed from a nearby kill site and transported to Clary Ranch for intensive processing and extraction of meat and marrow.

Colby (Frison and Todd 1986)

The Colby site is located in the Bighorn Basin in northern Wyoming and has been dated to 10,961 BP. It contains seven mammoths in association with several Clovis artifacts. During five field seasons between 1973 and 1978, archaeologists recovered the remains from multiple smaller species of animals. Colby has been interpreted as a winter camp where Paleoindians with Clovis toolkits might have hunted and processed mammoth.

Cooper (Bement 1999)

Cooper is a Folsom-age arroyo-trap bison kill site in northwest Oklahoma, dating to 10,050 ± 210 BP. The site is composed of three large bison bonebeds containing at least 68 animals. These bonebeds have been inferred to represent three large-scale kill episodes, during which these bison were hunted, killed, and butchered.

Domebo (Leonhardy 1966)

The Domebo site is located in central Oklahoma in Caddo County, dating to 11,091 BP. It is one of the rare archaeological sites that clearly features mammoth remains next to Paleoindian stone tools and projectile points. Archaeologists have identified 75 specimens at this site (NISP), interpreted to be the result of a Clovis mammoth kill.

Finley (Hill Jr 2008)

This site is located in the southwestern foothills of Wyoming. It is of Holocene age dating to 9009 BP. Subsurface investigations were conducted after 1940, when projectile points were observed on the surface of the site. Multiple universities have performed further tests on the Finley site. Archaeologists have identified 8,326 bison specimens at the site (NISP), including two bison bonebeds. Finley is currently thought to be a mass bison kill site.

Folsom (Meltzer 2006)

The site is located along Wild Horse Arroyo in northeastern New Mexico, approximately 14 miles south of the Colorado border and 10 miles west of the town of Folsom. Excavations at Folsom in the 1920s demonstrated the antiquity of the human presence on the North American continent. Paleoindians killed 32 bison and prepared them for transport at this site. The archaeological remains are dominated by low-utility skeletal elements and broken projectile points; high-utility bones are rare or absent. Archaeologists have determined that Folsom was a bison kill site – the type site for the Paleoindian Folsom culture and a keystone site in the history of North American archaeology.

Frasca (Fulgham and Stanford 1982)

Area I at the Frasca site (5LO19) is located in northeast Colorado near the city of Sterling. The site was discovered on a cut bank along Pawnee Creek, a tributary of the South Platte River. It is a Cody Complex-aged bison kill and processing site, consisting of at least 63 bison.

Frazier (Borresen 2002)

Frazier (5WL268) is located in northeastern Colorado. H. Marie Wormington initially discovered the site in the 1960s and determined it to be of Agate Basin age (~10kya). Archaeologists have identified a minimum of 44 bison individuals, largely from a cow-calf herd, and determined the site to be a bison kill-butcher site.

Hanson (Amick 1994)

The Hanson site is located in Wyoming near the Rocky Mountains. Radiocarbon dating has determined the site to be from 10,251 BP. Hanson represents an important site in the understanding of Paleoindian economy, land use, and mobility, as it has produced high-quality information about site age, chipped stone assemblages, and bison utilization. The site functioned as a Paleoindian lithic workshop.

Helen Lookingbill (Kornfeld et al. 2001)

The Helen Lookingbill site is a high-altitude (2620 masl) open site in the Wahakie Range of the Absaroka Mountains in northwest Wyoming. Archaeological remains indicate the site's usage from Paleoindian to Late Prehistoric periods, with each period being well represented. Major materials found include chipped stone, high frequencies of medium-sized mammals, and very low frequencies of bison. The pattern of skeletal elements is consistent with a kill-butcher site.

Hell Gap (Knell et al. 2002)

The Hell Gap site (48GO305) is located at 1,500 masl in eastern Wyoming and consists of five localities. Archaeologists have determined that materials are from four Paleoindian cultures: Midland, Agate Basin, Hell Gap, and Lusk. A total of 1,318 faunal specimens have been identified as Agate Basin material, 98.6% of which are bison (NISP=1,300).

Heron Eden (Corbeil 1995)

The Heron Eden site is located on the Great Plains of Saskatchewan, Canada. Radiocarbon dating has indicated that the site and its remains are from 9037 BP. This is an age range consistent with the Cody Complex and the Scottsbluff and Eden projectile points recovered at the site. The 22,901 faunal specimens identified at this site represent at least 37 animals. This site is believed to have been a multiple (at least two) bison kill/butchery site that took place in the winter. However, it is difficult to quantify the size of each individual event.

Horner (Frison and Todd 1987)

The Horner site is located in the northern Bighorn Basin of Wyoming. Archaeologists from Princeton University and the Smithsonian Institution first investigated the site between 1949 and 1952. Radiocarbon dating has indicated that systematic bison procurement occurred at the site for approximately 1,000 years around 9000 BP. The bison bonebed found contains chipped stone weapons and tools. It is the type site of the Cody Complex.

Howard Gully (Hurst et al. 2010)

Howard Gully (34GR121) is located in Oklahoma along the Osage Plains. The site has been radiocarbon dated to 10,021 BP. A total of 2,066 bone fragments were recovered from the site. Thirty-five were identifiable to skeletal element, representing the remains of two bison. Several projectile points recovered from this site resemble the San Patrice type frequently occurring east of the southern Great Plains. This site is thought to have functioned as a bison kill and processing site.

Hudson-Meng (Agenbroad 1978; Todd and Rapson 1999)

The Hudson-Meng site is located in the High Plains of Nebraska. Three radiocarbon dates have yielded an average expected date of 9418 BP. Faunal remains identified represent nearly 500 individuals of an extinct species of bison, seemingly in association with 21 Alberta points or point fragments and bone tools. The degree of human influence on the creation of the death assemblage has been explained by several competing hypotheses. These inferences range from viewing Hudson-Meng as a human butchery locality to seeing it as a naturally occurring multi-animal bonebed.

Jake Bluff (Bement and Carter 2003)

The Jake Bluff site is a multicomponent Clovis and Folsom site with sediment separating the two deposits. This site is located in northern Oklahoma near the Beaver River floodplain. Radiocarbon dating has indicated that this site is from 10,762 BP. Archaeologists have found a total of 167 specimen and complete projectile points at the site. Sediment samples from this site have been used to help construct the

paleoenvironment. Jake Bluff represents a Clovis-era bison kill site with an overlaying Folsom deposit.

James (“Jimmy”) Allen (Berman 1959; Mulloy 1959)

The James Allen site is located in the Wyoming Basin, close to 14-miles south of the town of Laramie. Radiocarbon dating has revealed this site to be from 8405 BP. This is the type site for the Allen type (previously known as “Yuma”), characterized by its lanceolate shape, lenticular cross-section, and oblique-parallel flake removal scars across the surface. Mulloy reported observing >30 Allen points and point fragments, mostly manufactured from fine-grained quartzites, in association with at least 15 individuals of an extinct species of bison (Berman 1959). The Jimmy Allen site is believed to have been a kill (or associated with nearby kill) and processing site.

Jerry Craig (Hill and Kornfeld 1999; Kornfeld and Frison 2000)

The Jerry Craig site is located in Middle Park, Colorado. This site dates to 9360 BP. Lithic artifacts include Cody or Cody-like projectile point fragments, and several with parallel-oblique flake removal. Associated bison remains recovered reflect the presence of at least seven individuals that died in late-summer/early-fall. Blood residue analysis associated with projectile points at the site suggests that Jerry Craig was a kill/processing site.

Jones Miller (Stanford 1984, 1999)

The Jones Miller site is located in Colorado and has been radiocarbon dated to 10,020 BP. At this site, more than 100 Hell Gap point and point fragments have been documented in

association with >41,000 bison bones representing a least 250 individuals, exhibiting evidence of butchery. Investigators have inferred that these remains are the result of a bison-pound kill and associated processing work.

Jurgens (Wheat 1979)

The Jurgens site is located in northeastern Colorado, approximately 50 miles south of the Wyoming border near the cities of Kersey and Greeley, Colorado. It is a Paleoindian site associated with the Cody Complex. Frank Frazier, a geologist and namesake of the Frazier Paleoindian site, discovered Jurgens in 1967. He then notified H. Marie Wormington, who visited the site with Joe-Ben Wheat on July 30, 1967. In total, approximately 75 bison individuals have been recovered from all areas. The site is composed of three areas that were used as kill/processing sites and a camp.

Laird (Hofman and Blackmar 1997)

Located in northeastern Sherman County, Kansas, the Laird site was discovered in 1990. Investigators reported 322 bison bone-fragments in association with a Dalton-like Paleoindian projectile point and lithic debitage. Identifiable bison remains indicate the presence of at least two individuals. This limited evidence suggests that the site functioned as a small bison kill site.

Lake Theo (Baxevanis 1997)

Lake Theo is a Folsom-aged bonebed, located in Caprock Canyons State Park in southeastern Briscoe County, Texas, dating to 10–12 kya. Artifacts were first found in 1972

on the surface at the edge of the lake. Testing in 1974 indicated that the site was a campsite and bison-butcher area composed of 6,919 bone specimens from an extinct type of bison, associated with Folsom projectile points. These bison specimens represent the remains of at least 12 individuals. Cultural modification of the bones includes cutmarks and intentional breakage. The site has been interpreted as a campsite and secondary butchery/processing locality.

Lamb Spring (McCartney 1983)

The Lamb Spring site is located south of Denver in central Colorado. Waldo Wedel and Dennis Stanford conducted excavations at this site in the 1960s and early 1980s. Excavations yielded a Late Paleoindian component, including diagnostic Cody-type projectile points and tools associated with 579 bison bones and bone fragments. Bison remains represent 27 mature male individuals that died in spring. It is believed to have been a Paleoindian bison kill and butchery site.

Levi Rockshelter (Alexander 1963)

The Levi Rockshelter site is a multicomponent site located in southeastern Texas. The earliest component (Zone II) dates to $10,000 \pm 125$ BP and is associated with a potential Clovis point. The Late Paleoindian component (Zone V) is associated with Angostura-type projectile points dating from 8262 ± 109 BP. This site represents a Paleoindian campsite.

Lime Creek (Jones 1999)

Lime Creek (24FT41) is a deeply buried, Late Paleoindian/early Archaic multicomponent site located in the Republican River basin of southwestern Nebraska. It is one of the Medicine Creek sites. Excavations were conducted from 1947 to 1950 after a flash flood revealed lithic debitage and bone. The Cody-aged component (Zone I) at Lime Creek dates to 9120 ± 510 BP. This component has yielded several lithic artifacts, including Scottsbluff and Milnesand projectile points. The faunal assemblage is diverse, representing 13 different animal taxa; but, it is dominated by bison, beaver, and pronghorn. The site is believed to have functioned as a Paleoindian camp.

Lindenmeier (Wilmsen and Roberts 1978)

The well-known Lindenmeier site is located in northern Colorado. Artifact collectors discovered the site in 1924, and Frank H. H. Roberts Jr. excavated it from 1934 to 1940. The site has revealed an extended period of occupation, although excavations have concentrated upon the Folsom component (dated to 10,600–10,720 BP). Several species of fauna have been identified, but the assemblage is dominated by 524 bison specimens representing at least 13 individuals. Evidence suggests that Lindenmeier functioned as a camp during Folsom times.

Lipscomb (Hofman and Todd 2001; Todd et al. 1992)

The Lipscomb site is located on the Southern Plains in North Texas. During its excavation in 1939 and 1946, archaeologists discovered a bison bonebed associated with Folsom projectile points. These bison remains have been dated to 10,820 BP. Upon later

investigation, the site seemed to represent a Folsom bison kill, consisting of at least 55 animals with a total of 1,202 identified specimens.

Lubbock Lake (Johnson and Holliday 1989)

Lubbock Lake is a well-known multicomponent archaeological site located in Texas. The different components vary widely in their radiocarbon dates, ranging from 200 BP to 11,100 BP, and in their site function, ranging from kill/processing, secondary processing, campsites, and even unknown functions. As a result, this site has given archaeologists plenty of insight into Paleoindian activity.

Mangus (Husted 1969)

The Mangus site (24CB221) is a multi-occupation rockshelter located in Bighorn Canyon on the bank of the Bighorn River in southern Carbon County, Montana. Excavation began in 1962, ultimately revealing three occupation levels. The lower of three, Occupation 1, dates to 8641 BP and has yielded several lanceolate and stemmed projectile points consistent with Late Paleoindian foothills/mountain archaeological cultures. Several “fire pits” suggest the long-term use of this site. The preferred mammals of Occupation 1 have been determined to be mule deer and cottontail rabbit. Mangus appears to have been used as a camp by late Paleoindian foragers.

Marks Beach (Holliday 1997; LaBelle and Meltzer 1996)

Marks Beach is a multicomponent site located on the High Plains of Texas, on the edge of Blackwater Draw. Radiocarbon dating has indicated that the site is from 10,301 BP. The

Marks Beach site was reinvestigated as a possible Early/Middle Holocene campsite near Blackwater Draw. However, the site is still believed to have functioned as a kill/processing site.

Medicine Lodge Creek (Walker 1975)

The Medicine Lodge Creek site is located in Big Horn County, Wyoming, on the west slope of the Big Horn Mountains at an elevation of 4,811 feet. The site's cultural components vary from Early Paleoindian to Late Prehistoric. Vertebrate faunal remains have been identified at all levels of the site. Most of the game present include mountain sheep, deer, and the occasional bison. Evidence at this site is consistent with an inference of a camp.

Meserve (Widga 2007)

The Meserve site is located along the South Platte River in Hall County, Nebraska. The site has been recently radiocarbon dated to 9380 ± 100 . A lanceolate projectile point (Meserve type), in association with an extinct species of bison, was recovered from this site. According to Widga (2007), more than 40 specimens can be attributed to at least four *bison occidentalis* individuals. No butchering marks have been observed.

Mill Iron (Frison 1996; Todd, et al. 1996)

Located in Wyoming, the Mill Iron site is found on the Missouri Plateau. The average of nine radiocarbon dates suggests that the site is from 11,076 BP. The site consists almost exclusively of bison remains that also indicate campsite activity. It is believed that Mill

Iron functioned as a kill/processing site; it is considered an outlier in terms of living-structure patterns.

Milnesand (Hill Jr. 2002)

The Milnesand site is located in New Mexico. This site has been estimated to be from around 10,000 BP, but radiocarbon dating has not confirmed the age. Hill (2002) reported a small bison faunal assemblage (NISP = 180). Interestingly, this small assemblage represents at least 33 bison individuals (Astragali MNI), indicating biases in either preservation or during recovery. Another interesting aspect of the Milnesand site is that there is evidence of multiple use/repeated use at different times of the year. Many more bison are believed to have been killed at this site, based on the number of projectile points present. However, poorly preserved faunal remains mean that the number of bison is likely underestimated. Although this site has been classified as a kill site in terms of its function, additional butchery activity might be represented by burned bone present in filled-in hearths.

Mummy Cave (Hughes 2003)

The Mummy Cave site is a rock shelter located on the eastern flank of the Absaroka Mountains in northwestern Wyoming. Gene Smith and Dan Witter discovered the site in 1957, and Bob Edgar began excavations in 1963. Archaeologists have identified 38 discrete occupational strata. The faunal remains include 15,174 bones and 4,223 specimens from 31 taxonomic groups. Bighorn sheep dominate the assemblage. Evidence at this site seems consistent with an interpretation of a camp.

Nelson (Kornfeld et al. 2007)

The Nelson site is located in Weld County, Colorado. This site is associated with the Cody Complex and has been radiocarbon dated to 9260 BP. The Nelson site is composed of a small and poorly preserved assemblage of bison remains (NISP = 212). Evidence of carcass butchery and exploitation is present including “green” bone fractures to access marrow. Investigators have been cautious in interpreting the site’s function based on such a small sample of poorly preserved bone. However, the bone assemblage composition at this site seems consistent with a winter kill site.

Norton (Hofman, et al. 1995)

Located in western Kansas, the Norton site has only been subject to limited recovery of faunal remains and incomplete excavation. Found in the High Plains, this site has been dated to 9080 BP and is believed to have been a kill and processing site. This site is known to be an Early Holocene bison bonebed, but the number of kills remains unknown due to the incomplete excavation.

O.V. Clary (Hill et al. 2008)

O.V. Clary is a site located on the Clary Ranch in western Nebraska. Pooled ¹⁴C dates temporally place this site at 9034 ± 32 BP (10, 212 ± 19 yCal. BP). It was a residential camp of the Allen/Frederick Complex, with evidence of occupation during the mid-summer, mid-winter, and late winter/early spring. Activities were organized around an intact hearth area, to which at least six bison carcasses were transported for processing and

consumption. The chipped stone assemblage (9,914) consists predominantly of microdebitage and 39 tools.

Olsen-Chubbuck (Wheat 1972)

The Olsen-Chubbuck site is located in east-central Colorado, in Cheyenne County near the city of Kit-Carson. It is an iconic North American Great Plains Paleoindian bison kill site associated with the Cody Complex, dating to 9394 ± 22 BP ($10,626 \pm 35$ yCal BP; pooled). Amateur archaeologists Sigurd Olsen and Jerry Chubbuck were responsible for the preliminary excavation and bringing the site to the attention of archaeologist Joe-Ben Wheat in the late 1950s. The site was excavated over two field seasons between 1958 and 1960, yielding the remains of at least 190 bison trapped and killed in an arroyo. Little evidence of processing or other subsistence behavior has been found, suggesting that this site was a task-specific kill site.

Perry Ranch (Hofman and Todd 1997; Hurst and Wyckoff 2005)

The Perry Ranch site is located in southwestern Oklahoma. The site has been radiocarbon dated to 8460 BP. Archaeological deposits at Perry Ranch consist of two Plainview type points associated with a bison bonebed, where the remains of at least two individuals are represented. Butchery marks are absent, although this is not surprising to investigators given the poor bone preservation. Evidence from Perry Ranch is consistent with an interpretation of a winter kill and processing site.

Plainview (M. E. Hill 2010; Holliday et al. 1999)

The Plainview site is located in the Texas panhandle. A secure radiocarbon date for this site remains problematic, but an estimate based on point typology is 10,000 BP. The bonebed is composed of 4,335 bison specimens, representing the remains of at least 84 individuals and potentially more than one death event. Currently, the site is inferred to have functioned as a fall/spring kill and processing site.

Rattlesnake Pass (Smith and McNees 1990)

The Rattlesnake Pass site is a short-term Folsom occupation site located in south-central Wyoming. Upon excavation, archaeologists discovered bison bones, flake tools, and flakes that carbon date to 9950–9770 BP. This site is important because its carbon dates challenge the previously established timeline of Folsom, indicating that the Folsom occupations may have been earlier than originally thought. The distribution of skeletal remains indicates the presence of two sites for the butchering and processing of bison.

Rex Rodgers (M. E. Hill 2010)

The Rex Rodgers site is located in northern Texas. Radiocarbon dating revealed this site to be from 9391 BP. Archaeologists have found 1,886 specimens at this site, largely bison remains. The remains indicate a Pleistocene bison kill and processing site at this location.

San Jon (Hill et al. 1995)

The San Jon site is located in eastern New Mexico on a dried “playa” lake. The Cody component of this site (Area 2) dates to 8360 BP. The San Jon bonebed contains the

remains of at least five bison individuals associated with Cody Complex-type points. Further evaluation of this site is necessary, as its function is still unknown.

Scottsbluff (Hill Jr 2008)

Scottsbluff is a multicomponent site located in Western Nebraska. It is the type site for the Scottsbluff point type. The average of two radiocarbon dates has yielded a date of 8809 ± 60 BP. The Scottsbluff bison assemblage is composed of 1,461 specimens, representing at least 26 individuals that died in late spring/early summer. Due to extensive fluvial disturbance, the site's association with artifacts and inferred function as a bison kill locality remains tenuous.

