# 5. Human Prey Choice in the Late Pleistocene and Its Relation to Megafaunal Extinctions

Todd A. Surovell<sup>\*</sup> and Nicole M. Waguespack Department of Anthropology University of Wyoming 1000 East University Avenue Laramie, WY 82071, USA surovell@uwyo.edu, nmwagues@uwyo.edu

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# Introduction

Like many dimensions of human behavior during the early phases of New World occupation, interpretations of Early Paleoindian subsistence practices are highly contentious. Different researchers examining the same faunal record have arrived at opposing conclusions regarding what Early Paleoindians were hunting, collecting, and eating. Some argue that Early Paleoindians were quintessentially "large game specialists;" others see a pattern of "generalized foraging." This debate has important implications for evaluating possible causes of Pleistocene extinctions. While at the core of the issue is a fundamentally simple question - "What did Early Paleoindians hunt?" - the interpretation of direct human involvement in the demise of multiple species of animals is clouded by larger issues concerning hunter-gatherer economics and climate change. Our concern is with the former, and we examine Early Paleoindian hunting from an ethnographic, zooarcheological, and behavioral ecological standpoint.

# Why Hunt Big Animals, Especially Really Big Ones?

Kurtén and Anderson (1980) estimated a woolly mammoth (*Mammuthus primigenius*) to have weighed over six metric tons, roughly 100 times the weight of an average human.

The magnitude of this size difference is unprecedented among predatory mammals and their prey. Even a wolf capturing an adult bull moose is killing an animal only about eight times its body weight. Yet, interpretations of Early Paleoindian subsistence frequently portray foraging societies as specialized hunters of Pleistocene megafauna. While the image of mammoth hunters is compelling, it remains difficult to conceive of megafaunal hunting as a habitual component of the food quest. This scenario challenges the limits of hunter-gatherer economic diversity as it is ethnographically known and more generally presents a unique predator-prey dynamic in prehistoric ecosystems.

Whether or not Pleistocene foragers of the Americas were capable of killing mammoths and other megafauna is not in question. Historic and recent hunter-gatherers are proficient at killing elephant sized game using hand propelled weapons (Hodgeson, 1926; Johnson et al., 1980; Duffy, 1984; Fisher, 1993) and replicative experiments indicate that Early Paleoindian weaponry is suitable for megafauna predation (Stanford, 1987; Frison, 1989). While we can comfortably assume that Pleistocene foragers of the Americas could hunt extremely large-bodied prey, we are left to explore the complex issue of why they would or would not have chosen to do so (e.g., Haynes, 2002a:198-200). In addition, questions regarding the potential human involvement in Pleistocene extinction necessitates that the degree of megafauna exploitation also be addressed. Exploring the personal motivations of Paleoindian hunters is well beyond our interpretive capacities. But the more general question of how foragers make economic decisions regarding prey selection can be addressed.

Given various options, how do hunter-gatherers choose which prey to pursue? Models and concepts derived from foraging theory, such as diet breadth ranking systems, predation risk, and variance, provide one means for exploring prey choice. According to the diet breadth model, a hunter can maximize net

<sup>\*</sup> Address for correspondence: surovell@uwyo.edu

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return rates by focusing on taxa whose post-encounter returns exceed the average environmental return rate (Charnov, 1976; Stephens and Krebs, 1986). Individual prey species can then be ranked according to their potential caloric returns relative to other prey. In its simplest form, the optimal diet is comprised of the highest ranked resources. Taking lower ranked taxa only serves to lower overall return rates, an unproductive activity from an evolutionary standpoint. Focusing one's subsistence efforts on high ranked items ensures worthwhile expenditure of a forager's time and energy. High ranked prey are often larger than lower ranked species because they provide greater caloric returns per unit of resource (Winterhalder, 1983; Winterhalder et al., 1988; Ugan, 2005). Although roughly comparable, prey rank and prey size are not necessarily the same. For instance, a mule deer and giant tortoise may be similar in weight but fundamental differences in how these animals are captured and butchered may result in disparate handling costs and hence alter their caloric returns and relative rank. For many predators, excessively largeand small-bodied prey (relative to predator size) may provide so little caloric return due to the difficulty involved in their capture that their rank is far lower than predicted by body size alone (Griffiths, 1980; Byers and Ugan, 2005).