Sheaman (Frison and Stanford 1982)

The Sheaman site is located in eastern Wyoming, near the Nebraska and South Dakota borders. Radiocarbon dating of associated artifacts has revealed this site to be from 10,690 BP. This site yielded a Goshen-type point and other lithic debitage associated with a single bison individual. Investigation of the site has identified it as a campsite.

Sorenson (Husted 1969)

The Sorenson site (24CB202) is a multi-occupation rockshelter located in Bighorn Canyon on the bank of the Bighorn River in southern Carbon County, Montana. Radiocarbon dates of Occupation 2 average to 7680 ± 177 BP. This component has yielded stone tools associated with Late Paleoindian foothills/mountain archaeological cultures, including two Lovell Constricted-type points. Several "fire pits" suggest the long-term use of this site.

The remains of a mule deer and bison individual have been recovered. Sorenson appears to have been used as a camp by late Paleoindian foragers.

Stewart's Cattle Guard (Jodry 1999)

Stewart's Cattle Guard is a Folsom site in southern Colorado that was exposed by wind deflation in the 1970s. Archaeologists recovered debris from butchery, bone marrow recovery, hide processing, and weapon manufacture and repair. The remains indicate that it was a processing camp where 49 bison were killed over a short period of time. Bison seem to have been abundant due to the natural grazing/travel corridor between the mountains and wetlands.

Upper Twin Mountain (Kornfeld and Frison 2000)

The Upper Twin Mountain site is located in northern Colorado between the northern Plains Goshen and the southern Plains Plainview. The remains of at least 15 adult bison have been identified along with 222 specimens dating to 10,392 BP. Faunal and stone remains indicate year-round occupation. At an altitude of 2,548 m, this site is the highest known Paleoindian bison bonebed. The site has also provided archaeologists with significant information about bison procurement.

Vermilion Lakes (Fedje et al. 1995)

Vermilion Lakes is a site located in Banff National Park, Alberta. It contains evidence for 12 cultural components. The site was investigated between 1983 and 1985, during the widening of the Trans-Canada Highway. Radiocarbon dates place the site between 10,800

and 9000 BP. The distribution of features and artifacts indicates a series of small temporary camps. Mountain sheep represent the dominant faunal remains.

Waugh (Hill Jr. and Hofman 1997)

The Waugh site (34HP42) is located in northwest Oklahoma. The site contains a bison bonebed associated with a Folsom point and hearth dating to 10,390 BP. The bonebed represents the remains of at least six bison individuals, including three males. Limited testing has been conducted at the site, and seasonality remains undetermined. The current inference is that Waugh functioned as a camp.

Wilson-Leonard (Collins 1998)

The Wilson-Leonard site is located in the Bushy Creek valley of southwestern Williamson County, Texas. It was recorded in 1973 and excavated in 1981–1984; the site was re-investigated in 1992 under Michael B. Collins. This site contains the most complete cultural sequence of any single site in central Texas, the oldest being the Clovis horizon. Directly above this horizon is a bonebed of extinct bison, along with a few artifacts resembling Folsom. Evidence drawn from the Paleoindian components is consistent with an inference of a camp site.

Winger (Mandel and Hofman 2003)

The Winger site is a deeply buried Late Paleoindian bison bonebed located in Stanton County, southwestern Kansas. Collagen from a bison rib sample yielded a ^{14}C date of 9080 BP. Archaeologists have recovered the remains of at least six bison individuals in

association with Frederick/Allen projectile points. Despite limited excavation, Winger is believed to have been a Paleoindian bison kill and processing site.

Abbreviations of skeletal element names used in table headers below.

CRN = Cranium;

MR = Mandible;

CE = Cervical 1-7;

TH = Thoracic 1-14;

LM = Lumbar 1-5;

SAC = Sacrum;

RB = Rib;

SC = Scapulae;

HM = Humerus;

RD = Radius;

UL = Ulna;

MC = Metacarpal;

IM = Innominate;

FM = Femur;

TA = Tibia;

MT = Metacarpal;

PH = Phalange

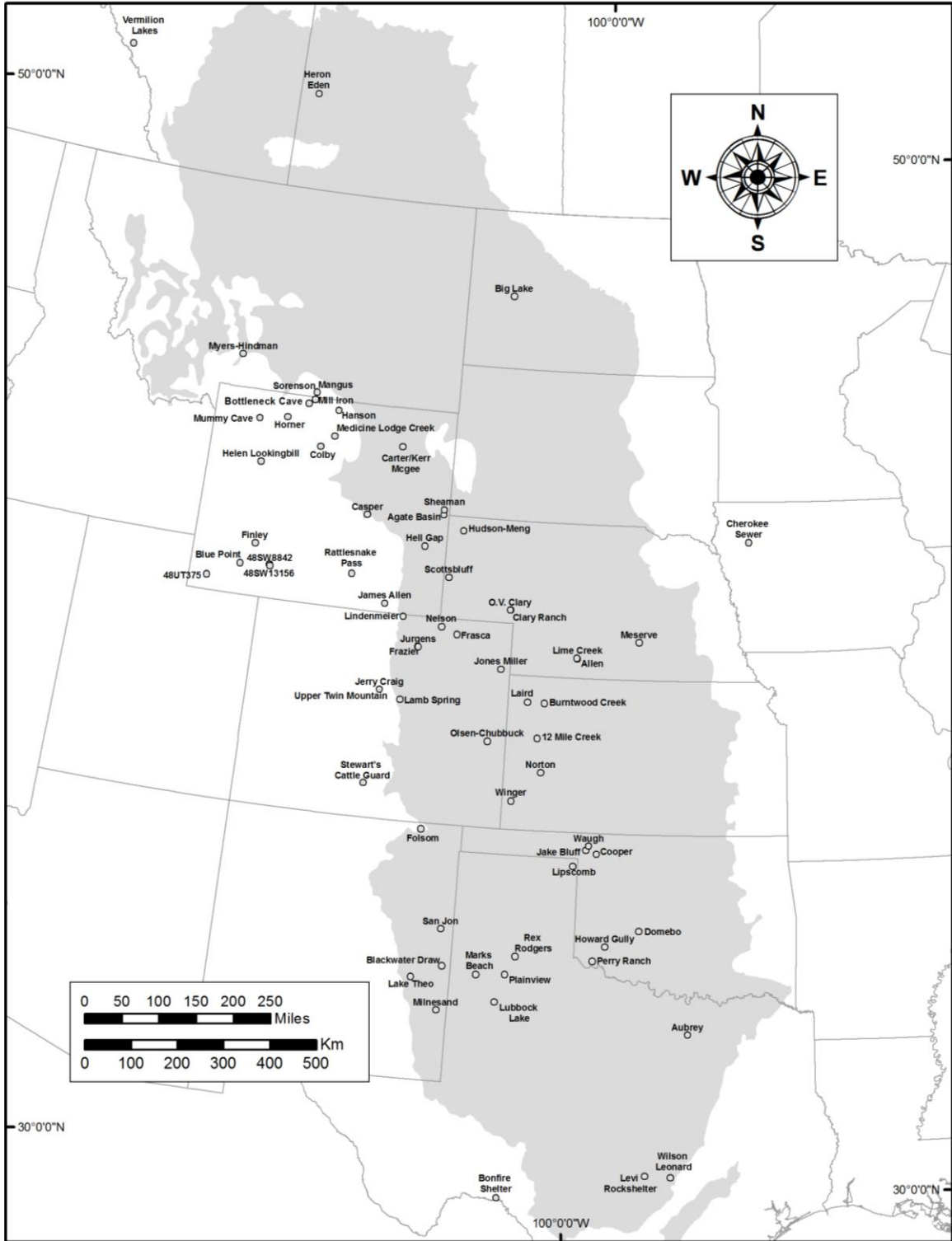


Figure A.1. Geographic distribution of Paleoindian sites mentioned in this chapter and Table A.1.

Appendix A.1 Geographical and zooarchaeological characteristics of archaeological sites used in this dissertation¹.

State	Site	Component	Date (cal BP)
Kansas	12 Mile Creek	All	12,409
Wyoming	48SW13156	I	9780
Wyoming	48SW8842	5	9380
Wyoming	48UT375	2	8723
Wyoming	48UT375	1	9444
Wyoming	Agate Basin	Folsom	12,764
Wyoming	Agate Basin	Agate Basin	12,341
Wyoming	Agate Basin	Hell Gap	12,356
Nebraska	Allen	OL2	8550
Nebraska	Allen	IZ	10,850
Nebraska	Allen	OL1	12,400
Texas	Aubrey	Camp A and B	13,477
Texas	Big Lake	All	8788
N. Mexico	Blackwater Draw	HPP 1961 Locality-3 Bonebed	11,975
N. Mexico	Blackwater Draw	HPP 1962-Locality 5 Bonebed	11,975
N. Mexico	Blackwater Draw	Sellards Clovis Bison Kill	12,700
N. Mexico	Blackwater Draw	Jelinek Bonebed	12,766
Wyoming	Blue Point	2	9106
Wyoming	Blue Point	1	10,904
Texas	Bonfire Shelter	Strat.A and B/C	11,390
Wyoming	Bottleneck Cave	III	8466
Wyoming	Bottleneck Cave	II	8641
Wyoming	Bottleneck Cave	I	8853
Kansas	Burntwood Creek	All	10,269
Wyoming	Carter/Kerr-Mcgee	Cody	7800
Wyoming	Carter/Kerr-Mcgee	Folsom	12,308

Appendix A.1 Geographical and zooarchaeological characteristics of archaeological sites used in this dissertation¹.

State	Site	Component	Date (cal BP)
Wyoming	Casper	All	11,583
Iowa	Cherokee Sewer	IIIA	8024
Nebraska	Clary Ranch	All	10,154
Wyoming	Colby	All	12,903
Oklahoma	Cooper	Upper Kill	11,508
Oklahoma	Cooper	Middle Kill	11,598
Oklahoma	Cooper	Lower Kill	11,622
Oklahoma	Domebo	All	12,995
Wyoming	Finley	WYO Station B	10,341
N. Mexico	Folsom	All	12,859
Colorado	Frasca	Area 1	9987
Colorado	Frazier	All	10,987
Wyoming	Hanson	All	12,040
Wyoming	Helen Lookingbill	Layer 7/9	9707
Wyoming	Helen Lookingbill	Layer 2/4	12,314
Wyoming	Hell Gap	Locality V Cody	9820
Saskatchewan, Canada	Heron Eden	All	10,148
Wyoming	Horner	I	9871
Wyoming	Horner	II	11,721
Oklahoma	Howard Gully	All	11,917
Nebraska	Hudson-Meng	All	11,266
Oklahoma	Jake Bluff	Unit I	12,798
Wyoming	James Allen	All	9455
Colorado	Jerry Craig	All	10,639
Colorado	Jones Miller	All	11,576

Appendix A.1 Geographical and zooarchaeological characteristics of archaeological sites used in this dissertation¹.

State	Site	Component	Date (cal BP)
Colorado	Jurgens	Area 3	10,217
Kansas	Laird	All	9471
Texas	Lake Theo	Folsom	12,412
Colorado	Lamb Spring	Cody-1980/1981	10,000
Texas	Levi Rockshelter	Zone IV	9249
Nebraska	Lime Creek	Zone I	10,329
Colorado	Lindenmeier	Folsom	12,469
Texas	Lipscomb	All	12,799
Texas	Lubbock Lake	FA5-8/10	8301
Texas	Lubbock Lake	FA6-3	9578
Texas	Lubbock Lake	GA5-2	9632
Texas	Lubbock Lake	FA5-7/GA5-3	10,514
Texas	Lubbock Lake	FA5-12	11,126
Texas	Lubbock Lake	FA6-11	11,422
Texas	Lubbock Lake	FA9-1	11,422
Texas	Lubbock Lake	FA5-17	11,498
Texas	Lubbock Lake	FA6-15	11,549
Texas	Lubbock Lake	GA12-5	11,549
Texas	Lubbock Lake	FA2-2	12,137
Texas	Lubbock Lake	FA6-8	12,137
Montana	Mangus	I	9692
Texas	Marks Beach	All	12,139
Wyoming	Medicine Lodge Creek	Fire Pit Level	9181
Wyoming	Medicine Lodge Creek	Pryor Stemmed	9210

Appendix A.1 Geographical and zooarchaeological characteristics of archaeological sites used in this dissertation¹.

State	Site	Component	Date (cal BP)
Wyoming	Medicine Lodge Creek	N. Paleo (6-ft deep)	9373
Wyoming	Medicine Lodge Creek	Fish Fauna	9520
Wyoming	Medicine Lodge Creek	North Paleo	9632
Wyoming	Medicine Lodge Creek	Cody	9912
Wyoming	Medicine Lodge Creek	23ft-deep deer	11,025
Nebraska	Meserve	All	10,612
Wyoming	Mill Iron	All	12,893
N. Mexico	Milnesand	All	10,000
Wyoming	Mummy Cave	Layer 13	8853
Wyoming	Mummy Cave	Layer 14	8872
Wyoming	Mummy Cave	Layer 12	9011
Wyoming	Mummy Cave	Layer 11	9102
Wyoming	Mummy Cave	Layer 10	9187
Wyoming	Mummy Cave	Layer 9	9294
Wyoming	Mummy Cave	Layer 8	9450
Wyoming	Mummy Cave	Layer 6	9481
Wyoming	Mummy Cave	Layer 7	9747
Wyoming	Mummy Cave	Layer 4	10,421
Wyoming	Mummy Cave	Layer 1	10,850
Montana	Myers-Hindman	Unit 1	10,005
Colorado	Nelson	All	10,460
Kansas	Norton	All	10,251
Nebraska	O.V. Clary	Middle	10,333

Appendix A.1 Geographical and zooarchaeological characteristics of archaeological sites used in this dissertation¹.

State	Site	Component	Date (cal BP)
Colorado	Olsen-Chubbuck	All	10,656
Oklahoma	Perry Ranch	All	9431
Texas	Plainview	All	11,975
Wyoming	Rattlesnake Pass	All	11,373
Texas	Rex Rodgers	All	10,642
Texas	San Jon	Area 2	9333
Nebraska	Scottsbluff	All	9893
Wyoming	Sheaman	All	12,614
Montana	Sorenson	II	8525
Colorado	Stewart's Cattle Guard	All	12,792
Colorado	Upper Twin Mountain	All	12,300
Alberta	Vermilion Lakes	6a	10,979
Alberta	Vermilion Lakes	8	11,497
Alberta	Vermilion Lakes	6b	11,950
Alberta	Vermilion Lakes	9a	12,174
Alberta	Vermilion Lakes	9b	12,729
Oklahoma	Waugh	All	12,301
Texas	Wilson Leonard	Unit II	10,493
Texas	Wilson Leonard	Upper Unit I	11,042
Texas	Wilson Leonard	EP Bonebed	13,097
Kansas	Winger	All	10,251

¹Geographic coordinates available from author (EOC).

Appendix A.2. Functional and recovery information of sites used.

Site	Component	Archaeological Culture	Site Function	Screening Used?	Screen Size (< or = 1/4-Inch)
12 Mile Creek	All	Clovis	K/P ⁴	N	None
48SW13156	I	Unknown	C ⁵	Y	<1/4"
48SW8842	5	Unknown	C	Y	<1/4"
48UT375	2	Unknown	C	Y	NA
48UT375	1	Unknown	C	Y	NA
Agate Basin	Folsom	Folsom	C	Y	<1/4"
Agate Basin	Agate Basin	Agate Basin	K/P	NA ²	NA
Agate Basin	Hell Gap	Hell Gap	K/P	NA	NA
Allen	OL2	Unknown	C	N	NA
Allen	IZ	Unknown	C	N	NA
Allen	OL1	Agate Basin/Hell Gap	C	N	NA
Aubrey	Camp A and B	Clovis	C	Y	<1/4"
Big Lake	All	Scottsbluff/Milnesand	K/P	NA	NA
Blackwater Draw	HPP 1961 Locality-3 Bonebed	Folsom	K/P	NA	NA NA
Blackwater Draw	HPP 1962-Locality 5 Bonebed	Folsom	K/P	NA	
Blackwater Draw	Sellards Clovis Bison Kill	Clovis	K/P	NA	NA
Blackwater Draw	Jelinek Bonebed	Unknown	K/P	NA	NA
Blue Point	2	Unknown	C	Y	<1/4"
Blue Point	1	Unknown	C	Y	<1/4"
Bonfire Shelter	Strat.A and B/C	Plainview and Folsom Agate Basin-Pryor	K/P	NA	NA
Bottleneck Cave	III	Stemmed	C	Y	1/4"
Bottleneck Cave	II	Unknown	C	Y	1/4"
Bottleneck Cave	I	Lovell Constricted	C	Y	1/4"
Burntwood Creek	All	Allen/Frederick	K/P	NA	NA

²NA: Not Applicable because datum was not used in this dissertation; ³NR: Not reported in sources cited/Unknown.; ⁴K/P: Kill/Processing; ⁵C: Camp

Appendix A.2. Functional and recovery information of sites used.

Site	Component	Archaeological Culture	Site Function	Screening Used?	Screen Size (< or = 1/4-Inch)
Carter/Kerr-Mcgee	Cody	Cody	K/P	NA	NA
Carter/Kerr-Mcgee	Folsom	Folsom	Unknown	NA	NA
Casper	All	Hell Gap	K/P	NA	NA
					NA
Cherokee Sewer	IIIA	Agate Basin	K/P	NA	
Clary Ranch	All	Allen/Frederick	K/P	NA	NA
Colby	All	Clovis	C	Y	<1/4"
Cooper	Upper Kill	Folsom	K/P	NA	NA
Cooper	Middle Kill	Folsom	K/P	NA	NA
Cooper	Lower Kill	Folsom	K/P	NA	NA
Domebo	All	Clovis	K/P	NA	NA
Finley	WYO Station B	Cody	K/P	NA	NA
Folsom	All	Folsom	K/P	NA	NA
					NA
Frasca	Area 1	Cody	K/P	NA	
Frazier	All	Agate Basin	K/P	NA	NA
Hanson	All	Folsom	C	NA	NA
Helen Lookingbill	Layer 7/9	Fishtail Lanceolate	C	Y	<1/4"
Helen Lookingbill	Layer 2/4	Hell Gap	C	Y	<1/4"
Hell Gap	Locality V Cody	Cody	C	Y	1/4"
Heron Eden	All	Scottsbluff	K/P	NA	<1/4"
Horner	I	Alberta/Cody	C	Y	1/4"
Horner	II	Cody	K/P	NA	<1/4"
Howard Gully	All	San Patrice	K/P	NA	<1/4"
Hudson-Meng	All	Alberta	K/P	NA	NA
Jake Bluff	Unit I	Clovis	K/P	NA	<1/4"
James Allen	All	Allen/Frederick	K/P	NA	NA
Jerry Craig	All	Cody	K/P	NA	<1/4"

Appendix A.2. Functional and recovery information of sites used.

Site	Component	Archaeological Culture	Site Function	Screening Used?	Screen Size (< or = 1/4-Inch)
Jones Miller	All	Hell Gap	K/P	NA	<1/4"
Jurgens	Area 3	Firstview	K/P	NA	NA
Laird	All	Dalton	K/P	NA	<1/4" <1/4"
Lake Theo	Folsom	Folsom	C	N	
Lamb Spring	Cody-1980/1981	Cody	K/P	NA	NA
Levi Rockshelter	Zone IV	Angostura	C	NA	NA
Lime Creek	Zone I	Cody	C	N	NA NA
Lindenmeier	Folsom	Folsom	C	Y	
Lipscomb	All	Folsom	K/P	NA	NA
Lubbock Lake	FA5-8/10	Firstview	K/P	NA	NA
Lubbock Lake	FA6-3	Firstview	C	NA	NA
Lubbock Lake	GA5-2	Firstview	K/P	NA	NA
Lubbock Lake	FA5-7/GA5-3	Unknown	K/P	NA	NA
Lubbock Lake	FA5-12	Plainview	K/P	NA	NA
Lubbock Lake	FA6-11	Plainview	K/P	NA	NA
Lubbock Lake	FA9-1	Plainview	K/P	NA	NA
Lubbock Lake	FA5-17	Lubbock	K/P	NA	NA
Lubbock Lake	FA6-15	Unknown	K/P	NA	NA
Lubbock Lake	GA12-5	Plainview	K/P	NA	NA
Lubbock Lake	FA2-2	Unknown	K/P	NA	NA
Lubbock Lake	FA6-8	Folsom	K/P	NA	NA
Mangus	I	Agate Basin-Cody	C	Y	1/4"
Marks Beach	All	Unknown	K/P	NA	NA

Appendix A.2. Functional and recovery information of sites used.

Site	Component	Archaeological Culture	Site Function	Screening Used?	Screen Size (< or = 1/4-Inch)
Medicine Lodge Creek	Fire Pit Level	Lovell Constricted	C	Y	<1/4"
Medicine Lodge Creek	Pryor Stemmed	Pryor Stemmed	C	Y	<1/4" <1/4"
Medicine Lodge Creek	N. Paleo (6-ft deep)	Unknown	C	Y	<1/4"
Medicine Lodge Creek	Fish Fauna	Foothill-Mountain	C	Y	<1/4"
Medicine Lodge Creek	North Paleo	Unknown	C	Y	<1/4"
Medicine Lodge Creek	Cody	Cody	C	Y	<1/4"
Medicine Lodge Creek	23ft-deep deer	Goshen	C	Y	
Meserve	All	Meserve	Unknown	NA	NA
Mill Iron	All	Goshen	K/P	NA	NA
Milnesand	All	Milnesand	K/P	NA	NA
Mummy Cave	Layer 13	Unknown	C	Y	1/4"
Mummy Cave	Layer 14	Lovell Constricted	C	Y	1/4"
Mummy Cave	Layer 12	Angostura	C	Y	1/4"
Mummy Cave	Layer 11	Angostura	C	Y	1/4"
Mummy Cave	Layer 10	Angostura	C	Y	1/4"
Mummy Cave	Layer 9	Angostura	C	Y	1/4"
Mummy Cave	Layer 8	Angostura	C	Y	1/4"
Mummy Cave	Layer 6	Unknown	C	Y	1/4"
Mummy Cave	Layer 7	Unknown	C	Y	1/4"
Mummy Cave	Layer 4	Unknown	C	Y	1/4"
Mummy Cave	Layer 1	Unknown	C	Y	1/4"

Appendix A.2. Functional and recovery information of sites used.

Site	Component	Archaeological Culture	Site Function	Screening Used?	Screen Size (< or = 1/4-Inch)
					NA
Myers-Hindman	Unit 1	Agate Basin	C	Y	
Nelson	All	Cody	Unknown	NA	NA
Norton	All	Allen/Frederick	K/P	NA	NA
O.V. Clary	Middle	Frederick/Allen	C	Y	<1/4"
Olsen-Chubbuck	All	Firstview	K/P	NA	NA
Perry Ranch	All	Plainview	K/P	NA	NA
Plainview	All	Plainview	K/P	NA	NA
Rattlesnake Pass	All	Folsom	K/P	NA	NA
Rex Rodgers	All	Plainview	K/P	NA	NA
San Jon	Area 2	Firstview	Unknown	NA	NA
Scottsbluff	All	Cody	Unknown	NA	NA
					NA
Sheaman	All	Goshen	C	NA	
Sorenson	II	Lovell Constricted	C	Y	1/4"
Stewart's Cattle Guard	All	Folsom	C	Y	<1/4"
Upper Twin Mountain	All	Goshen	K/P	NA	NA
Vermilion Lakes	6a	Unknown	C	Y	<1/4"
Vermilion Lakes	8	Unknown	C	Y	<1/4"
Vermilion Lakes	6b	Unknown	C	Y	<1/4"
Vermilion Lakes	9a	Unknown	C	Y	<1/4"
Vermilion Lakes	9b	Unknown	C	Y	<1/4"
Waugh	All	Folsom	C	Y	<1/4"
Wilson Leonard	Unit II	Angostura	C	Y	<1/4"
Wilson Leonard	Upper Unit I	Wilson	C	Y	<1/4"
Wilson Leonard	EP Bonebed	Unknown	C	Y	<1/4"
Winger	All	Allen/Frederick	K/P	NA	NA

Appendix A.3. Faunal information of sites and components used in this dissertation.

Site	Component	Label	Habitat	Margalef Index	NTAXA	N (NISP)	MAMMOTH
12 Mile Creek	All	12MC	Plains/Rolling Hills	NA	NA	NA	NA
48SW13156	I	NA	Plains/Rolling Hills	0.2	1	169	0
48SW8842	5	NA	Plains/Rolling Hills	0.14	1	1643	0
48UT375	2	NA	Plains/Rolling Hills	0.61	2	26	0
48UT375	1	NA	Plains/Rolling Hills	0.25	2	3175	0
Agate Basin	Folsom	NA	Plains/Rolling Hills	0.97	7	1336	0
Agate Basin	Agate Basin	NA	Plains/Rolling Hills	NA	NA	NA	NA
Agate Basin	Hell Gap	NA	Plains/Rolling Hills	NA	NA	NA	NA
Allen	OL2	NA	Alluvial Valley	2.65	15	289	0
Allen	IZ	NA	Alluvial Valley	2.25	14	510	0
Allen	OL1	NA	Alluvial Valley	1.83	14	2071	0
Aubrey	Camp A and B	NA	Alluvial Valley	1.13	8	1172	0
Big Lake	All	NA	Plains/Rolling Hills	NA	NA	NA	NA
Blackwater Draw	HPP 1961 Locality-3 Bonebed	BWD12	Plains/Rolling Hills	NA	NA	NA	NA
Blackwater Draw	HPP 1962-Locality 5 Bonebed	BWD15	Plains/Rolling Hills	NA	NA	NA	NA
Blackwater Draw	Sellards Clovis Bison Kill	BWD7	Plains/Rolling Hills	NA	NA	NA	NA
Blackwater Draw	Jelinek Bonebed	BWD1	Plains/Rolling Hills	NA	NA	NA	NA
Blue Point	2	NA	Plains/Rolling Hills	1.16	3	75	0
Blue Point	1	NA	Plains/Rolling Hills	1.05	5	119	0
Bonfire Shelter	Strat.A and B/C	BFS	Plains/Rolling Hills	NA	NA	NA	NA
Bottleneck Cave	III	NA	Foothills/Mountain	1.62	6	40	0
Bottleneck Cave	II	NA	Foothills/Mountain	1.17	3	12	0
Bottleneck Cave	I	NA	Foothills/Mountain	1.67	3	5	0
Burntwood Creek	All	BRC	Plains/Rolling Hills	NA	NA	NA	NA

Appendix A.3. Faunal information of sites and components used in this dissertation.

Site	Component	Label	Habitat	Margalef Index	NTAXA	N (NISP)	MAMMOTH
Carter/Kerr-Mcgee	Cody	NA	Plains/Rolling Hills	NA	NA	NA	NA
Carter/Kerr-Mcgee	Folsom	NA	Plains/Rolling Hills	NA	NA	NA	NA
Casper	All	NA	Plains/Rolling Hills	NA	NA	NA	NA
Cherokee Sewer	IIIA	CS	Alluvial Valley	NA	NA	NA	NA
Clary Ranch	All	CR	Plains/Rolling Hills	NA	NA	NA	NA
Colby	All	NA	Foothills/Mountain	0.16	1	463	463
Cooper	Upper Kill	CPRU	Plains/Rolling Hills	NA	NA	NA	NA
Cooper	Middle Kill	CPRM	Plains/Rolling Hills	NA	NA	NA	NA
Cooper	Lower Kill	CPRL	Plains/Rolling Hills	NA	NA	NA	NA
Domebo	All	NA	Plains/Rolling Hills	NA	NA	NA	NA
Finley	WYO Station B	NA	Plains/Rolling Hills	NA	NA	NA	NA
Folsom	All	FOL	Foothills/Mountain	NA	NA	NA	NA
Frasca	Area 1	NA	Plains/Rolling Hills	NA	NA	NA	NA
Frazier	All	FRAZ	Alluvial Valley	NA	NA	NA	NA
Hanson	All	NA	Foothills/Mountain	NA	NA	NA	NA
Helen Lookingbill	Layer 7/9	NA	Foothills/Mountain	0.48	4	531	0
Helen Lookingbill	Layer 2/4	NA	Foothills/Mountain	1.24	3	25	0
Hell Gap	Locality V Cody	NA	Foothills/Mountain	0.69	4	342	0
Heron Eden	All	NA	Plains/Rolling Hills	NA	NA	NA	NA
Horner	I	HORN1	Foothills/Mountain	0.52	4	2157	0
Horner	II	NA	Foothills/Mountain	NA	NA	NA	NA
Howard Gully	All	NA	Plains/Rolling Hills	NA	NA	NA	NA
Hudson-Meng	All	NA	Plains/Rolling Hills	NA	NA	NA	NA
Jake Bluff	Unit I	JB	Plains/Rolling Hills	NA	NA	NA	NA
James Allen	All	NA	Plains/Rolling Hills	NA	NA	NA	NA
Jerry Craig	All	JC	Foothills/Mountain	NA	NA	NA	NA

Appendix A.3. Faunal information of sites and components used in this dissertation.

Site	Component	Label	Habitat	Margalef Index	NTAXA	N (NISP)	MAMMOTH
Jones Miller	All	NA	Plains/Rolling Hills	NA	NA	NA	NA
Jurgens	Area 3	JURG3	Alluvial Valley	NA	NA	NA	NA
Laird	All	NA	Plains/Rolling Hills	NA	NA	NA	NA
Lake Theo	Folsom	LKTH	Plains/Rolling Hills	0.11	1	6919	0
Lamb Spring	Cody-1980/1981	LMSP	Plains/Rolling Hills	NA	NA	NA	NA
Levi Rockshelter	Zone IV	NA	Alluvial Valley	NA	NA	NA	NA
Lime Creek	Zone I	NA	Alluvial Valley	1.74	13	1212	0
Lindenmeier	Folsom	NA	Plains/Rolling Hills	1.09	7	604	0
Lipscomb	All	LIPS	Plains/Rolling Hills	NA	NA	NA	NA
Lubbock Lake	FA5-8/10	NA	Plains/Rolling Hills	NA	NA	NA	NA
Lubbock Lake	FA6-3	NA	Plains/Rolling Hills	NA	NA	NA	NA
Lubbock Lake	GA5-2	NA	Plains/Rolling Hills	NA	NA	NA	NA
Lubbock Lake	FA5-7/GA5-3	NA	Plains/Rolling Hills	NA	NA	NA	NA
Lubbock Lake	FA5-12	NA	Plains/Rolling Hills	NA	NA	NA	NA
Lubbock Lake	FA6-11	NA	Plains/Rolling Hills	NA	NA	NA	NA
Lubbock Lake	FA9-1	NA	Plains/Rolling Hills	NA	NA	NA	NA
Lubbock Lake	FA5-17	NA	Plains/Rolling Hills	NA	NA	NA	NA
Lubbock Lake	FA6-15	NA	Plains/Rolling Hills	NA	NA	NA	NA
Lubbock Lake	GA12-5	NA	Plains/Rolling Hills	NA	NA	NA	NA
Lubbock Lake	FA2-2	NA	Plains/Rolling Hills	NA	NA	NA	NA
Lubbock Lake	FA6-8	NA	Plains/Rolling Hills	NA	NA	NA	NA
Mangus	I	NA	Foothills/Mountain	0.91	2	8	0

Appendix A.3. Faunal information of sites and components used in this dissertation.

Site	Component	Label	Habitat	Margalef Index	NTAXA	N (NISP)	MAMMOTH
Marks Beach	All	NA	Plains/Rolling Hills	NA	NA	NA	NA
Medicine Lodge Creek	Fire Pit Level	NA	Foothills/Mountain	2.19	10	95	0
Medicine Lodge Creek	Pryor Stemmed	NA	Foothills/Mountain	2.27	9	52	0
Medicine Lodge Creek	N. Paleo (6-ft deep)	NA	Foothills/Mountain	2.27	7	14	0
Medicine Lodge Creek	Fish Fauna	NA	Foothills/Mountain	0.56	1	5	0
Medicine Lodge Creek	North Paleo	NA	Foothills/Mountain	2.59	7	14	0
Medicine Lodge Creek	Cody	NA	Foothills/Mountain	1.5	5	27	0
Medicine Lodge Creek	23ft-deep deer	NA	Foothills/Mountain	1.43	6	65	0
Meserve	All	NA	Alluvial Valley	NA	NA	NA	NA
Mill Iron	All	NA	Foothills/Mountain	NA	NA	NA	NA
Milnesand	All	MILSN	Plains/Rolling Hills	NA	NA	NA	NA
Mummy Cave	Layer 13	NA	Foothills/Mountain	0.72	1	3	0
Mummy Cave	Layer 14	NA	Foothills/Mountain	1.44	4	15	0
Mummy Cave	Layer 12	NA	Foothills/Mountain	1.3	6	101	0
Mummy Cave	Layer 11	NA	Foothills/Mountain	0.46	2	75	0
Mummy Cave	Layer 10	NA	Foothills/Mountain	1.07	5	107	0
Mummy Cave	Layer 9	NA	Foothills/Mountain	0.47	2	73	0
Mummy Cave	Layer 8	NA	Foothills/Mountain	1.01	4	52	0
Mummy Cave	Layer 6	NA	Foothills/Mountain	1.67	6	35	0
Mummy Cave	Layer 7	NA	Foothills/Mountain	1.44	2	3	0

Appendix A.3. Faunal information of sites and components used in this dissertation.

Site	Component	Label	Habitat	Margalef Index	NTAXA	N (NISP)	MAMMOTH
Mummy Cave	Layer 4	NA	Foothills/Mountain	2.42	7	17	0
Mummy Cave	Layer 1	NA	Foothills/Mountain	1.5	5	27	0
Myers-Hindman	Unit 1	NA	Foothills/Mountain	1.38	5	37	0
Nelson	All	NA	Plains/Rolling Hills	NA	NA	NA	NA
Norton	All	NO	Plains/Rolling Hills	NA	NA	NA	NA
O.V. Clary	Middle	NA	Plains/Rolling Hills	0.56	4	1339	0
Olsen-Chubbuck	All	OLCH	Plains/Rolling Hills	NA	NA	NA	NA
Perry Ranch	All	NA	Plains/Rolling Hills	NA	NA	NA	NA
Plainview	All	PLAIN	Plains/Rolling Hills	NA	NA	NA	NA
Rattlesnake Pass	All	NA	Plains/Rolling Hills	NA	NA	NA	NA
Rex Rodgers	All	RXRD	Plains/Rolling Hills	NA	NA	NA	NA
San Jon	Area 2	SNJN	Plains/Rolling Hills	NA	NA	NA	NA
Scottsbluff	All	SCTS	Plains/Rolling Hills	NA	NA	NA	NA
Sheaman	All	NA	Plains/Rolling Hills	NA	NA	NA	NA
Sorenson	II	NA	Foothills/Mountain	1.82	2	2	0
Stewart's Cattle Guard	All	NA	Foothills/Mountain	0.25	2	3501	0
Upper Twin Mountain	All	NA	Foothills/Mountain	NA	NA	NA	NA
Vermilion Lakes	6a	NA	Foothills/Mountain	0.72	1	3	0
Vermilion Lakes	8	NA	Foothills/Mountain	0.64	3	109	0
Vermilion Lakes	6b	NA	Foothills/Mountain	0.72	1	3	0
Vermilion Lakes	9a	NA	Foothills/Mountain	0.76	2	13	0
Vermilion Lakes	9b	NA	Foothills/Mountain	0.4	1	11	0
Waugh	All	NA	Plains/Rolling Hills	0.17	1	416	0
Wilson Leonard	Unit II	NA	Alluvial Valley	1.51	8	201	0

Appendix A.3. Faunal information of sites and components used in this dissertation.

Site	Component	Label	Habitat	Margalef Index	NTAXA	N (NISP)	MAMMOTH
Wilson Leonard	Upper Unit I	NA	Alluvial Valley	1.7	8	111	0
Wilson Leonard	EP Bonebed	NA	Alluvial Valley	0.91	4	81	0
Winger	All	NA	Plains/Rolling Hills	NA	NA	NA	NA

Appendix A.4. Faunal information of sites and components used in this dissertation.

Site	Component	BISON _(NISP)	BEAR	ELK	CARIBOU	BIGHORN SHEEP	DEER
12 Mile Creek	All	871	NA	NA	NA	NA	NA
48SW13156	I	0	0	0	0	0	0
48SW8842	5	0	0	0	0	0	0
48UT375	2	0	0	0	0	0	0
48UT375	1	0	0	0	0	0	0
Agate Basin	Folsom	1033	1033	0	0	0	0
Agate Basin	Agate Basin	3179	NA	NA	NA	NA	NA
Agate Basin	Hell Gap	986	NA	NA	NA	NA	NA
Allen	OL2	16	1	0	0	0	28
Allen	IZ	115	0	0	0	0	54
Allen	OL1	835	0	0	0	0	75
Aubrey	Camp A and B	401	0	0	0	0	17
Big Lake	All	NR	NA	NA	NA	NA	NA
Blackwater Draw	HPP 1961 Locality-3 Bonebed	64	NA	NA	NA	NA	NA
Blackwater Draw	HPP 1962-Locality 5 Bonebed	41	NA	NA	NA	NA	NA
Blackwater Draw	Sellards Clovis Bison Kill	35	NA	NA	NA	NA	NA
Blackwater Draw	Jelinek Bonebed	67	NA	NA	NA	NA	NA
Blue Point	2	0	0	0	0	0	1
Blue Point	1	39	0	2	0	0	0
Bonfire Shelter	Strat.A and B/C	2261	NA	NA	NA	NA	NA
Bottleneck Cave	III	2	0	0	0	10	20
Bottleneck Cave	II	0	0	0	0	7	4
Bottleneck Cave	I	1	0	0	0	2	2
Burntwood Creek	All	1577	NA	NA	NA	NA	NA
Carter/Kerr-Mcgee	Cody	NR	NA	NA	NA	NA	NA
Carter/Kerr-Mcgee	Folsom	NR	NA	NA	NA	NA	NA
Casper	All	7146	NA	NA	NA	NA	NA

Appendix A.4. Faunal information of sites and components used in this dissertation.

Site	Component	BISON _(NISP)	BEAR	ELK	CARIBOU	BIGHORN SHEEP	DEER
Cherokee Sewer	IIIA	144	NA	NA	NA	NA	NA
Clary Ranch	All	1841	NA	NA	NA	NA	NA
Colby	All	0	0	0	0	0	0
Cooper	Upper Kill	900	NA	NA	NA	NA	NA
Cooper	Middle Kill	1200	NA	NA	NA	NA	NA
Cooper	Lower Kill	1450	NA	NA	NA	NA	NA
Domebo	All	0	NA	NA	NA	NA	NA
Finley	WYO Station B	8033	NA	NA	NA	NA	NA
Folsom	All	3640	NA	NA	NA	NA	NA
Frasca	Area 1	7526	NA	NA	NA	NA	NA
Frazier	All	1175	NA	NA	NA	NA	NA
Hanson	All	NR	NA	NA	NA	NA	NA
Helen Lookingbill	Layer 7/9	3	0	2	0	1	525
Helen Lookingbill	Layer 2/4	3	0	0	0	0	21
Hell Gap	Locality V Cody	333	0	0	0	0	1
Heron Eden	All	22,898	NA	NA	NA	NA	NA
Horner	I	2141	0	0	0	0	10
Horner	II	7082	NA	NA	NA	NA	NA
Howard Gully	All	11	NA	NA	NA	NA	NA
Hudson-Meng	All	13,039	NA	NA	NA	NA	NA
Jake Bluff	Unit I	167	NA	NA	NA	NA	NA
James Allen	All	NR	NA	NA	NA	NA	NA
Jerry Craig	All	326	NA	NA	NA	NA	NA
Jones Miller	All	41,000	NA	NA	NA	NA	NA
Jurgens	Area 3	2955	NA	NA	NA	NA	NA

Appendix A.4. Faunal information of sites and components used in this dissertation.