The "zero-one rule" of the diet breadth model predicts that a species will either always be taken or always be ignored upon encounter (Stephens and Krebs, 1986:20-21). From an optimality standpoint an individual predator should always pursue high ranked prey upon encounter and never pursue low ranked items, assuming that the ranking of resources remains constant relative to a fixed average environmental return rate. For as long as high ranked prey species are frequently encountered, low ranked prey are not profitable. Rarely, if ever, can the rank of available prey be considered constant. In a risk-sensitive model, that allows for variation in environmental and prey-specific return rates (e.g., Winterhalder et al., 1999), the optimal diet will consist of a more diverse mix of high and low ranked prey. For example, if a forager encounters a low-ranked prey item in circumstances in which handling costs are minimal, the effective return rate for that animal is enhanced, and it should be exploited (e.g., Madsen and Schmitt, 1988). Temporary scarcity of high-ranked prey could also cause low-ranked prey to be included in the diet (Krebs and McCleery, 1984). In addition, optimal diet breadth should vary for different segments of a foraging population with respect to age, skill, mobility patterns, time constraints, and, for humans, access to hunting technology. By allowing for contingencies such as fluctuations in prey encounter rate, capture efficiency, and capture success rate, variation in the relative ranking of available prey more realistically accounts for the diversity of prey likely to be pursued and captured by a demographically variable group over a period of time.

Thus, although the diet breadth model would generally predict use of the largest encountered prey, it does not imply that the highest ranked resources are always the largest available or that small prey are universally low ranked. Studies of diet breadth in both ethnographic and prehistoric human contexts do commonly indicate that large prey are high ranked and pursued when encountered (Winterhalder, 1981; Hill et al., 1985; Hawkes, 1991; Smith, 1991). However what constitutes "large" prey depends on the species available within the hunting environment and the inherent behavioral/physiological properties of the hunter (Hill et al., 1985; Bailey, 1991; Bird and Bird, 2000; Walker et al., 2002). Although subject to ecological, individual forager, and cultural conditions, prey size remains an important attribute of non-human and human predation strategies. Large prey can provide great economic payoffs, whether these are measured in total weight, calories, or nutrients procured. Given the choice between procuring a 1,000 kg animal and a 20 kg animal with comparable handling costs, why not choose the larger?

The potential caloric benefits of large animals are frequently matched by social (Testart, 1986; Condon et al., 1995; Cox et al., 1999; Gurven et al., 2000; Wiessner, 2002) and/or reproductive benefits (Hawkes, 1991; Kaplan et al., 2000; Marlowe, 2001, 2003) enjoyed by hunters capable of procuring large game in many hunter-gatherer societies. The ability to reliably procure large-bodied game, animals with returns which exceed the immediate caloric needs of the procurer and their dependants, requires successfully capturing prey that are likely to be encountered far less frequently than smaller prey. The combination of providing excess resources and procuring comparatively rare prey animals often brings enhanced social prestige upon the hunter. The larger the resource package, the greater the opportunity to share and exchange hunted prey with others. Large prey animals provide a commodity, utilized among hunter-gatherer societies across the globe, as a widely shared and exchanged resource conferring social benefits (in the form of social capital, economic security, and mating/marriage opportunities) to successful hunters. Thus there are clear economic and social incentives for capable hunters to actively pursue the largest game species available to them. If such social mechanisms were in place among early foragers of the Americas, Pleistocene megafauna presented an obvious medium for attaching social value to hunted prey. The combination of social and economic payoffs provides theoretical impetus for taking seriously the possibility that Pleistocene foragers consistently included megafauna in their subsistence economy.

### The Drawbacks of Hunting Really Big Prey

While the potential windfall of calories and social advantages resulting from large animal predation is well documented among subsistence hunting societies from across the globe, it must also be acknowledged that such behavior has its drawbacks and may present an unfeasible economic strategy in many socio-environmental contexts. Negative aspects of large game predation include specific costs incurred to the hunter (in the form of risk and reduced post-encounter caloric returns when hunted prey is widely shared), costs distributed among cooperative individuals (variance in return rates), and more general issues concerning the abundance and processing costs associated with extremely large game.