Site	Component	BISON_(NISP)	BEAR	ELK	CARIBOU	BIGHORN SHEEP	DEER
Laird	All	322	NA	NA	NA	NA	NA
Lake Theo	Folsom	6919	0	0	0	0	0
Lamb Spring	Cody-1980/1981	579	NA	NA	NA	NA	NA
Levi Rockshelter	Zone IV	NR	NA	NA	NA	NA	NA
Lime Creek	Zone I	114	0	0	0	0	44
Lindenmeier	Folsom	524	0	0	0	0	6
Lipscomb	All	1202	NA	NA	NA	NA	NA
Lubbock Lake	FA5-8/10	NR	NA	NA	NA	NA	NA
Lubbock Lake	FA6-3	NR	NA	NA	NA	NA	NA
Lubbock Lake	GA5-2	NR	NA	NA	NA	NA	NA
Lubbock Lake	FA5-7/GA5-3	NR	NA	NA	NA	NA	NA
Lubbock Lake	FA5-12	NR	NA	NA	NA	NA	NA
Lubbock Lake	FA6-11	NR	NA	NA	NA	NA	NA
Lubbock Lake	FA9-1	NR	NA	NA	NA	NA	NA
Lubbock Lake	FA5-17	NR	NA	NA	NA	NA	NA
Lubbock Lake	FA6-15	NR	NA	NA	NA	NA	NA
Lubbock Lake	GA12-5	NR	NA	NA	NA	NA	NA
Lubbock Lake	FA2-2	NR	NA	NA	NA	NA	NA
Lubbock Lake	FA6-8	NR	NA	NA	NA	NA	NA
Mangus	I	0	0	0	0	0	3
Marks Beach	All	NR	NA	NA	NA	NA	NA
Medicine Lodge Creek	Fire Pit Level	0	21	0	0	5	1
Medicine Lodge Creek	Pryor Stemmed	1	0	0	0	18	6

Appendix A.4. Faunal information of sites and components used in this dissertation.

Site	Component	BISON _(NISP)	BEAR	ELK	CARIBOU	BIGHORN SHEEP	DEER
Medicine Lodge Creek	N. Paleo (6-ft deep)	4	0	0	0	2	3
Medicine Lodge Creek	Fish Fauna	0	0	0	0	0	0
Medicine Lodge Creek	North Paleo	4	0	0	0	2	3
Medicine Lodge Creek	Cody	2	0	0	0	1	2
Medicine Lodge Creek	23ft-deep deer	2	0	0	0	0	23
Meserve	All	NR	NA	NA	NA	NA	NA
Mill Iron	All	655	NA	NA	NA	NA	NA
Milnesand	All	161	NA	NA	NA	NA	NA
Mummy Cave	Layer 13	0	0	0	0	3	0
Mummy Cave	Layer 14	0	0	0	0	10	0
Mummy Cave	Layer 12	0	0	0	0	86	0
Mummy Cave	Layer 11	0	0	0	0	73	2
Mummy Cave	Layer 10	0	0	0	0	99	0
Mummy Cave	Layer 9	0	0	0	0	72	0
Mummy Cave	Layer 8	0	1	0	0	43	6
Mummy Cave	Layer 6	0	0	0	0	3	6
Mummy Cave	Layer 7	0	0	0	0	0	2
Mummy Cave	Layer 4	0	0	0	0	2	3
Mummy Cave	Layer 1	0	0	0	0	3	0
Myers-Hindman	Unit 1	14	0	0	0	9	10
Nelson	All	212	NA	NA	NA	NA	NA
Norton	All	1441	NA	NA	NA	NA	NA
O.V. Clary	Middle	1231	0	0	0	0	0
Olsen-Chubbuck	All	5370	NA	NA	NA	NA	NA

Appendix A.4. Faunal information of sites and components used in this dissertation.

Site	Component	BISON_(NISP)	BEAR	ELK	CARIBOU	BIGHORN SHEEP	DEER
Perry Ranch	All	112	NA	NA	NA	NA	NA
Plainview	All	3784	NA	NA	NA	NA	NA
Rattlesnake Pass	All	419	NA	NA	NA	NA	NA
Rex Rodgers	All	1885	NA	NA	NA	NA	NA
San Jon	Area 2	231	NA	NA	NA	NA	NA
Scottsbluff	All	1461	NA	NA	NA	NA	NA
Sheaman	All	13	NA	NA	NA	NA	NA
Sorenson	II	1	0	0	0	0	1
Stewart's Cattle Guard	All	3500	0	0	0	0	0
Upper Twin Mountain	All	222	NA	NA	NA	NA	NA
Vermilion Lakes	6a	0	0	0	0	3	0
Vermilion Lakes	8	2	2	0	0	84	0
Vermilion Lakes	6b	0	0	0	0	3	0
Vermilion Lakes	9a	0	0	0	2	11	0
Vermilion Lakes	9b	0	0	0	0	11	0
Waugh	All	416	416	0	0	0	0
Wilson Leonard	Unit II	0	0	0	0	0	1
Wilson Leonard	Upper Unit I	1	1	0	0	0	6
Wilson Leonard	EP Bonebed	36	36	0	0	0	0
Winger	All	NR	NA	NA	NA	NA	NA

Appendix A.4. Faunal information of sites and components used in this dissertation.

SITE	COMPONENT	PRONGHORN	WOLF	CANIDAE	BEAVER	BADGER	LYNX	PORCUPINE
12 Mile Creek	All	NA	NA	NA	NA	NA	NA	NA
48SW13156	I	0	0	0	0	0	0	0
48SW8842	5	0	0	0	0	0	0	0
48UT375	2	0	0	0	0	0	0	0
48UT375	1	0	0	0	0	0	0	0
Agate Basin	Folsom	297	2	1	0	0	0	0
Agate Basin	Agate Basin	NA	NA	NA	NA	NA	NA	NA
Agate Basin	Hell Gap	NA	NA	NA	NA	NA	NA	NA
Allen	OL2	17	0	7	0	2	0	2
Allen	IZ	46	0	10	0	6	0	0
Allen	OL1	34	0	12	1	13	0	0
Aubrey	Camp A and B	0	0	0	0	0	0	0
Big Lake	All	NA	NA	NA	NA	NA	NA	NA
Blackwater Draw	HPP 1961 Locality-3 Bonebed	NA	NA	NA	NA	NA	NA	NA
Blackwater Draw	HPP 1962-Localitiy 5 Bonebed	NA	NA	NA	NA	NA	NA	NA
Blackwater Draw	Sellards Clovis Bison Kill	NA	NA	NA	NA	NA	NA	NA
Blackwater Draw	Jelinek Bonebed	NA	NA	NA	NA	NA	NA	NA
Blue Point	2	0	0	0	0	0	0	0
Blue Point	1	1	0	0	0	0	0	0
Bonfire Shelter	Strat.A and B/C	NA	NA	NA	NA	NA	NA	NA
Bottleneck Cave	III	0	0	0	0	0	0	0
Bottleneck Cave	II	0	0	0	0	0	0	0
Bottleneck Cave	I	0	0	0	0	0	0	0
Burntwood Creek	All	NA	NA	NA	NA	NA	NA	NA
Carter/Kerr-Mcgee	Cody	NA	NA	NA	NA	NA	NA	NA
Carter/Kerr-Mcgee	Folsom	NA	NA	NA	NA	NA	NA	NA
Casper	All	NA	NA	NA	NA	NA	NA	NA

Appendix A.4. Faunal information of sites and components used in this dissertation.

SITE	COMPONENT	PRONGHORN	WOLF	CANIDAE	BEAVER	BADGER	LYNX	PORCUPINE
Cherokee Sewer	IIIA	NA	NA	NA	NA	NA	NA	NA
Clary Ranch	All	NA	NA	NA	NA	NA	NA	NA
Colby	All	0	0	0	0	0	0	0
Cooper	Upper Kill	NA	NA	NA	NA	NA	NA	NA
Cooper	Middle Kill	NA	NA	NA	NA	NA	NA	NA
Cooper	Lower Kill	NA	NA	NA	NA	NA	NA	NA
Domebo	All	NA	NA	NA	NA	NA	NA	NA
Finley	WYO Station B	NA	NA	NA	NA	NA	NA	NA
Folsom	All	NA	NA	NA	NA	NA	NA	NA
Frasca	Area 1	NA	NA	NA	NA	NA	NA	NA
Frazier	All	NA	NA	NA	NA	NA	NA	NA
Hanson	All	NA	NA	NA	NA	NA	NA	NA
Helen Lookingbill	Layer 7/9	0	0	0	0	0	0	0
Helen Lookingbill	Layer 2/4	0	0	0	0	0	0	0
Hell Gap	Locality V Cody	0	0	7	0	0	0	0
Heron Eden	All	NA	NA	NA	NA	NA	NA	NA
Horner	I	3	0	0	0	0	0	0
Horner	II	NA	NA	NA	NA	NA	NA	NA
Howard Gully	All	NA	NA	NA	NA	NA	NA	NA
Hudson-Meng	All	NA	NA	NA	NA	NA	NA	NA
Jake Bluff	Unit I	NA	NA	NA	NA	NA	NA	NA
James Allen	All	NA	NA	NA	NA	NA	NA	NA
Jerry Craig	All	NA	NA	NA	NA	NA	NA	NA
Jones Miller	All	NA	NA	NA	NA	NA	NA	NA

Appendix A.4. Faunal information of sites and components used in this dissertation.

SITE	COMPONENT	PRONGHORN	WOLF	CANIDAE	BEAVER	BADGER	LYNX	PORCUPINE
Jurgens	Area 3	NA	NA	NA	NA	NA	NA	NA
Laird	All	NA	NA	NA	NA	NA	NA	NA
Lake Theo	Folsom	0	0	0	0	0	0	0
Lamb Spring	Cody-1980/1981	NA	NA	NA	NA	NA	NA	NA
Levi Rockshelter	Zone IV	NA	NA	NA	NA	NA	NA	NA
Lime Creek	Zone I	239	0	1	218	0	0	0
Lindenmeier	Folsom	10	0	13	0	0	0	0
Lipscomb	All	NA	NA	NA	NA	NA	NA	NA
Lubbock Lake	FA5-8/10	NA	NA	NA	NA	NA	NA	NA
Lubbock Lake	FA6-3	NA	NA	NA	NA	NA	NA	NA
Lubbock Lake	GA5-2	NA	NA	NA	NA	NA	NA	NA
Lubbock Lake	FA5-7/GA5-3	NA	NA	NA	NA	NA	NA	NA
Lubbock Lake	FA5-12	NA	NA	NA	NA	NA	NA	NA
Lubbock Lake	FA6-11	NA	NA	NA	NA	NA	NA	NA
Lubbock Lake	FA9-1	NA	NA	NA	NA	NA	NA	NA
Lubbock Lake	FA5-17	NA	NA	NA	NA	NA	NA	NA
Lubbock Lake	FA6-15	NA	NA	NA	NA	NA	NA	NA
Lubbock Lake	GA12-5	NA	NA	NA	NA	NA	NA	NA
Lubbock Lake	FA2-2	NA	NA	NA	NA	NA	NA	NA
Lubbock Lake	FA6-8	NA	NA	NA	NA	NA	NA	NA
Mangus	I	0	0	0	0	0	0	0
Marks Beach	All	NA	NA	NA	NA	NA	NA	NA
Medicine Lodge Creek	Fire Pit Level	0	0	0	12	0	0	3

Appendix A.4. Faunal information of sites and components used in this dissertation.

SITE	COMPONENT	PRONGHORN	WOLF	CANIDAE	BEAVER	BADGER	LYNX	PORCUPINE
Medicine Lodge Creek	Pryor Stemmed	0	0	0	2	0	1	0
Medicine Lodge Creek	N. Paleo (6-ft deep)	0	0	0	1	0	0	0
Medicine Lodge Creek	Fish Fauna	0	0	0	0	0	0	0
Medicine Lodge Creek	North Paleo	0	0	0	1	0	0	0
Medicine Lodge Creek	Cody	0	0	0	0	0	0	0
Medicine Lodge Creek	23ft-deep deer	0	0	0	0	0	0	0
Meserve	All	NA	NA	NA	NA	NA	NA	NA
Mill Iron	All	NA	NA	NA	NA	NA	NA	NA
Milnesand	All	NA	NA	NA	NA	NA	NA	NA
Mummy Cave	Layer 13	0	0	0	0	0	0	0
Mummy Cave	Layer 14	0	0	0	0	0	0	0
Mummy Cave	Layer 12	0	0	0	0	0	0	9
Mummy Cave	Layer 11	2	0	0	0	0	0	0
Mummy Cave	Layer 10	0	0	0	0	0	0	3
Mummy Cave	Layer 9	0	0	0	0	0	0	0
Mummy Cave	Layer 8	6	0	0	0	0	0	2
Mummy Cave	Layer 6	6	0	0	0	0	0	9
Mummy Cave	Layer 7	2	0	0	0	0	0	0
Mummy Cave	Layer 4	3	0	1	2	0	0	0
Mummy Cave	Layer 1	0	0	0	0	0	0	0

Appendix A.4. Faunal information of sites and components used in this dissertation.

SITE	COMPONENT	PRONGHORN	WOLF	CANIDAE	BEAVER	BADGER	LYNX	PORCUPINE
Myers-Hindman	Unit 1	10	0	0	0	0	0	0
Nelson	All	NA	NA	NA	NA	NA	NA	NA
Norton	All	NA	NA	NA	NA	NA	NA	NA
O.V. Clary	Middle	0	0	1	0	0	0	0
Olsen-Chubbuck	All	NA	NA	NA	NA	NA	NA	NA
Perry Ranch	All	NA	NA	NA	NA	NA	NA	NA
Plainview	All	NA	NA	NA	NA	NA	NA	NA
Rattlesnake Pass	All	NA	NA	NA	NA	NA	NA	NA
Rex Rodgers	All	NA	NA	NA	NA	NA	NA	NA
San Jon	Area 2	NA	NA	NA	NA	NA	NA	NA
Scottsbluff	All	NA	NA	NA	NA	NA	NA	NA
Sheaman	All	NA	NA	NA	NA	NA	NA	NA
Sorenson	II	0	0	0	0	0	0	0
Stewart's Cattle Guard	All	0	1	0	0	0	0	0
Upper Twin Mountain	All	NA	NA	NA	NA	NA	NA	NA
Vermilion Lakes	6a	0	0	0	0	0	0	0
Vermilion Lakes	8	0	0	0	0	0	0	0
Vermilion Lakes	6b	0	0	0	0	0	0	0
Vermilion Lakes	9a	0	0	0	0	0	0	0
Vermilion Lakes	9b	0	0	0	0	0	0	0
Waugh	All	0	0	0	0	0	0	0
Wilson Leonard	Unit II	0	0	4	0	0	0	0
Wilson Leonard	Upper Unit I	0	0	3	0	0	0	0

Appendix A.4. Faunal information of sites and components used in this dissertation.

SITE	COMPONENT	PRONGHORN	WOLF	CANIDAE	BEAVER	BADGER	LYNX	PORCUPINE
Wilson Leonard	EP Bonebed	0	0	0	0	0	0	0
Winger	All	NA	NA	NA	NA	NA	NA	NA

Appendix A.4. Faunal information of sites and components used in this dissertation.

Site	Component	FOX	RACCOON	SKUNK	HARE/RABBIT	MARMOT	MUSKRAT	MUSTELID
12 Mile Creek	All	NA	NA	NA	NA	NA	NA	NA
48SW13156	I	0	0	0	0	0	0	0
48SW8842	5	0	0	0	1643	0	0	0
48UT375	2	0	0	0	1	0	0	0
48UT375	1	0	0	0	26	0	0	0
Agate Basin	Folsom	1	0	1	1	0	0	0
Agate Basin	Agate Basin	NA	NA	NA	NA	NA	NA	NA
Agate Basin	Hell Gap	NA	NA	NA	NA	NA	NA	NA
Allen	OL2	0	0	0	86	0	0	0
Allen	IZ	0	4	0	151	0	0	0
Allen	OL1	3	0	0	757	0	0	0
Aubrey	Camp A and B	0	0	0	0	0	0	0
Big Lake	All	NA	NA	NA	NA	NA	NA	NA
	HPP 1961							
Blackwater Draw	Locality-3							
	Bonebed	NA	NA	NA	NA	NA	NA	NA
	HPP 1962-							
Blackwater Draw	Locality 5							
	Bonebed	NA	NA	NA	NA	NA	NA	NA
Blackwater Draw	Sellards Clovis							
	Bison Kill	NA	NA	NA	NA	NA	NA	NA
Blackwater Draw	Jelinek Bonebed	NA	NA	NA	NA	NA	NA	NA
Blue Point	2	0	0	0	53	0	0	0
Blue Point	1	0	0	0	64	0	0	0
Bonfire Shelter	Strat.A and B/C	NA	NA	NA	NA	NA	NA	NA
Bottleneck Cave	III	4	0	0	2	0	0	0
Bottleneck Cave	II	0	0	0	0	0	0	0
Bottleneck Cave	I	0	0	0	0	0	0	0

Appendix A.4. Faunal information of sites and components used in this dissertation.

Site	Component	FOX	RACCOON	SKUNK	HARE/RABBIT	MARMOT	MUSKRAT	MUSTELID
Burntwood Creek	All	NA	NA	NA	NA	NA	NA	NA
Carter/Kerr-Mcgee	Cody	NA	NA	NA	NA	NA	NA	NA
Carter/Kerr-Mcgee	Folsom	NA	NA	NA	NA	NA	NA	NA
Casper	All	NA	NA	NA	NA	NA	NA	NA
Cherokee Sewer	IIIA	NA	NA	NA	NA	NA	NA	NA
Clary Ranch	All	NA	NA	NA	NA	NA	NA	NA
Colby	All	0	0	0	0	0	0	0
Cooper	Upper Kill	NA	NA	NA	NA	NA	NA	NA
Cooper	Middle Kill	NA	NA	NA	NA	NA	NA	NA
Cooper	Lower Kill	NA	NA	NA	NA	NA	NA	NA
Domebo	All	NA	NA	NA	NA	NA	NA	NA
Finley	WYO Station B	NA	NA	NA	NA	NA	NA	NA
Folsom	All	NA	NA	NA	NA	NA	NA	NA
Frasca	Area 1	NA	NA	NA	NA	NA	NA	NA
Frazier	All	NA	NA	NA	NA	NA	NA	NA
Hanson	All	NA	NA	NA	NA	NA	NA	NA
Helen Lookingbill	Layer 7/9	0	0	0	0	0	0	0
Helen Lookingbill	Layer 2/4	0	0	0	0	0	0	0
Hell Gap	Locality V Cody	0	0	0	1	0	0	0
Heron Eden	All	NA	NA	NA	NA	NA	NA	NA
Horner	I	0	0	0	0	0	0	0
Horner	II	NA	NA	NA	NA	NA	NA	NA
Howard Gully	All	NA	NA	NA	NA	NA	NA	NA

Appendix A.4. Faunal information of sites and components used in this dissertation.

Site	Component	FOX	RACCOON	SKUNK	HARE/RABBIT	MARMOT	MUSKRAT	MUSTELID
Hudson-Meng	All	NA	NA	NA	NA	NA	NA	NA
Jake Bluff	Unit I	NA	NA	NA	NA	NA	NA	NA
James Allen	All	NA	NA	NA	NA	NA	NA	NA
Jerry Craig	All	NA	NA	NA	NA	NA	NA	NA
Jones Miller	All	NA	NA	NA	NA	NA	NA	NA
Jurgens	Area 3	NA	NA	NA	NA	NA	NA	NA
Laird	All	NA	NA	NA	NA	NA	NA	NA
Lake Theo	Folsom	0	0	0	0	0	0	0
Lamb Spring	Cody-1980/1981	NA	NA	NA	NA	NA	NA	NA
Levi								
Rockshelter	Zone IV	NA	NA	NA	NA	NA	NA	NA
Lime Creek	Zone I	0	2	0	1	0	0	0
Lindenmeier	Folsom	13	0	0	36	0	0	0
Lipscomb	All	NA	NA	NA	NA	NA	NA	NA
Lubbock Lake	FA5-8/10	NA	NA	NA	NA	NA	NA	NA
Lubbock Lake	FA6-3	NA	NA	NA	NA	NA	NA	NA
Lubbock Lake	GA5-2	NA	NA	NA	NA	NA	NA	NA
Lubbock Lake	FA5-7/GA5-3	NA	NA	NA	NA	NA	NA	NA
Lubbock Lake	FA5-12	NA	NA	NA	NA	NA	NA	NA
Lubbock Lake	FA6-11	NA	NA	NA	NA	NA	NA	NA
Lubbock Lake	FA9-1	NA	NA	NA	NA	NA	NA	NA
Lubbock Lake	FA5-17	NA	NA	NA	NA	NA	NA	NA
Lubbock Lake	FA6-15	NA	NA	NA	NA	NA	NA	NA
Lubbock Lake	GA12-5	NA	NA	NA	NA	NA	NA	NA
Lubbock Lake	FA2-2	NA	NA	NA	NA	NA	NA	NA
Lubbock Lake	FA6-8	NA	NA	NA	NA	NA	NA	NA
Mangus	I	0	0	0	5	0	0	0

Appendix A.4. Faunal information of sites and components used in this dissertation.

Site	Component	FOX	RACCOON	SKUNK	HARE/RABBIT	MARMOT	MUSKRAT	MUSTELID
Marks Beach	All	NA	NA	NA	NA	NA	NA	NA
Medicine Lodge Creek	Fire Pit Level	0	0	0	23	0	0	0
Medicine Lodge Creek	Pryor Stemmed	0	0	0	7	0	0	0
Medicine Lodge Creek	N. Paleo (6-ft deep)	0	0	0	0	0	1	0
Medicine Lodge Creek	Fish Fauna	0	0	0	0	0	0	0
Medicine Lodge Creek	North Paleo	0	0	0	0	0	1	0
Medicine Lodge Creek	Cody	0	0	0	0	0	0	0
Medicine Lodge Creek	23ft-deep deer	0	0	0	4	0	0	1
Meserve	All	NA	NA	NA	NA	NA	NA	NA
Mill Iron	All	NA	NA	NA	NA	NA	NA	NA
Milnesand	All	NA	NA	NA	NA	NA	NA	NA
Mummy Cave	Layer 13	0	0	0	0	0	0	0
Mummy Cave	Layer 14	0	0	0	3	0	0	0
Mummy Cave	Layer 12	0	0	0	2	1	0	0
Mummy Cave	Layer 11	0	0	0	0	0	0	0
Mummy Cave	Layer 10	0	0	0	1	0	0	0
Mummy Cave	Layer 9	0	0	0	0	0	0	0
Mummy Cave	Layer 8	0	0	0	0	0	0	0
Mummy Cave	Layer 6	0	0	0	9	0	0	0
Mummy Cave	Layer 7	0	0	0	1	0	0	0
Mummy Cave	Layer 4	0	0	0	4	4	0	0
Mummy Cave	Layer 1	1	0	0	5	0	0	0

Appendix A.4. Faunal information of sites and components used in this dissertation.

Site	Component	FOX	RACCOON	SKUNK	HARE/RABBIT	MARMOT	MUSKRAT	MUSTELID
Myers-Hindman	Unit 1	0	0	0	0	0	0	0
Nelson	All	NA	NA	NA	NA	NA	NA	NA
Norton	All	NA	NA	NA	NA	NA	NA	NA
O.V. Clary	Middle	0	0	0	0	0	0	0
Olsen-Chubbuck	All	NA	NA	NA	NA	NA	NA	NA
Perry Ranch	All	NA	NA	NA	NA	NA	NA	NA
Plainview	All	NA	NA	NA	NA	NA	NA	NA
Rattlesnake Pass	All	NA	NA	NA	NA	NA	NA	NA
Rex Rodgers	All	NA	NA	NA	NA	NA	NA	NA
San Jon	Area 2	NA	NA	NA	NA	NA	NA	NA
Scottsbluff	All	NA	NA	NA	NA	NA	NA	NA
Sheaman	All	NA	NA	NA	NA	NA	NA	NA
Sorenson	II	0	0	0	0	0	0	0
Stewart's Cattle Guard	All	0	0	0	0	0	0	0
Upper Twin Mountain	All	NA	NA	NA	NA	NA	NA	NA
Vermilion Lakes	6a	0	0	0	0	0	0	0
Vermilion Lakes	8	0	0	0	23	0	0	0
Vermilion Lakes	6b	0	0	0	0	0	0	0
Vermilion Lakes	9a	0	0	0	0	0	0	0
Vermilion Lakes	9b	0	0	0	0	0	0	0
Waugh	All	0	0	0	0	0	0	0

Appendix A.4. Faunal information of sites and components used in this dissertation.

Site	Component	FOX	RACCOON	SKUNK	HARE/RABBIT	MARMOT	MUSKRAT	MUSTELID
Wilson Leonard	Unit II	0	0	0	59	0	0	0
Wilson Leonard	Upper Unit I	0	0	0	52	0	0	0
Wilson Leonard	EP Bonebed	0	0	0	29	0	0	0
Winger	All	NA	NA	NA	NA	NA	NA	NA

Appendix A.4. Faunal information of sites and components used in this dissertation.

SITE	COMPONENT	PRAIRIE DOG	RODENT/SMMAM	BIRD	TURTLE	SNAKES	LIZARD
12 Mile Creek	All	NA	NA	NA	NA	NA	NA
48SW13156	I	0	169	0	0	0	0
48SW8842	5	0	0	0	0	0	0
48UT375	2	0	25	1	0	0	0
48UT375	1	0	3149	0	0	0	0
Agate Basin	Folsom	0	0	0	0	0	0
Agate Basin	Agate Basin	NA	NA	NA	NA	NA	NA
Agate Basin	Hell Gap	NA	NA	NA	NA	NA	NA
Allen	OL2	37	53	19	7	5	0
Allen	IZ	56	16	28	8	10	0
Allen	OL1	150	48	14	85	2	0
Aubrey	Camp A and B	0	127	7	478	113	0
Big Lake	All	NA	NA	NA	NA	NA	NA
	HPP 1961						
Blackwater Draw	Locality-3						
	Bonebed	NA	NA	NA	NA	NA	NA
	HPP 1962-						
Blackwater Draw	Locality 5						
	Bonebed	NA	NA	NA	NA	NA	NA
Blackwater Draw	Sellards Clovis						
	Bison Kill	NA	NA	NA	NA	NA	NA
Blackwater Draw	Jelinek						
	Bonebed	NA	NA	NA	NA	NA	NA
Blue Point	2	0	21	0	0	0	0
Blue Point	1	0	13	0	0	0	0
Bonfire Shelter	Strat.A and B/C	NA	NA	NA	NA	NA	NA
Bottleneck Cave	III	0	2	0	0	0	0
Bottleneck Cave	II	0	1	0	0	0	0

Appendix A.4. Faunal information of sites and components used in this dissertation.

SITE	COMPONENT	PRAIRIE DOG	RODENT/SMMAM	BIRD	TURTLE	SNAKES	LIZARD
Bottleneck Cave	I	0	0	0	0	0	0
Burntwood Creek	All	NA	NA	NA	NA	NA	NA
Carter/Kerr-Mcgee	Cody	NA	NA	NA	NA	NA	NA
Carter/Kerr-Mcgee	Folsom	NA	NA	NA	NA	NA	NA
Casper	All	NA	NA	NA	NA	NA	NA
Cherokee Sewer	IIIA	NA	NA	NA	NA	NA	NA
Clary Ranch	All	NA	NA	NA	NA	NA	NA
Colby	All	0	0	0	0	0	0
Cooper	Upper Kill	NA	NA	NA	NA	NA	NA
Cooper	Middle Kill	NA	NA	NA	NA	NA	NA
Cooper	Lower Kill	NA	NA	NA	NA	NA	NA
Domebo	All	NA	NA	NA	NA	NA	NA
Finley	WYO Station B	NA	NA	NA	NA	NA	NA
Folsom	All	NA	NA	NA	NA	NA	NA
Frasca	Area 1	NA	NA	NA	NA	NA	NA
Frazier	All	NA	NA	NA	NA	NA	NA
Hanson	All	NA	NA	NA	NA	NA	NA
Helen							
Lookingbill	Layer 7/9	0	0	0	0	0	0
Helen							
Lookingbill	Layer 2/4	0	1	0	0	0	0
Hell Gap	Locality V Cody	0	0	0	0	0	0
Heron Eden	All	NA	NA	NA	NA	NA	NA
Horner	I	0	0	0	3	0	0
Horner	II	NA	NA	NA	NA	NA	NA

Appendix A.4. Faunal information of sites and components used in this dissertation.

SITE	COMPONENT	PRAIRIE DOG	RODENT/SMMAM	BIRD	TURTLE	SNAKES	LIZARD
Howard Gully	All	NA	NA	NA	NA	NA	NA
Hudson-Meng	All	NA	NA	NA	NA	NA	NA
Jake Bluff	Unit I	NA	NA	NA	NA	NA	NA
James Allen	All	NA	NA	NA	NA	NA	NA
Jerry Craig	All	NA	NA	NA	NA	NA	NA
Jones Miller	All	NA	NA	NA	NA	NA	NA
Jurgens	Area 3	NA	NA	NA	NA	NA	NA
Laird	All	NA	NA	NA	NA	NA	NA
Lake Theo	Folsom	0	0	0	0	0	0
Lamb Spring	Cody-1980/1981	NA	NA	NA	NA	NA	NA
Levi	Zone IV	NA	NA	NA	NA	NA	NA
Rockshelter	Zone I	28	0	107	57	0	0
Lime Creek							
Lindenmeier	Folsom	0	380	0	2	0	0
Lipscomb	All	NA	NA	NA	NA	NA	NA
Lubbock Lake	FA5-8/10	NA	NA	NA	NA	NA	NA
Lubbock Lake	FA6-3	NA	NA	NA	NA	NA	NA
Lubbock Lake	GA5-2	NA	NA	NA	NA	NA	NA
Lubbock Lake	FA5-7/GA5-3	NA	NA	NA	NA	NA	NA
Lubbock Lake	FA5-12	NA	NA	NA	NA	NA	NA
Lubbock Lake	FA6-11	NA	NA	NA	NA	NA	NA
Lubbock Lake	FA9-1	NA	NA	NA	NA	NA	NA
Lubbock Lake	FA5-17	NA	NA	NA	NA	NA	NA
Lubbock Lake	FA6-15	NA	NA	NA	NA	NA	NA

Appendix A.4. Faunal information of sites and components used in this dissertation.

SITE	COMPONENT	PRAIRIE DOG	RODENT/SMMAM	BIRD	TURTLE	SNAKES	LIZARD
Lubbock Lake	GA12-5	NA	NA	NA	NA	NA	NA
Lubbock Lake	FA2-2	NA	NA	NA	NA	NA	NA
Lubbock Lake	FA6-8	NA	NA	NA	NA	NA	NA
Mangus	I	0	0	0	0	0	0
Marks Beach	All	NA	NA	NA	NA	NA	NA
Medicine Lodge Creek	Fire Pit Level	0	21	2	0	0	2
Medicine Lodge Creek	Pryor Stemmed	0	14	2	0	0	0
Medicine Lodge Creek	N. Paleo (6-ft deep)	0	2	1	0	0	0
Medicine Lodge Creek	Fish Fauna	0	5	0	0	0	0
Medicine Lodge Creek	North Paleo	0	2	1	0	0	0
Medicine Lodge Creek	Cody	0	6	16	0	0	0
Medicine Lodge Creek	23ft-deep deer	0	34	1	0	0	0
Meserve	All	NA	NA	NA	NA	NA	NA
Mill Iron	All	NA	NA	NA	NA	NA	NA
Milnesand	All	NA	NA	NA	NA	NA	NA
Mummy Cave	Layer 13	0	0	0	0	0	0
Mummy Cave	Layer 14	0	1	0	0	0	0
Mummy Cave	Layer 12	0	2	1	0	0	0
Mummy Cave	Layer 11	0	0	0	0	0	0
Mummy Cave	Layer 10	0	3	1	0	0	0
Mummy Cave	Layer 9	0	1	0	0	0	0
Mummy Cave	Layer 8	0	0	0	0	0	0

Appendix A.4. Faunal information of sites and components used in this dissertation.

SITE	COMPONENT	PRAIRIE DOG	RODENT/SMMAM	BIRD	TURTLE	SNAKES	LIZARD
Mummy Cave	Layer 6	0	7	1	0	0	0
Mummy Cave	Layer 7	0	0	0	0	0	0
Mummy Cave	Layer 4	0	1	0	0	0	0
Mummy Cave	Layer 1	0	17	1	0	0	0
Myers-Hindman	Unit 1	0	0	0	0	0	0
Nelson	All	NA	NA	NA	NA	NA	NA
Norton	All	NA	NA	NA	NA	NA	NA
O.V. Clary	Middle	0	0	54	53	0	0
Olsen-Chubbuck	All	NA	NA	NA	NA	NA	NA
Perry Ranch	All	NA	NA	NA	NA	NA	NA
Plainview	All	NA	NA	NA	NA	NA	NA
Rattlesnake Pass	All	NA	NA	NA	NA	NA	NA
Rex Rodgers	All	NA	NA	NA	NA	NA	NA
San Jon	Area 2	NA	NA	NA	NA	NA	NA
Scottsbluff	All	NA	NA	NA	NA	NA	NA
Sheaman	All	NA	NA	NA	NA	NA	NA
Sorenson	II	0	0	0	0	0	0
Stewart's Cattle Guard	All	0	0	0	0	0	0
Upper Twin Mountain	All	NA	NA	NA	NA	NA	NA
Vermilion Lakes	6a	0	0	0	0	0	0
Vermilion Lakes	8	0	0	0	0	0	0
Vermilion Lakes	6b	0	0	0	0	0	0

Appendix A.4. Faunal information of sites and components used in this dissertation.

SITE	COMPONENT	PRAIRIE DOG	RODENT/SMMAM	BIRD	TURTLE	SNAKES	LIZARD
Vermilion Lakes	9a	0	0	0	0	0	0
Vermilion Lakes	9b	0	0	0	0	0	0
Waugh Wilson	All	0	0	0	0	0	0
Leonard Wilson	Unit II	0	17	1	19	15	0
Leonard Wilson	Upper Unit I	0	6	2	27	14	0
Leonard	EP Bonebed	0	11	0	5	0	0
Winger	All	NA	NA	NA	NA	NA	NA

Appendix A.4. Faunal information of sites and components used in this dissertation.

SITE	COMPONENT	AMPHIBIANS	FISH	MOLLUSKS	BISON				
					MNI	CRN	MR	CE	TH
12 Mile Creek	All	NA	NA	NA	13	2	5	25	53
48SW13156	I	0	0	0	0	NA	NA	NA	NA
48SW8842	5	0	0	0	0	NA	NA	NA	NA
48UT375	2	0	0	0	0	NA	NA	NA	NA
48UT375	1	0	0	0	0	NA	NA	NA	NA
Agate Basin	Folsom	0	0	0	11	NA	NA	NA	NA
Agate Basin	Agate Basin	NA	NA	NA	53	NA	NA	NA	NA
Agate Basin	Hell Gap	NA	NA	NA	16	NA	NA	NA	NA
Allen	OL2	6	3	0	2	NA	NA	NA	NA
Allen	IZ	3	3	0	3	NA	NA	NA	NA
Allen	OL1	42	0	0	12	NA	NA	NA	NA
Aubrey	Camp A and B	8	21	0	5	NA	NA	NA	NA
Big Lake	All	NA	NA	NA	10	NA	NA	NA	NA
Blackwater Draw	HPP 1961 Locality-3 Bonebed	NA	NA	NA	3	3	1	0	0
	HPP 1962-Locality 5 Bonebed	NA	NA	NA	3	0	0	0	0
Blackwater Draw	Sellards Clovis Bison Kill	NA	NA	NA	7	4	5	0	0
Blackwater Draw	Jelinek Bonebed	NA	NA	NA	4	0	2	5	1
Blue Point	2	0	0	0	0	NA	NA	NA	NA
Blue Point	1	0	0	0	0	NA	NA	NA	NA
Bonfire Shelter	Strat.A and B/C	NA	NA	NA	24	5	26	57	65
Bottleneck Cave	III	0	0	0	0	NA	NA	NA	NA
Bottleneck Cave	II	0	0	0	0	NA	NA	NA	NA
Bottleneck Cave	I	0	0	0	0	NA	NA	NA	NA
Burntwood Creek	All	NA	NA	NA	32	3	55	25	13
Carter/Kerr- Mcgee	Cody	NA	NA	NA	47	NA	NA	NA	NA

Appendix A.4. Faunal information of sites and components used in this dissertation.

SITE	COMPONENT	AMPHIBIANS	FISH	MOLLUSKS	BISON				
					MNI	CRN	MR	CE	TH
Carter/Kerr-Mcgee	Folsom	NA	NA	NA	1	NA	NA	NA	NA
Casper	All	NA	NA	NA	74	NA	NA	NA	NA
Cherokee Sewer	IIIA	NA	NA	NA	8	0	6	0	0
Clary Ranch	All	NA	NA	NA	41	13	20	48	34
Colby	All	0	0	0	0	NA	NA	NA	NA
Cooper	Upper Kill	NA	NA	NA	29	19	0	32	55
Cooper	Middle Kill	NA	NA	NA	29	16	0	15	17
Cooper	Lower Kill	NA	NA	NA	20	14	0	10	15
Domebo	All	NA	NA	NA	1	NA	NA	NA	NA
Finley	WYO Station B	NA	NA	NA	82	NA	NA	NA	NA
Folsom	All	NA	NA	NA	32	11	57	126	187
Frasca	Area 1	NA	NA	NA	63	NA	NA	NA	NA
Frazier	All	NA	NA	NA	44	5	27	24	33
Hanson	All	NA	NA	NA	4	NA	NA	NA	NA
Helen									
Lookingbill	Layer 7/9	0	0	0	1	NA	NA	NA	NA
Helen									
Lookingbill	Layer 2/4	0	0	0	1	NA	NA	NA	NA
Hell Gap	Locality V Cody	0	0	0	7	NA	NA	NA	NA
Heron Eden	All	NA	NA	NA	37	NA	NA	NA	NA
Horner	I	0	0	0	158	7	29	14	20
Horner	II	NA	NA	NA	65	NA	NA	NA	NA
Howard Gully	All	NA	NA	NA	2	NA	NA	NA	NA
Hudson-Meng	All	NA	NA	NA	474	NA	NA	NA	NA
Jake Bluff	Unit I	NA	NA	NA	22	NA	NA	NA	NA
James Allen	All	NA	NA	NA	15	NA	NA	NA	NA

Appendix A.4. Faunal information of sites and components used in this dissertation.