Hunting large prey involves a certain degree of risk. A hunter must be willing/able to absorb the potential risk of failing to successfully capture encountered prey and the consequences of coming home empty-handed as well as the potential risk of injury involved in pursuit and capture (i.e., not coming home at all). Risk is generally interpreted to increase with prey size (Griffiths, 1980; Jochim, 1981; Bird et al., 2002) and undoubtedly the successful pursuit and capture of Pleistocene sized megafauna clearly entailed the risk of being fatally stomped-on, gored, kicked, and other "unsuccessful" outcomes. However, a certain degree of risk is associated with hunting regardless of the prey being pursued. Assuming equal search times, you are just as likely to be bitten by a snake or trip and break your leg while hunting rabbits as you are hunting mammoth. Fatal attacks on human foragers by other animals such as jaguars and snakes occur more commonly while hunting than engaging in other activities (Treves and Naughton-Treves, 1999), suggesting that time spent hunting is also time a hunter is at higher risk for personal injury regardless of the prey pursued. But it must also be acknowledged that there is a greater probability of being injured or killed by a mammoth than by a rabbit. Obviously the risks involved must be outweighed by the potential benefits, or else people would never choose to pursue potentially dangerous prey animals.

While the vast majority of anthropologists would shudder at the thought of approaching 1,000+ kg animals armed only with hand propelled weaponry, our hesitance cannot and should not be imposed onto others. Recent forager-level hunters of elephant (e.g., Marks, 1976; Steinhart, 2000) and whale (e.g., Boeri, 1983; Alvard and Nolin, 2002) are well aware of the potential risks involved in their predatory endeavors. Although mediated to some extent through careful planning, labor organization, and technology, the risks stay quite high, yet hunters remain undeterred. In some ethnographic cases the pursuit of large dangerous animals serves to increase the social prestige associated with hunting, while in others it may simply result from economic necessity. Either way, the many gruesome risks that we can imagine befalling a Pleistocene hunter of megafauna are plausible but not necessarily accurate reasons for not pursuing the available large game species of the Pleistocene.

Likewise, variance in hunting returns increases with prey size as the hunting of large prey is subject to a more pronounced boom and bust cycle (Hawkes et al., 1991; Waguespack, 2003). Unless large prey are spatially aggregated (which they may be due to behavioral or habitat attributes), their populations are generally thinly spread across the landscape. Compounding the distributional effect is the simple fact that large animals exist at lower numbers than small animals in any given environment. In general, hunted resources exhibit a great degree of variance among individual return rates. Put simply, associated hunters individually pursuing game are likely to experience differential success rates and such differences are only exacerbated when large prey is the focus of predation. Whether variance is measured as an individual's hunting returns over a period of time or among multiple individuals within a given time period, a high degree of variance in the subsistence economy can be a problem that must be mediated. Numerous mechanisms can alleviate intra-group variance. Practices such as food sharing (Cashdan, 1985; Hawkes, 1992; Waguespack, 2002), food storage (Testart, 1982; Hayden, 1994), and cooperative hunting (Smith, 1991; Alvard and Nolin, 2002) have been identified as successful means of redistributing resources among an aggregate of consumers by minimizing the variance in returns between procurers. However the extent to which these "pre-" and "post-kill" mechanisms were employed by Pleistocene foragers of the Americas is not known.

In addition to risk and variance, there are more general concerns that must be acknowledged concerning large game predation. All things being equal, the larger an animal is, the lower its population density. So it must be kept in mind that if the frequency with which prey are encountered is directly related to their density, it can be expected that a hunter would have lower encounter rates and fewer opportunities to capture large prey items. The frequency of encounter should have no impact on prey rank, but if large high ranked prey are rarely encountered it simply cannot provide a consistent or frequent source of calories. For instance, mid-1900s ethnographic reports concerning the Ju/'hoansi of Africa indicate that giraffe was considered a prized resource (providing a windfall of calories and prestige) (Lee, 1979:230-232), but the species was so rarely brought down that it played little role in the everyday subsistence economy. Thus, however highly ranked giraffe might be, characterizing the Jul'hoansi as specialized giraffe hunters would be wholly inappropriate since the vast majority of their kills and caloric intake is derived from smaller game species.