SITE	COMPONENT	AMPHIBIANS	FISH	MOLLUSKS	BISON				
					MNI	CRN	MR	CE	TH
Jerry Craig	All	NA	NA	NA	7	1	14	3	2
Jones Miller	All	NA	NA	NA	250	NA	NA	NA	NA
Jurgens	Area 3	NA	NA	NA	36	32	61	0	0
Laird	All	NA	NA	NA	2	NA	NA	NA	NA
Lake Theo	Folsom	0	0	0	12	2	8	10	5
Lamb Spring	Cody-1980/1981	NA	NA	NA	28	8	13	50	53
Levi Rockshelter	Zone IV	NA	NA	NA	1	NA	NA	NA	NA
Lime Creek	Zone I	0	0	2	3	NA	NA	NA	NA
Lindenmeier	Folsom	0	0	0	13	NA	NA	NA	NA
Lipscomb	All	NA	NA	NA	56	0	47	39	0
Lubbock Lake	FA5-8/10	NA	NA	NA	2	NA	NA	NA	NA
Lubbock Lake	FA6-3	NA	NA	NA	7	NA	NA	NA	NA
Lubbock Lake	GA5-2	NA	NA	NA	1	NA	NA	NA	NA
Lubbock Lake	FA5-7/GA5-3	NA	NA	NA	6	NA	NA	NA	NA
Lubbock Lake	FA5-12	NA	NA	NA	4	NA	NA	NA	NA
Lubbock Lake	FA6-11	NA	NA	NA	6	NA	NA	NA	NA
Lubbock Lake	FA9-1	NA	NA	NA	5	NA	NA	NA	NA
Lubbock Lake	FA5-17	NA	NA	NA	4	NA	NA	NA	NA
Lubbock Lake	FA6-15	NA	NA	NA	1	NA	NA	NA	NA
Lubbock Lake	GA12-5	NA	NA	NA	3	NA	NA	NA	NA
Lubbock Lake	FA2-2	NA	NA	NA	3	NA	NA	NA	NA
Lubbock Lake	FA6-8	NA	NA	NA	3	NA	NA	NA	NA
Mangus	I	0	0	0	0	NA	NA	NA	NA

Appendix A.4. Faunal information of sites and components used in this dissertation.

SITE	COMPONENT	AMPHIBIANS	FISH	MOLLUSKS	BISON				
					MNI	CRN	MR	CE	TH
Marks Beach	All	NA	NA	NA	1	NA	NA	NA	NA
Medicine Lodge Creek	Fire Pit Level	0	5	0	0	NA	NA	NA	NA
Medicine Lodge Creek	Pryor Stemmed	0	0	0	1	NA	NA	NA	NA
Medicine Lodge Creek	N. Paleo (6-ft deep)	0	0	0	0	NA	NA	NA	NA
Medicine Lodge Creek	Fish Fauna	0	0	0	0	NA	NA	NA	NA
Medicine Lodge Creek	North Paleo	0	0	0	0	NA	NA	NA	NA
Medicine Lodge Creek	Cody	0	0	0	1	NA	NA	NA	NA
Medicine Lodge Creek	23ft-deep deer	0	0	0	1	NA	NA	NA	NA
Meserve	All	NA	NA	NA	4	NA	NA	NA	NA
Mill Iron	All	NA	NA	NA	34	NA	NA	NA	NA
Milnesand	All	NA	NA	NA	33	1	6	1	1
Mummy Cave	Layer 13	0	0	0	0	NA	NA	NA	NA
Mummy Cave	Layer 14	0	0	0	0	NA	NA	NA	NA
Mummy Cave	Layer 12	0	0	0	0	NA	NA	NA	NA
Mummy Cave	Layer 11	0	0	0	0	NA	NA	NA	NA
Mummy Cave	Layer 10	0	0	0	0	NA	NA	NA	NA
Mummy Cave	Layer 9	0	0	0	0	NA	NA	NA	NA
Mummy Cave	Layer 8	0	0	0	0	NA	NA	NA	NA
Mummy Cave	Layer 6	0	0	0	0	NA	NA	NA	NA
Mummy Cave	Layer 7	0	0	0	0	NA	NA	NA	NA
Mummy Cave	Layer 4	0	0	0	0	NA	NA	NA	NA

Appendix A.4. Faunal information of sites and components used in this dissertation.

SITE	COMPONENT	AMPHIBIANS	FISH	MOLLUSKS	BISON				
					MNI	CRN	MR	CE	TH
Mummy Cave	Layer 1	0	0	0	0	NA	NA	NA	NA
Myers-Hindman	Unit 1	0	0	0	2	NA	NA	NA	NA
Nelson	All	NA	NA	NA	5	NA	NA	NA	NA
Norton	All	NA	NA	NA	8	8	6	3	14
O.V. Clary	Middle	0	0		6	NA	NA	NA	NA
Olsen-Chubbuck	All	NA	NA	NA	190	64	102	313	865
Perry Ranch	All	NA	NA	NA	2	NA	NA	NA	NA
Plainview	All	NA	NA	NA	84	0	0	0	0
Rattlesnake Pass	All	NA	NA	NA	2	NA	NA	NA	NA
Rex Rodgers	All	NA	NA	NA	6	6	9	13	9
San Jon	Area 2	NA	NA	NA	5	5	5	1	0
Scottsbluff	All	NA	NA	NA	26	NR	NR	NR	NR
Sheaman	All	NA	NA	NA	1	NA	NA	NA	NA
Sorenson	II	0	0	0	1	NA	NA	NA	NA
Stewart's Cattle Guard	All	0	0	0	49	NA	NA	NA	NA
Upper Twin Mountain	All	NA	NA	NA	15	NA	NA	NA	NA
Vermilion Lakes	6a	0	0	0	0	NA	NA	NA	NA
Vermilion Lakes	8	0	0	0	1	NA	NA	NA	NA
Vermilion Lakes	6b	0	0	0	0	NA	NA	NA	NA
Vermilion Lakes	9a	0	0	0	0	NA	NA	NA	NA
Vermilion Lakes	9b	0	0	0	0	NA	NA	NA	NA
Waugh	All	0	0	0	6	NA	NA	NA	NA
Wilson Leonard	Unit II	0	85	0	0	NA	NA	NA	NA
Wilson Leonard	Upper Unit I	0	0	0	1	NA	NA	NA	NA

Appendix A.4. Faunal information of sites and components used in this dissertation.

SITE	COMPONENT	AMPHIBIANS	FISH	MOLLUSKS	BISON				
					MNI	CRN	MR	CE	TH
Wilson Leonard	EP Bonebed	0	0	0	2	NA	NA	NA	NA
Winger	All	NA	NA	NA	6	NA	NA	NA	NA

Appendix A.4. Faunal information of sites and components used in this dissertation.

SITE	COMPONENT	LM	SAC	RB	SC	HM	RD	UL	MC	IM
12 Mile Creek	All	18	3	34	6	8	10	8	16	3
48SW13156	I	NA	NA	NA	NA	NA	NA	NA	NA	NA
48SW8842	5	NA	NA	NA	NA	NA	NA	NA	NA	NA
48UT375	2	NA	NA	NA	NA	NA	NA	NA	NA	NA
48UT375	1	NA	NA	NA	NA	NA	NA	NA	NA	NA
Agate Basin	Folsom	NA	NA	NA	NA	NA	NA	NA	NA	NA
Agate Basin	Agate Basin	NA	NA	NA	NA	NA	NA	NA	NA	NA
Agate Basin	Hell Gap	NA	NA	NA	NA	NA	NA	NA	NA	NA
Allen	OL2	NA	NA	NA	NA	NA	NA	NA	NA	NA
Allen	IZ	NA	NA	NA	NA	NA	NA	NA	NA	NA
Allen	OL1	NA	NA	NA	NA	NA	NA	NA	NA	NA
Aubrey	Camp A and B	NA	NA	NA	NA	NA	NA	NA	NA	NA
Big Lake	All	NA	NA	NA	NA	NA	NA	NA	NA	NA
Blackwater Draw	HPP 1961 Locality- 3 Bonebed	0	0	16	1	2	0	1	0	1
Blackwater Draw	HPP 1962-Locality 5 Bonebed	0	0	3	1	2	2	0	0	2
Blackwater Draw	Sellards Clovis Bison Kill	0	0	0	3	0	0	0	0	0
Blackwater Draw	Jelinek Bonebed	2	0	12	0	1	2	0	1	2
Blue Point	2	NA	NA	NA	NA	NA	NA	NA	NA	NA
Blue Point	1	NA	NA	NA	NA	NA	NA	NA	NA	NA
Bonfire Shelter	Strat.A and B/C	42	13	43	13	30	26	18	18	16
Bottleneck Cave	III	NA	NA	NA	NA	NA	NA	NA	NA	NA
Bottleneck Cave	II	NA	NA	NA	NA	NA	NA	NA	NA	NA
Bottleneck Cave	I	NA	NA	NA	NA	NA	NA	NA	NA	NA
Burntwood Creek	All	0	0	9	0	5	5	2	23	0
Carter/Kerr-Mcgee	Cody	NA	NA	NA	NA	NA	NA	NA	NA	NA
Carter/Kerr-Mcgee	Folsom	NA	NA	NA	NA	NA	NA	NA	NA	NA
Casper	All	NA	NA	NA	NA	NA	NA	NA	NA	NA

Appendix A.4. Faunal information of sites and components used in this dissertation.

SITE	COMPONENT	LM	SAC	RB	SC	HM	RD	UL	MC	IM
Cherokee Sewer	IIIA	0	2	0	9	3	11	12	7	5
Clary Ranch	All	20	8	82	18	42	25	21	21	26
Colby	All	NA	NA	NA	NA	NA	NA	NA	NA	NA
Cooper	Upper Kill	18	15	65	34	34	31	33	32	20
Cooper	Middle Kill	15	10	29	29	30	33	27	29	0
Cooper	Lower Kill	13	6	16	23	21	24	21	18	13
Domebo	All	NA	NA	NA	NA	NA	NA	NA	NA	NA
Finley	WYO Station B	NA	NA	NA	NA	NA	NA	NA	NA	NA
Folsom	All	93	15	280	26	30	39	32	43	29
Frasca	Area 1	NA	NA	NA	NA	NA	NA	NA	NA	NA
Frazier	All	12	14	16	41	29	36	0	41	0
Hanson	All	NA	NA	NA	NA	NA	NA	NA	NA	NA
Helen Lookingbill	Layer 7/9	NA	NA	NA	NA	NA	NA	NA	NA	NA
Helen Lookingbill	Layer 2/4	NA	NA	NA	NA	NA	NA	NA	NA	NA
Hell Gap	Locality V Cody	NA	NA	NA	NA	NA	NA	NA	NA	NA
Heron Eden	All	NA	NA	NA	NA	NA	NA	NA	NA	NA
Horner	I	15	7	257	25	41	36	23	35	29
Horner	II	NA	NA	NA	NA	NA	NA	NA	NA	NA
Howard Gully	All	NA	NA	NA	NA	NA	NA	NA	NA	NA
Hudson-Meng	All	NA	NA	NA	NA	NA	NA	NA	NA	NA
Jake Bluff	Unit I	NA	NA	NA	NA	NA	NA	NA	NA	NA
James Allen	All	NA	NA	NA	NA	NA	NA	NA	NA	NA
Jerry Craig	All	4	0	1	1	2	3	2	3	1
Jones Miller	All	NA	NA	NA	NA	NA	NA	NA	NA	NA
Jurgens	Area 3	0	0	0	66	42	53	32	69	34

Appendix A.4. Faunal information of sites and components used in this dissertation.

SITE	COMPONENT	LM	SAC	RB	SC	HM	RD	UL	MC	IM
Laird	All	NA	NA	NA	NA	NA	NA	NA	NA	NA
Lake Theo	Folsom	5	1	0	3	8	4	5	11	1
Lamb Spring	Cody-1980/1981	26	3	69	12	15	14	15	9	15
Levi Rockshelter	Zone IV	NA	NA	NA	NA	NA	NA	NA	NA	NA
Lime Creek	Zone I	NA	NA	NA	NA	NA	NA	NA	NA	NA
Lindenmeier	Folsom	NA	NA	NA	NA	NA	NA	NA	NA	NA
Lipscomb	All	0	14	0	34	49	56	43	96	0
Lubbock Lake	FA5-8/10	NA	NA	NA	NA	NA	NA	NA	NA	NA
Lubbock Lake	FA6-3	NA	NA	NA	NA	NA	NA	NA	NA	NA
Lubbock Lake	GA5-2	NA	NA	NA	NA	NA	NA	NA	NA	NA
Lubbock Lake	FA5-7/GA5-3	NA	NA	NA	NA	NA	NA	NA	NA	NA
Lubbock Lake	FA5-12	NA	NA	NA	NA	NA	NA	NA	NA	NA
Lubbock Lake	FA6-11	NA	NA	NA	NA	NA	NA	NA	NA	NA
Lubbock Lake	FA9-1	NA	NA	NA	NA	NA	NA	NA	NA	NA
Lubbock Lake	FA5-17	NA	NA	NA	NA	NA	NA	NA	NA	NA
Lubbock Lake	FA6-15	NA	NA	NA	NA	NA	NA	NA	NA	NA
Lubbock Lake	GA12-5	NA	NA	NA	NA	NA	NA	NA	NA	NA
Lubbock Lake	FA2-2	NA	NA	NA	NA	NA	NA	NA	NA	NA
Lubbock Lake	FA6-8	NA	NA	NA	NA	NA	NA	NA	NA	NA
Mangus	I	NA	NA	NA	NA	NA	NA	NA	NA	NA
Marks Beach	All	NA	NA	NA	NA	NA	NA	NA	NA	NA
Medicine Lodge Creek	Fire Pit Level	NA	NA	NA	NA	NA	NA	NA	NA	NA
Medicine Lodge Creek	Pryor Stemmed	NA	NA	NA	NA	NA	NA	NA	NA	NA

Appendix A.4. Faunal information of sites and components used in this dissertation.

SITE	COMPONENT	LM	SAC	RB	SC	HM	RD	UL	MC	IM
Medicine Lodge Creek	N. Paleo (6-ft deep)	NA	NA	NA	NA	NA	NA	NA	NA	NA
Medicine Lodge Creek	Fish Fauna	NA	NA	NA	NA	NA	NA	NA	NA	NA
Medicine Lodge Creek	North Paleo	NA	NA	NA	NA	NA	NA	NA	NA	NA
Medicine Lodge Creek	Cody	NA	NA	NA	NA	NA	NA	NA	NA	NA
Medicine Lodge Creek	23ft-deep deer	NA	NA	NA	NA	NA	NA	NA	NA	NA
Meserve	All	NA	NA	NA	NA	NA	NA	NA	NA	NA
Mill Iron	All	NA	NA	NA	NA	NA	NA	NA	NA	NA
Milnesand	All	0	0	1	2	6	6	2	8	1
Mummy Cave	Layer 13	NA	NA	NA	NA	NA	NA	NA	NA	NA
Mummy Cave	Layer 14	NA	NA	NA	NA	NA	NA	NA	NA	NA
Mummy Cave	Layer 12	NA	NA	NA	NA	NA	NA	NA	NA	NA
Mummy Cave	Layer 11	NA	NA	NA	NA	NA	NA	NA	NA	NA
Mummy Cave	Layer 10	NA	NA	NA	NA	NA	NA	NA	NA	NA
Mummy Cave	Layer 9	NA	NA	NA	NA	NA	NA	NA	NA	NA
Mummy Cave	Layer 8	NA	NA	NA	NA	NA	NA	NA	NA	NA
Mummy Cave	Layer 6	NA	NA	NA	NA	NA	NA	NA	NA	NA
Mummy Cave	Layer 7	NA	NA	NA	NA	NA	NA	NA	NA	NA
Mummy Cave	Layer 4	NA	NA	NA	NA	NA	NA	NA	NA	NA
Mummy Cave	Layer 1	NA	NA	NA	NA	NA	NA	NA	NA	NA
Myers-Hindman	Unit 1	NA	NA	NA	NA	NA	NA	NA	NA	NA
Nelson	All	NA	NA	NA	NA	NA	NA	NA	NA	NA
Norton	All	7	3	31	11	5	6	2	2	5
O.V. Clary	Middle	NA	NA	NA	NA	NA	NA	NA	NA	NA
Olsen-Chubbuck	All	320	64	1120	99	95	86	69	0	64

Appendix A.4. Faunal information of sites and components used in this dissertation.

SITE	COMPONENT	LM	SAC	RB	SC	HM	RD	UL	MC	IM
Perry Ranch	All	NA	NA	NA	NA	NA	NA	NA	NA	NA
Plainview	All	0	0	192	16	27	17	5	23	4
Rattlesnake Pass	All	NA	NA	NA	NA	NA	NA	NA	NA	NA
Rex Rodgers	All	9	0	10	3	2	5	4	7	0
San Jon	Area 2	1	0	0	1	2	3	3	6	1
Scottsbluff	All	NR	NR	NR	NR	NR	NR	NR	NR	NR
Sheaman	All	NA	NA	NA	NA	NA	NA	NA	NA	NA
Sorenson	II	NA	NA	NA	NA	NA	NA	NA	NA	NA
Stewart's Cattle Guard	All	NA	NA	NA	NA	NA	NA	NA	NA	NA
Upper Twin Mountain	All	NA	NA	NA	NA	NA	NA	NA	NA	NA
Vermilion Lakes	6a	NA	NA	NA	NA	NA	NA	NA	NA	NA
Vermilion Lakes	8	NA	NA	NA	NA	NA	NA	NA	NA	NA
Vermilion Lakes	6b	NA	NA	NA	NA	NA	NA	NA	NA	NA
Vermilion Lakes	9a	NA	NA	NA	NA	NA	NA	NA	NA	NA
Vermilion Lakes	9b	NA	NA	NA	NA	NA	NA	NA	NA	NA
Waugh	All	NA	NA	NA	NA	NA	NA	NA	NA	NA
Wilson Leonard	Unit II	NA	NA	NA	NA	NA	NA	NA	NA	NA
Wilson Leonard	Upper Unit I	NA	NA	NA	NA	NA	NA	NA	NA	NA
Wilson Leonard	EP Bonebed	NA	NA	NA	NA	NA	NA	NA	NA	NA
Winger	All	NA	NA	NA	NA	NA	NA	NA	NA	NA

Appendix A.4. Faunal information of sites and components used in this dissertation.

SITE	COMPONENT	SAC	RB	SC	HM	RD	UL	MC	IM	FM
12 Mile Creek	All	3	34	6	8	10	8	16	3	10
48SW13156	I	NA	NA	NA	NA	NA	NA	NA	NA	NA
48SW8842	5	NA	NA	NA	NA	NA	NA	NA	NA	NA
48UT375	2	NA	NA	NA	NA	NA	NA	NA	NA	NA
48UT375	1	NA	NA	NA	NA	NA	NA	NA	NA	NA
Agate Basin	Folsom	NA	NA	NA	NA	NA	NA	NA	NA	NA
Agate Basin	Agate Basin	NA	NA	NA	NA	NA	NA	NA	NA	NA
Agate Basin	Hell Gap	NA	NA	NA	NA	NA	NA	NA	NA	NA
Allen	OL2	NA	NA	NA	NA	NA	NA	NA	NA	NA
Allen	IZ	NA	NA	NA	NA	NA	NA	NA	NA	NA
Allen	OL1	NA	NA	NA	NA	NA	NA	NA	NA	NA
Aubrey	Camp A and B	NA	NA	NA	NA	NA	NA	NA	NA	NA
Big Lake	All	NA	NA	NA	NA	NA	NA	NA	NA	NA
Blackwater Draw	HPP 1961 Locality-3 Bonebed	0	16	1	2	0	1	0	1	2
Blackwater Draw	HPP 1962-Locality 5 Bonebed	0	3	1	2	2	0	0	2	0
Blackwater Draw	Sellards Clovis Bison Kill	0	0	3	0	0	0	0	0	0
Blackwater Draw	Jelinek Bonebed	0	12	0	1	2	0	1	2	3
Blue Point	2	NA	NA	NA	NA	NA	NA	NA	NA	NA
Blue Point	1	NA	NA	NA	NA	NA	NA	NA	NA	NA
Bonfire Shelter	Strat.A and B/C	13	43	13	30	26	18	18	16	33
Bottleneck Cave	III	NA	NA	NA	NA	NA	NA	NA	NA	NA
Bottleneck Cave	II	NA	NA	NA	NA	NA	NA	NA	NA	NA
Bottleneck Cave	I	NA	NA	NA	NA	NA	NA	NA	NA	NA
Burntwood Creek	All	0	9	0	5	5	2	23	0	1
Carter/Kerr-Mcgee	Cody	NA	NA	NA	NA	NA	NA	NA	NA	NA
Carter/Kerr-Mcgee	Folsom	NA	NA	NA	NA	NA	NA	NA	NA	NA
Casper	All	NA	NA	NA	NA	NA	NA	NA	NA	NA

Appendix A.4. Faunal information of sites and components used in this dissertation.