One additional concern is the potential handling costs associated with extremely large game. It has been argued that the positive relationship between caloric benefits and game size has an upper limit – whereby at some point prey became so large that the handling costs (e.g., transport, butchery, and processing activities that render a kill edible) become so high that caloric return rates begin to drop. The time and energy required to handle fauna the size of mammoths has been modeled to be so costly that return rates make them no more profitable than far smaller prey (the size of deer or bison) (Byers and Ugan, 2005). It is easy to imagine why disarticulating and transporting a mammoth carcass would be exceedingly costly, as moving a single limb would require multiple handlers. Much like risk and variance, however, handling costs can be behaviorally altered. Estimated handling costs based on butchery and processing of African elephants by Efe and Lese hunters include the costs of a crew of butchers traveling to the kill site, establishing a temporary camp, dismembering and butchering, the building of drying racks, the stripping of meat for drying, and transporting the meat back to residential locations (Byers and Ugan, 2005). In this case, elephant kills are infrequent occurrences (Duffy, 1984; Fisher, 1993) and butchery appears to present a costly diversion of labor and resources. However, while recent ethnographic examples attest to the enormous handling costs associated with extremely large prey, two things must be kept in mind: (1) Efe and Lese peoples are still willing to accept these handling costs, and (2) if extremely large-bodied prey are killed comparatively more frequently, then mobility regimes and labor could be organized in ways to reduce handling costs. Ethnographic examples of other high handling costs endeavors, such as whale butchery and the processing of mass bison and caribou kills, suggest that coordination between hunters and butchers (e.g., organized logistical and residential mobility to ensure labor availability and cost effective transport of people and resources) effectively maintain high return rates for large prey by decreasing handling costs.

It should be clear that how foragers make decisions regarding which prey to pursue involves the relative costs, benefits, and attributes of the socio-ecological context in which hunting occurs. Large game in particular can have enormous benefits and exceedingly high costs. Theoretically, Pleistocene foragers were capable of megafauna predation and generally agreed upon attributes of the Early Paleoindian lifestyle such as low population density, frequent residential mobility, relatively high investment in hunting technology, and minimal game processing all support the plausibility that megafauna was consistently utilized. While assuming that low human population levels rendered megafauna a sufficiently abundant source of calories, that mobility served to enhance large game encounter rates, and that technological investment and minimal resource processing indicate some degree of economic "success" all seem plausible, the fact remains that regular predation of extremely large prey presents something of an anomaly among ethnographically known foragers. This may be reason enough for many archeologists to dismiss the potential role of megafauna hunting in Pleistocene societies. However, doing so runs the dangerous risk of limiting huntergatherer diversity of the past to the documented present. Similarly, assuming that Pleistocene hunters preferred megafauna as prey simply because they could, belies the unique socio-environmental attributes that make such a strategy possible (e.g., behavioral means of mediating risk, variance, and handling costs).

# Identifying Early Paleoindian Diet Breadth

If the extinction of >30 genera of mammalian megafauna in North America was caused directly or indirectly by human hunting, there should be archeological evidence indicating that humans not only hunted, but preferentially hunted, now extinct fauna. As outlined above, there is compelling, albeit purely theoretical, reasons why this may have been the case. Furthermore, because animal populations are capable of sustaining some level of predation depending upon their speciesspecific demographic attributes (e.g., Brook and Bowman, 2005; Mithen, 1993; Stiner et al., 1999, 2000; Alroy, 2001), the degree to which Early Paleoindians focused their subsistence efforts upon large mammals relates directly to the plausibility of the Overkill hypothesis (Alroy, 2001). If humans only rarely killed large mammals, then human hunting alone may not be sufficient to explain Pleistocene extinctions. If large mammals were regularly and preferentially targeted, Overkill is plausible. Thus, determining whether and to what extent Early Paleoindians hunted extinct fauna is critical to the Overkill debate (Martin, 1973, 1984; Martin and Steadman, 1999; Grayson, 2001; Grayson and Meltzer, 2002, 2003; Haynes, 2002a, b).

#### A Brief Review of Recent Research

A number of recent studies have examined the Early Paleoindian faunal record to address the question of what the first people in North America hunted and/or should have hunted (Grayson and Meltzer, 2002; Haynes, 2002a, b; Waguespack and Surovell, 2003; Barton et al., 2004; Cannon and Meltzer, 2004; Byers and Ugan, 2005). Among these studies, two camps have emerged: (1) Those who believe that Early Paleoindians were "large game specialists" and were characterized by a "narrow diet breadth" (Haynes 2002a,b: Waguespack and Surovell, 2003; Barton et al., 2004), and (2) Those who believe that Early Paleoindians were "generalists" and were characterized by a "broad diet breadth" (Grayson and Meltzer, 2002; Cannon and Meltzer, 2004; Byers and Ugan, 2005).