SITE	COMPONENT	SAC	RB	SC	HM	RD	UL	MC	IM	FM
Cherokee Sewer	IIIA	2	0	9	3	11	12	7	5	3
Clary Ranch	All	8	82	18	42	25	21	21	26	18
Colby	All	NA	NA	NA	NA	NA	NA	NA	NA	NA
Cooper	Upper Kill	15	65	34	34	31	33	32	20	36
Cooper	Middle Kill	10	29	29	30	33	27	29	0	32
Cooper	Lower Kill	6	16	23	21	24	21	18	13	21
Domebo	All	NA	NA	NA	NA	NA	NA	NA	NA	NA
Finley	WYO Station B	NA	NA	NA	NA	NA	NA	NA	NA	NA
Folsom	All	15	280	26	30	39	32	43	29	28
Frasca	Area 1	NA	NA	NA	NA	NA	NA	NA	NA	NA
Frazier	All	14	16	41	29	36	0	41	0	23
Hanson	All	NA	NA	NA	NA	NA	NA	NA	NA	NA
Helen Lookingbill	Layer 7/9	NA	NA	NA	NA	NA	NA	NA	NA	NA
Helen Lookingbill	Layer 2/4	NA	NA	NA	NA	NA	NA	NA	NA	NA
Hell Gap	Locality V Cody	NA	NA	NA	NA	NA	NA	NA	NA	NA
Heron Eden	All	NA	NA	NA	NA	NA	NA	NA	NA	NA
Horner	I	7	257	25	41	36	23	35	29	39
Horner	II	NA	NA	NA	NA	NA	NA	NA	NA	NA
Howard Gully	All	NA	NA	NA	NA	NA	NA	NA	NA	NA
Hudson-Meng	All	NA	NA	NA	NA	NA	NA	NA	NA	NA
Jake Bluff	Unit I	NA	NA	NA	NA	NA	NA	NA	NA	NA
James Allen	All	NA	NA	NA	NA	NA	NA	NA	NA	NA
Jerry Craig	All	0	1	1	2	3	2	3	1	0
Jones Miller	All	NA	NA	NA	NA	NA	NA	NA	NA	NA
Jurgens	Area 3	0	0	66	42	53	32	69	34	60

Appendix A.4. Faunal information of sites and components used in this dissertation.

SITE	COMPONENT	SAC	RB	SC	HM	RD	UL	MC	IM	FM
Laird	All	NA	NA	NA	NA	NA	NA	NA	NA	NA
Lake Theo	Folsom	1	0	3	8	4	5	11	1	1
Lamb Spring	Cody-1980/1981	3	69	12	15	14	15	9	15	14
Levi Rockshelter	Zone IV	NA	NA	NA	NA	NA	NA	NA	NA	NA
Lime Creek	Zone I	NA	NA	NA	NA	NA	NA	NA	NA	NA
Lindenmeier	Folsom	NA	NA	NA	NA	NA	NA	NA	NA	NA
Lipscomb	All	14	0	34	49	56	43	96	0	36
Lubbock Lake	FA5-8/10	NA	NA	NA	NA	NA	NA	NA	NA	NA
Lubbock Lake	FA6-3	NA	NA	NA	NA	NA	NA	NA	NA	NA
Lubbock Lake	GA5-2	NA	NA	NA	NA	NA	NA	NA	NA	NA
Lubbock Lake	FA5-7/GA5-3	NA	NA	NA	NA	NA	NA	NA	NA	NA
Lubbock Lake	FA5-12	NA	NA	NA	NA	NA	NA	NA	NA	NA
Lubbock Lake	FA6-11	NA	NA	NA	NA	NA	NA	NA	NA	NA
Lubbock Lake	FA9-1	NA	NA	NA	NA	NA	NA	NA	NA	NA
Lubbock Lake	FA5-17	NA	NA	NA	NA	NA	NA	NA	NA	NA
Lubbock Lake	FA6-15	NA	NA	NA	NA	NA	NA	NA	NA	NA
Lubbock Lake	GA12-5	NA	NA	NA	NA	NA	NA	NA	NA	NA
Lubbock Lake	FA2-2	NA	NA	NA	NA	NA	NA	NA	NA	NA
Lubbock Lake	FA6-8	NA	NA	NA	NA	NA	NA	NA	NA	NA
Mangus	I	NA	NA	NA	NA	NA	NA	NA	NA	NA
Marks Beach	All	NA	NA	NA	NA	NA	NA	NA	NA	NA
Medicine Lodge Creek	Fire Pit Level	NA	NA	NA	NA	NA	NA	NA	NA	NA
Medicine Lodge Creek	Pryor Stemmed	NA	NA	NA	NA	NA	NA	NA	NA	NA

Appendix A.4. Faunal information of sites and components used in this dissertation.

SITE	COMPONENT	SAC	RB	SC	HM	RD	UL	MC	IM	FM
Medicine Lodge Creek	N. Paleo (6-ft deep)	NA	NA	NA	NA	NA	NA	NA	NA	NA
Medicine Lodge Creek	Fish Fauna	NA	NA	NA	NA	NA	NA	NA	NA	NA
Medicine Lodge Creek	North Paleo	NA	NA	NA	NA	NA	NA	NA	NA	NA
Medicine Lodge Creek	Cody	NA	NA	NA	NA	NA	NA	NA	NA	NA
Medicine Lodge Creek	23ft-deep deer	NA	NA	NA	NA	NA	NA	NA	NA	NA
Meserve	All	NA	NA	NA	NA	NA	NA	NA	NA	NA
Mill Iron	All	NA	NA	NA	NA	NA	NA	NA	NA	NA
Milnesand	All	0	1	2	6	6	2	8	1	1
Mummy Cave	Layer 13	NA	NA	NA	NA	NA	NA	NA	NA	NA
Mummy Cave	Layer 14	NA	NA	NA	NA	NA	NA	NA	NA	NA
Mummy Cave	Layer 12	NA	NA	NA	NA	NA	NA	NA	NA	NA
Mummy Cave	Layer 11	NA	NA	NA	NA	NA	NA	NA	NA	NA
Mummy Cave	Layer 10	NA	NA	NA	NA	NA	NA	NA	NA	NA
Mummy Cave	Layer 9	NA	NA	NA	NA	NA	NA	NA	NA	NA
Mummy Cave	Layer 8	NA	NA	NA	NA	NA	NA	NA	NA	NA
Mummy Cave	Layer 6	NA	NA	NA	NA	NA	NA	NA	NA	NA
Mummy Cave	Layer 7	NA	NA	NA	NA	NA	NA	NA	NA	NA
Mummy Cave	Layer 4	NA	NA	NA	NA	NA	NA	NA	NA	NA
Mummy Cave	Layer 1	NA	NA	NA	NA	NA	NA	NA	NA	NA
Myers-Hindman	Unit 1	NA	NA	NA	NA	NA	NA	NA	NA	NA
Nelson	All	NA	NA	NA	NA	NA	NA	NA	NA	NA
Norton	All	3	31	11	5	6	2	2	5	7
O.V. Clary	Middle	NA	NA	NA	NA	NA	NA	NA	NA	NA
Olsen-Chubbuck	All	64	1120	99	95	86	69	0	64	85

Appendix A.4. Faunal information of sites and components used in this dissertation.

SITE	COMPONENT	SAC	RB	SC	HM	RD	UL	MC	IM	FM
Perry Ranch	All	NA	NA	NA	NA	NA	NA	NA	NA	NA
Plainview	All	0	192	16	27	17	5	23	4	18
Rattlesnake Pass	All	NA	NA	NA	NA	NA	NA	NA	NA	NA
Rex Rodgers	All	0	10	3	2	5	4	7	0	2
San Jon	Area 2	0	0	1	2	3	3	6	1	0
Scottsbluff	All	NR	NR	NR	NR	NR	NR	NR	NR	NR
Sheaman	All	NA	NA	NA	NA	NA	NA	NA	NA	NA
Sorenson	II	NA	NA	NA	NA	NA	NA	NA	NA	NA
Stewart's Cattle Guard	All	NA	NA	NA	NA	NA	NA	NA	NA	NA
Upper Twin Mountain	All	NA	NA	NA	NA	NA	NA	NA	NA	NA
Vermilion Lakes	6a	NA	NA	NA	NA	NA	NA	NA	NA	NA
Vermilion Lakes	8	NA	NA	NA	NA	NA	NA	NA	NA	NA
Vermilion Lakes	6b	NA	NA	NA	NA	NA	NA	NA	NA	NA
Vermilion Lakes	9a	NA	NA	NA	NA	NA	NA	NA	NA	NA
Vermilion Lakes	9b	NA	NA	NA	NA	NA	NA	NA	NA	NA
Waugh	All	NA	NA	NA	NA	NA	NA	NA	NA	NA
Wilson Leonard	Unit II	NA	NA	NA	NA	NA	NA	NA	NA	NA
Wilson Leonard	Upper Unit I	NA	NA	NA	NA	NA	NA	NA	NA	NA
Wilson Leonard	EP Bonebed	NA	NA	NA	NA	NA	NA	NA	NA	NA
Winger	All	NA	NA	NA	NA	NA	NA	NA	NA	NA

Appendix A.4. Faunal information of sites and components used in this dissertation.

SITE	COMPONENT	TA	MT	PH	REFERENCE
12 Mile Creek	All	14	10	165	Hill 2002
48SW13156	I	NA	NA	NA	Byers et al. 2005
48SW8842	5	NA	NA	NA	Byers et al. 2005
48UT375	2	NA	NA	NA	Smith et al. 2003
48UT375	1	NA	NA	NA	Smith et al. 2003
Agate Basin	Folsom	NA	NA	NA	Hill 2001
Agate Basin	Agate Basin	NA	NA	NA	Hill 2001
Agate Basin	Hell Gap	NA	NA	NA	Hill 2001
Allen	OL2	NA	NA	NA	Hudson 2007
Allen	IZ	NA	NA	NA	Hudson 2007
Allen	OL1	NA	NA	NA	Hudson 2007
Aubrey	Camp A and B	NA	NA	NA	Ferring 2001
Big Lake	All	NA	NA	NA	Turpin et al. 1997
Blackwater Draw	HPP 1961 Locality-3 Bonebed	2	0	20	Hester 1972
Blackwater Draw	HPP 1962-Locality 5 Bonebed	1	0	0	Hester 1972
Blackwater Draw	Sellards Clovis Bison Kill	1	0	4	Hester 1972 Hester 1973, Johnson and Holliday 1997
Blackwater Draw	Jelinek Bonebed	4	5	6	Johnson and Pastor 2003
Blue Point	2	NA	NA	NA	Johnson and Pastor 2003
Blue Point	1	NA	NA	NA	Byerly et al. 2004 and 2005
Bonfire Shelter	Strat.A and B/C	26	14	171	Husted 1969
Bottleneck Cave	III	NA	NA	NA	Husted 1969
Bottleneck Cave	II	NA	NA	NA	Husted 1969
Bottleneck Cave	I	NA	NA	NA	Husted 1969
Burntwood Creek	All	3	12	577	Hill et al. 1992
Carter/Kerr-Mcgee	Cody	NA	NA	NA	Frison 1984
Carter/Kerr-Mcgee	Folsom	NA	NA	NA	Frison 1984
Casper	All	NA	NA	NA	Todd et al. 1997
Cherokee Sewer	IIIA	14	0	0	Pyle 1980
Clary Ranch	All	29	19	157	Hill 2001 Frison and Todd 1986
Colby	All	NA	NA	NA	Bement 1999
Cooper	Upper Kill	40	42	312	Bement 1999
Cooper	Middle Kill	32	29	242	Bement 1999
Cooper	Lower Kill	17	15	149	Bement 1999

Appendix A.4. Faunal information of sites and components used in this dissertation.

SITE	COMPONENT	TA	MT	PH	REFERENCE
Domebo	All	NA	NA	NA	Leonhardy 1966
Finley	WYO Station B	NA	NA	NA	Hill Jr. 2008
Folsom	All	32	49	507	Baxevanis 1997, Meltzer 2006
Frasca	Area 1	NA	NA	NA	Fulgham and Stanford 1982
Frazier	All	37	44	341	Borresen 2002
Hanson	All	NA	NA	NA	Amick 1994 (Table 5.2)
Helen Lookingbill	Layer 7/9	NA	NA	NA	Larson et al. 1995, Kornfeld et al. 2001
Helen Lookingbill	Layer 2/4	NA	NA	NA	Larson et al. 1995, Kornfeld et al. 2001
Hell Gap	Locality V Cody	NA	NA	NA	Knell et al. 2002
Heron Eden	All	NA	NA	NA	Corbeil 1995
Horner	I	40	44	82	Frison and Todd 1987
Horner	II	NA	NA	NA	Frison and Todd 1987
Howard Gully	All	NA	NA	NA	Hurst et al. 2010
Hudson-Meng	All	NA	NA	NA	Agenbroad 1978
Jake Bluff	Unit I	NA	NA	NA	Bement and Carter 2003, 2010
James Allen	All	NA	NA	NA	Berman 1959; Mulloy 1959
Jerry Craig	All	0	0	4	Hill and Kornfeld 1999
Jones Miller	All	NA	NA	NA	Stanford 1999
Jurgens	Area 3	74	62	0	Wheat 1979
Laird	All	NA	NA	NA	Hofman and Blackmar 1997
Lake Theo	Folsom	6	4	56	Baxevanis 1997
Lamb Spring	Cody-1980/1981	17	13	89	McCartney 1983
Levi Rockshelter	Zone IV	NA	NA	NA	Alexander 1963, 1982
Lime Creek	Zone I	NA	NA	NA	Jones 1999
Lindenmeier	Folsom	NA	NA	NA	Wilmsen and Roberts 1978

Appendix A.4. Faunal information of sites and components used in this dissertation.

SITE	COMPONENT	TA	MT	PH	REFERENCE
Lipscomb	All	37	67	153	Todd et al. 1992, Hofman and Todd 2001
Lubbock Lake	FA5-8/10	NA	NA	NA	Johnson and Holliday 1989
Lubbock Lake	FA6-3	NA	NA	NA	Johnson and Holliday 1989
Lubbock Lake	GA5-2	NA	NA	NA	Johnson and Holliday 1989
Lubbock Lake	FA5-7/GA5-3	NA	NA	NA	Johnson and Holliday 1989
Lubbock Lake	FA5-12	NA	NA	NA	Johnson and Holliday 1989
Lubbock Lake	FA6-11	NA	NA	NA	Johnson and Holliday 1989
Lubbock Lake	FA9-1	NA	NA	NA	Johnson and Holliday 1989
Lubbock Lake	FA5-17	NA	NA	NA	Knudson et al. 1998, Johnson and Holliday 1989
Lubbock Lake	FA6-15	NA	NA	NA	Johnson and Holliday 1989
Lubbock Lake	GA12-5	NA	NA	NA	Johnson and Holliday 1989
Lubbock Lake	FA2-2	NA	NA	NA	Johnson and Holliday 1989
Lubbock Lake	FA6-8	NA	NA	NA	Holliday 1989
Mangus	I	NA	NA	NA	Husted 1969 Holliday 1997; LaBelle and Meltzer 1996
Marks Beach	All	NA	NA	NA	
Medicine Lodge Creek	Fire Pit Level	NA	NA	NA	Walker 1975
Medicine Lodge Creek	Pryor Stemmed	NA	NA	NA	Walker 1975
Medicine Lodge Creek	N. Paleo (6-ft deep)	NA	NA	NA	Walker 1975
Medicine Lodge Creek	Fish Fauna	NA	NA	NA	Walker 1975
Medicine Lodge Creek	North Paleo	NA	NA	NA	Walker 1975
Medicine Lodge Creek	Cody	NA	NA	NA	Walker 1975
Medicine Lodge Creek	23ft-deep deer	NA	NA	NA	Walker 1975

Appendix A.4. Faunal information of sites and components used in this dissertation.

SITE	COMPONENT	TA	MT	PH	REFERENCE
Meserve	All	NA	NA	NA	Wigda 2007
Mill Iron	All	NA	NA	NA	Frison 1996
Milnesand	All	0	2	38	Hill 2002
Mummy Cave	Layer 13	NA	NA	NA	Hughes 2003
Mummy Cave	Layer 14	NA	NA	NA	Hughes 2003
Mummy Cave	Layer 12	NA	NA	NA	Hughes 2003
Mummy Cave	Layer 11	NA	NA	NA	Hughes 2003
Mummy Cave	Layer 10	NA	NA	NA	Hughes 2003
Mummy Cave	Layer 9	NA	NA	NA	Hughes 2003
Mummy Cave	Layer 8	NA	NA	NA	Hughes 2003
Mummy Cave	Layer 6	NA	NA	NA	Hughes 2003
Mummy Cave	Layer 7	NA	NA	NA	Hughes 2003
Mummy Cave	Layer 4	NA	NA	NA	Hughes 2003
Mummy Cave	Layer 1	NA	NA	NA	Hughes 2003
Myers-Hindman	Unit 1	NA	NA	NA	Cannon and Cannon 2004
Nelson	All	NA	NA	NA	Kornfeld et al. 2007
Norton	All	8	6	41	Hofman et al. 1995
O.V. Clary	Middle	NA	NA	NA	Hill et al. 2001, 2008, 2011
Olsen-Chubbuck	All	92	0	875	Wheat 1972
Perry Ranch	All	NA	NA	NA	Hofman and Todd 1997
Plainview	All	19	27	30	Hill 2010a, Guffee 1979
Rattlesnake Pass	All	NA	NA	NA	Smith and McNees 1990
Rex Rodgers	All	2	4	42	Hill 2010b
San Jon	Area 2	2	6	79	Hill et al. 1995
Scottsbluff	All	NR	NR	NR	Hill Jr. 2008; P
Sheaman	All	NA	NA	NA	Frison and Stanford 1982; Hill 2001
Sorenson	II	NA	NA	NA	Husted 1969
Stewart's Cattle Guard	All	NA	NA	NA	Jodry 1999
Upper Twin Mountain	All	NA	NA	NA	Kornfeld and Frison 2000
Vermilion Lakes	6a	NA	NA	NA	Fedje et al. 1995
Vermilion Lakes	8	NA	NA	NA	Fedje et al. 1995
Vermilion Lakes	6b	NA	NA	NA	Fedje et al. 1995
Vermilion Lakes	9a	NA	NA	NA	Fedje et al. 1995
Vermilion Lakes	9b	NA	NA	NA	Fedje et al. 1995

Appendix A.4. Faunal information of sites and components used in this dissertation.

SITE	COMPONENT	TA	MT	PH	REFERENCE
Waugh	All	NA	NA	NA	Hill and Hofman 1997
Wilson Leonard	Unit II	NA	NA	NA	Collins 1998, Baker 1998
Wilson Leonard	Upper Unit I	NA	NA	NA	Collins 1998, Baker 1998
Wilson Leonard	EP Bonebed	NA	NA	NA	Collins 1998, Baker 1998
Winger	All	NA	NA	NA	Mandel and Hofman 2003

APPENDIX B: A METHOD TO CORRECT “BULK-CARBON” CONVENTIONAL RADIOCARBON DATES

Samples of lake sediment pollen assemblages are commonly used for paleoenvironmental reconstructions. Information derived from the latter is critically limited by the accuracy and precision of their ^{14}C ages (Grimm and Jacobson Jr. 2003). The case for more accurate and precise ^{14}C ages has been demonstrated by comparing, for example, dates derived using conventional radiometric techniques (requiring bulk carbon samples) and those derived using accelerator mass spectrometry (AMS; Grimm et al. 2009).

Conventional ^{14}C ages measurements are made by estimating the radioactive decay of individual carbon atoms either through gas proportional counting or liquid scintillation. These methods require large amounts of carbon: anywhere between 20 grams for charcoal and 50 grams for organic/woody material. Problems in accuracy and precision of the final date estimate arise when the provenance of components of such bulk samples is unknown or uncontrolled. By contrast, the use of AMS only requires between 10–50 milligrams of charcoal and 20–50 milligrams of organic/woody material to detect and count atoms directly. This sensitivity greatly increases the accuracy and precision of the date estimate.

Grimm et al. (2009) empirically demonstrated that differences exist between the two radiocarbon dating methods (Appendix Figure B.1). They compared radiocarbon dates based on AMS and dates derived from bulk carbon obtained from pollen cores at four lakes in Illinois, South Dakota, Wisconsin, and North Dakota. They found that the conventional methods seemed to consistently overestimate the AMS-derived dates. At its most extreme, this overestimation was as great as almost 2,000 years. One possible explanation for this

discrepancy is that a considerable amount of old carbon from geological sources may have been gradually incorporated into the conventional samples. However, even though the bias in Grimm et al.'s sample is consistent, it might not always be older or systematic if the depositional processes for lake layers change; moreover, this bias depends on the sources of the carbon.

This problem limits the utility of pollen as proxy data for studying climate-driven vegetation dynamics at sub-millennial scales. The majority of pollen records available for study were dated well before the current methods of ^{14}C dating were available (~90%). Dates derived using these methods are likely to be sparse, inaccurate, and/or imprecise ^{14}C ages. Nonetheless, these records contain unique information about local vegetation history and thus there is value in retaining them in integrative analyses. Therefore, the question is whether the bias in conventional radiocarbon methods can be modeled, and whether a correction can be applied to conventional radiocarbon dates.

The dates derived using conventional methods for Grimm et al.'s (2009) four samples appear to be systematically biased and older than the AMS results (Appendix Figure B.1). I modeled this bias in order to obtain a correction based on the observed relationship between the conventional radiocarbon and AMS methods.

To do this, I followed this series of steps:

1. First, using linear models, I modeled the relationship between each radiocarbon method as a function of the depth from each lake used in Grimm et al. (2009). For each of the four lakes, two models were computed to reflect both the conventional and AMS dates predicted by the lake depth. Consequently, eight models were created in total.

2. The accuracy of each linear model was assessed using the coefficient of determination (R^2).
3. Values of the prediction were systematically generated at equal intervals for each model, using each model's equation, within the limits of the data. The results of this step were two sets of predicted values for each radiocarbon method at each lake.
4. The relationship between predicted values was then modeled to:
 - a. determine the average relationship between the two radiocarbon methods;
 - b. model AMS as a function of conventional carbon dates.

Results

I fit a linear model to each radiocarbon method as a function of the depth at each lake. Visually, the linear fits looked very good, ranging between R^2 0.68 and 0.99 (Figure SM2.2). The between fit predictions also looked good. This procedure yielded the following correction equation:

$$\text{AMS} = -1654.93 + 1.07 \times \text{Conventional}.$$

Test application

Quaternary paleoecologists are very interested in what is known as the Younger Dryas cold event. The Younger Dryas stadial, also referred to as the “Big Freeze,” was a geologically brief period of cold climatic conditions and drought that occurred between approximately 11,000 and 10,000 radiocarbon years BP (before present).

Using the modern analogue technique for paleoenvironmental variable reconstruction (Appendix Figure B.3), I computed the mean annual temperatures between around 15,000 and 6,000 years ago. The top panel of Appendix Figure B.3 illustrates a cold

“dip” in temperature, which could be interpreted as the Younger Dryas. However, the onset and conclusion of this reconstructed event are temporally too early for what is believed to be the time span of the Younger Dryas. Observing the same climate data after correction (bottom panel), however, the dip is quite consistent with the timeline of the Younger Dryas event.

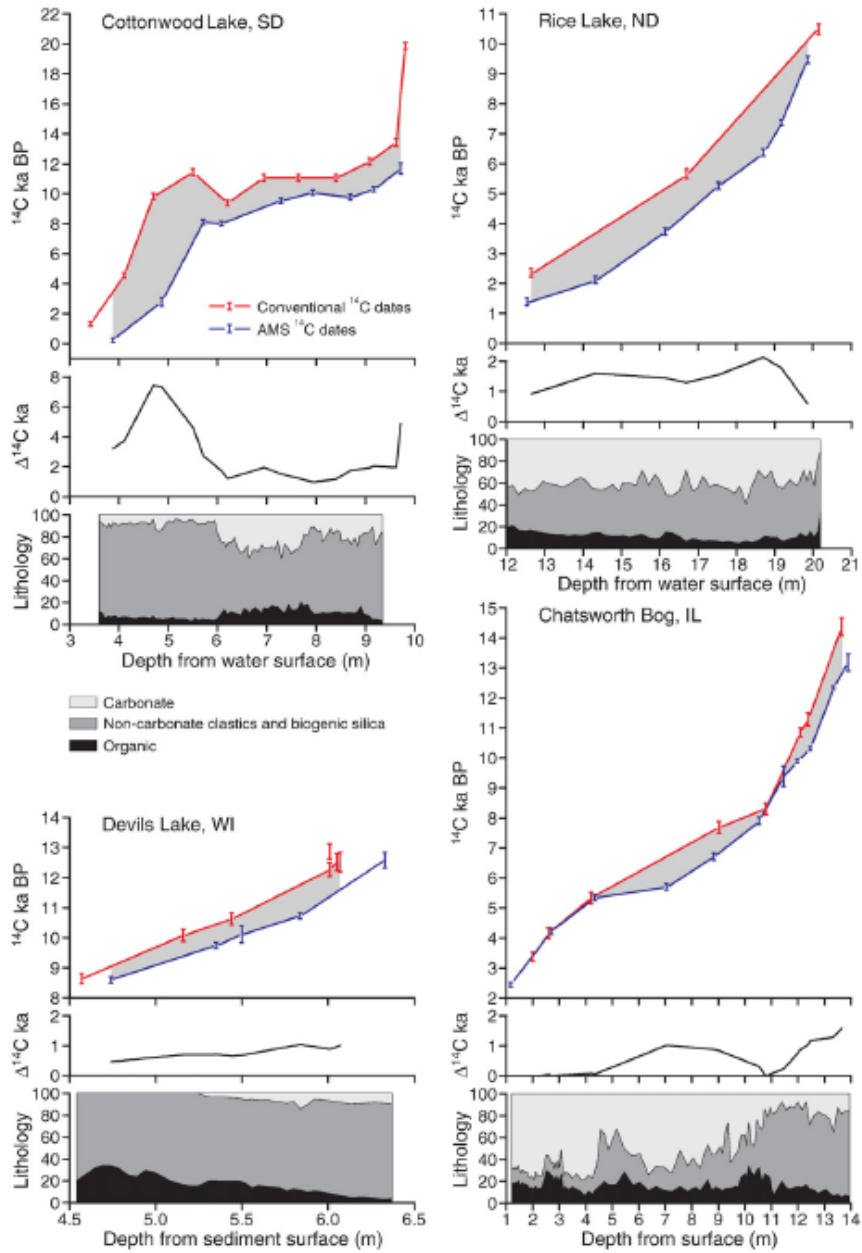


Figure B.1. Figure 2 from Grimm et al. 2009: Age-depth graphs (^{14}C yr BP) based on conventional (red) and AMS (blue) ^{14}C dates for the four study sites. The dates are shown with 2σ error bars. Depths on the horizontal axes are shown as originally published. The vertical scales are the same for all graphs except for Cottonwood Lake, which is half the scale of the others. The vertical distance between the AMS and the conventional chronologies, represented by the gray area, is the difference (Δ) or estimated reservoir, which is shown on the graph below each age-depth graph. The sediment composition based on loss-on-ignition is shown below each difference graph. The sediment key is shown below the graph for Cottonwood Lake.

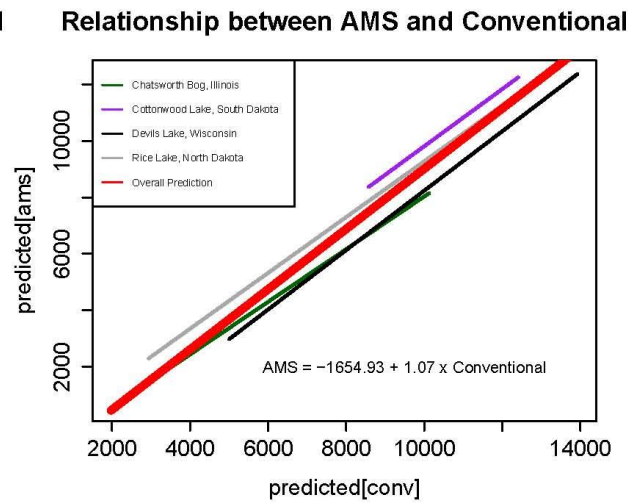
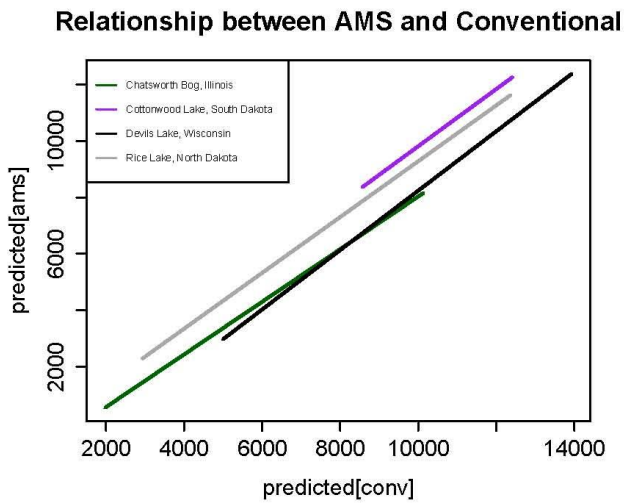
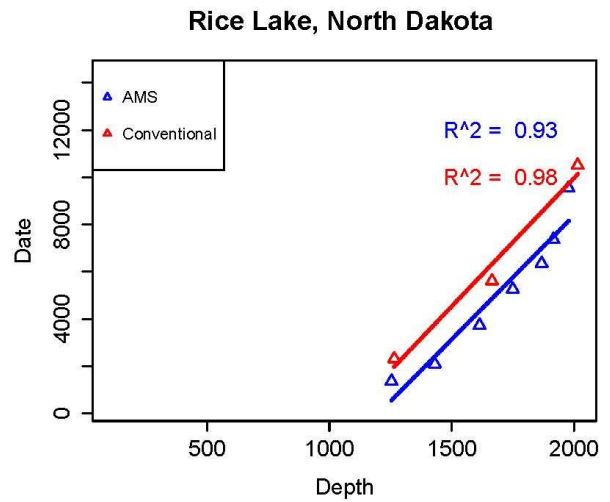
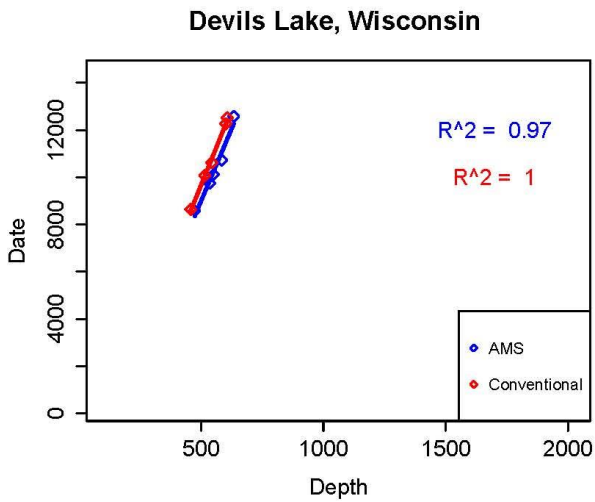
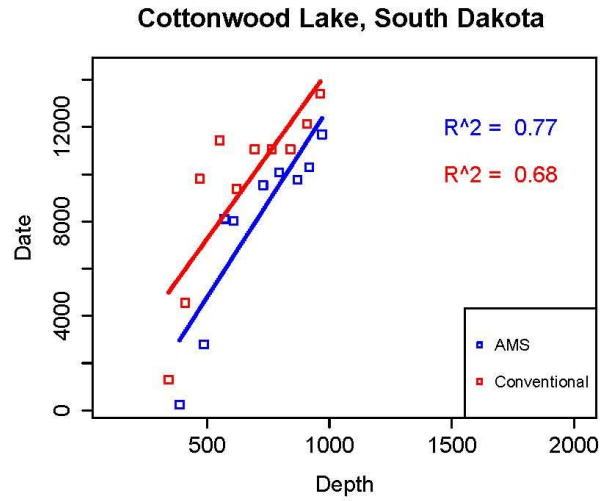
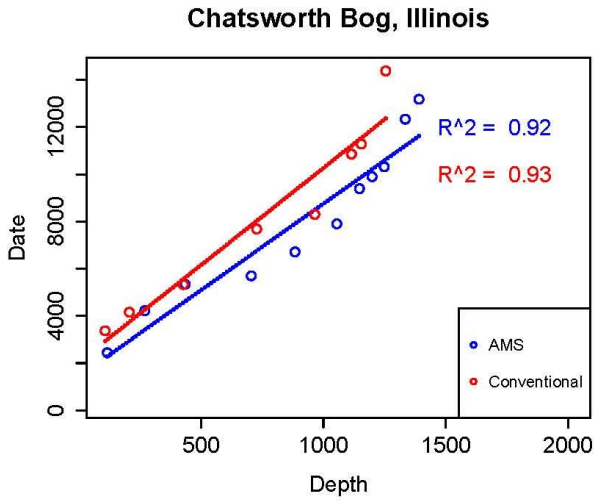


Figure B.2. Methods described in text. Data from Grimm et al., 2009.

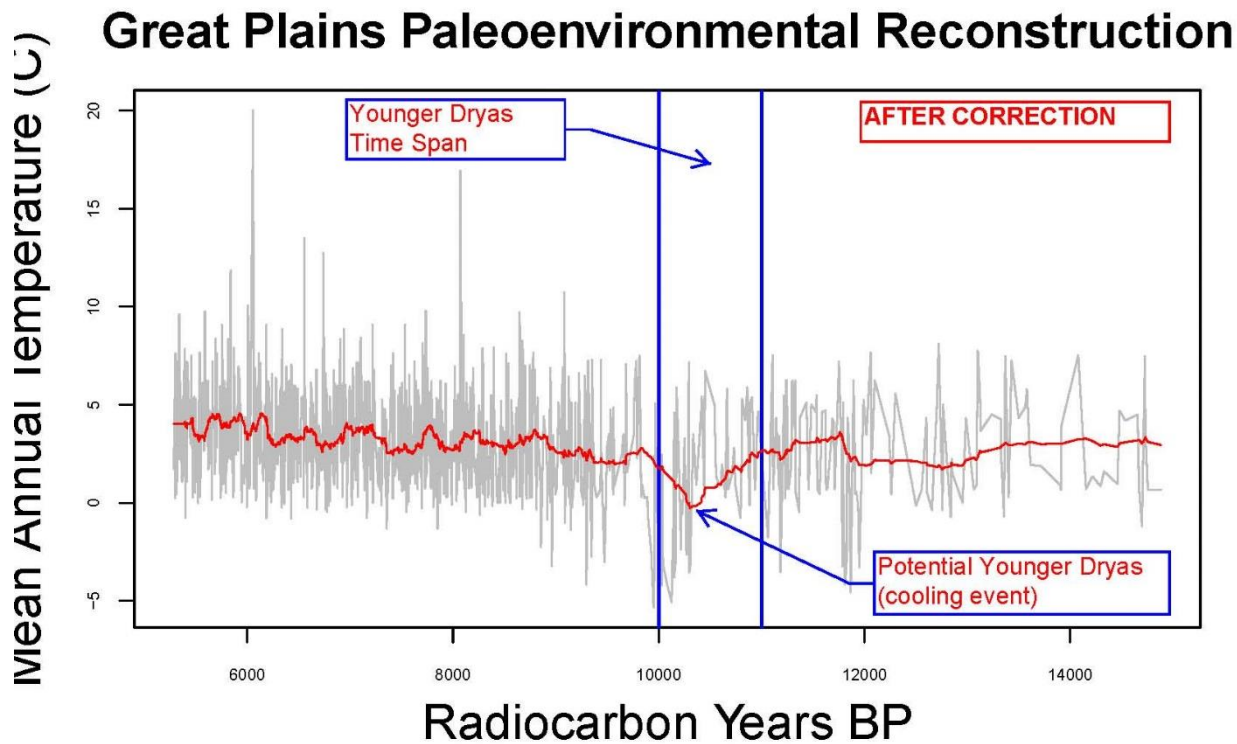
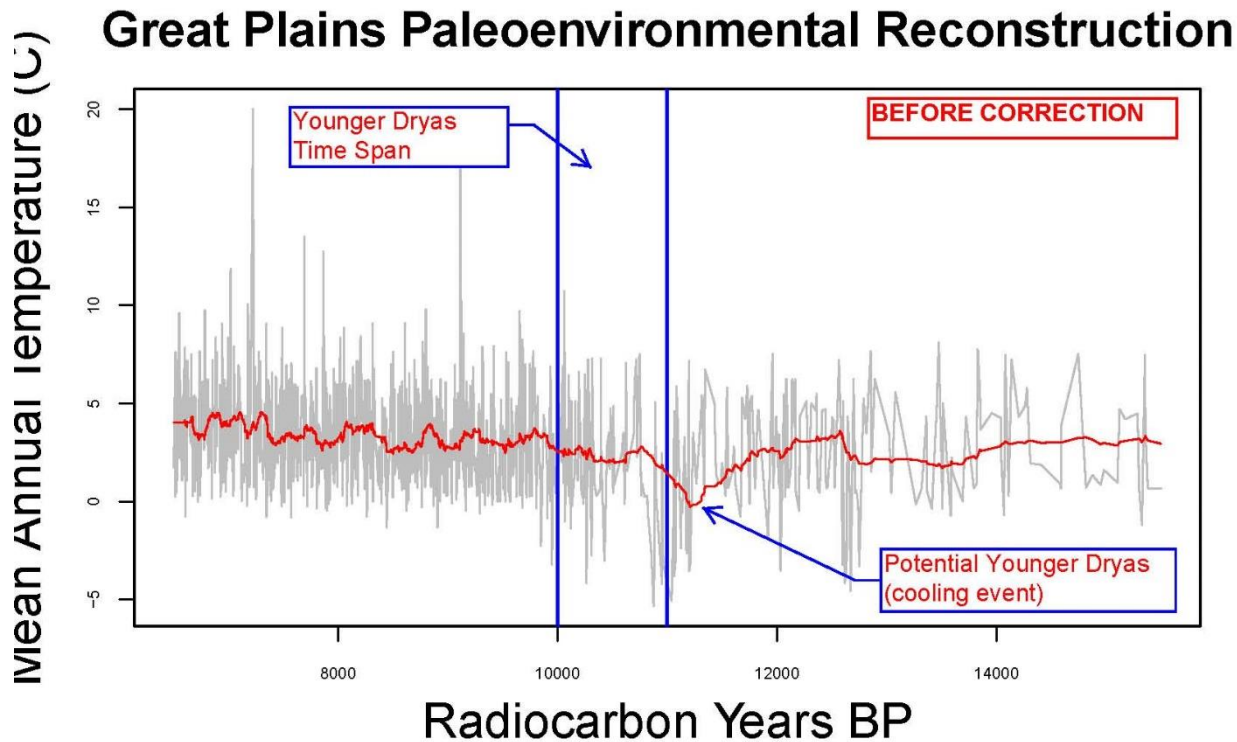


Figure B.3. Paleoenvironmental reconstruction before (top) and after (bottom) correction.