For the sake of brevity, we focus on three studies which have attempted to systematically examine the question. In 2003, we constructed a dataset of faunal remains from 33 late Pleistocene archeological sites in North America (Waguespack and Surovell, 2003). Examining the relationship between body size and archeological abundance, we found that large mammals were the most abundant and regularly occurring animals in Early Paleoindian faunal assemblages. Because there is a strong inverse correlation between body size and population density among animals, we argued that this faunal record could only have been produced by hunter-gatherers who were bypassing opportunities to take small game in favor of concentrating on larger prey. Furthermore, we argued that large game specialization is expected for the first inhabitants of North America since small numbers of highly mobile foragers could maintain fairly regular access to large-bodied animals. We considered the Pleistocene landscapes of the Americas to present a relatively unique demographic and ecological context for a hunter-gatherer subsistence strategy, comparatively rare in the modern ethnographic record, to have emerged.

Examining the same record, Cannon and Meltzer (2004) arrived at a very different conclusion. They concluded that "the faunal record provides little support for the idea that all, or even any, Early Paleoindian foragers were megafaunal specialists" (Cannon and Meltzer, 2004:1955). There are two primary reasons they invoke to explain this difference of opinion. The first is methodological. While we included all fauna recovered from Clovis components, whether strong evidence for subsistence use existed or not, Cannon and Meltzer (2004) only included animals for which "secure" subsistence associations were present. The second is bias. Cannon and Meltzer (2004) performed a number of statistical tests designed to demonstrate that the current sample of late Pleistocene archeological sites is a poor reflection of Paleoindian diets because it is highly biased in favor of large game. They argue that greater probabilities of discovery and research attention are afforded to mammoth-bearing archeological deposits resulting in an over-representation of large fauna sites in the record. Finally, Cannon and Meltzer (2004) suggested that Early Paleoindian diets would have varied considerably across the continent in response to environmental variability and therefore prey species availability.

Byers and Ugan (2005) took a slightly different approach, asking the question: "Should we expect large game specialization in the late Pleistocene?" Using known relationships between body size, return rates, handling costs, and population density, they built a formal prey-choice model based on estimated encounter rates, handling costs, and return rates, which allowed them to predict which species should have been included in Early Paleoindian diets given a foraging goal of maximizing post-encounter returns. Using various estimates of encounter rates for large mammals, they concluded that Paleoindians would have regularly killed animals at least down to the size of hares upon encounter, or possibly even smaller mammals such as ground squirrels. Their model causes them "to question whether Paleoindian subsistence would ever have been narrow and specialized..." (Byers and Ugan, 2005:1633) given the wide array of prey species available to them.

Despite these disagreements, it is our contention that there is actually more common ground among these studies than is immediately apparent. For example, we all agree what the Early Paleoindian faunal evidence looks like in terms of species representation, although there are clear differences about how datasets should be constructed and interpreted. From our perspective, there are two major points of disagreement. First is the extent the record is biased and how accurately it reflects Paleoindian prey choice decisions; second is how the terms "large game specialist" and "generalist" should be defined. We begin with the latter question.

#### Measuring Diet Breadth

Strangely, though much has been written about "diet breadth" and whether Early Paleoindians were "large game specialists" or "generalized foragers," rarely are these phrases defined in the Paleoindian literature. We believe this simple fact explains much of the disagreement about Early Paleoindian subsistence. As we demonstrate below, despite claims to the contrary, some aspects of the argument do not concern the prey species targeted by Paleoindians nor the composition of the faunal record. Instead, they are about what we should label Early Paleoindian subsistence practices.

Two basic approaches to the problem can be identified. One approach is to define the term large game specialist so narrowly (usually implicitly) that it must be false. It is essentially argued that if late Pleistocene foragers used any resources that are not large bodied mammals, whether plant or animal, then Early Paleoindians were not large game specialists (Byers and Ugan, 2005:1637). By this definition, there is no disagreement whatsoever about whether Clovis peoples were large game specialists. They were not. There is archeological evidence of the use of small mammals, reptiles, and possibly birds and fish in the late Pleistocene archeological record of North America (e.g., Haynes and Haury, 1982; Dent and Kauffman, 1985; Johnson, 1987; Storck and Spiess, 1994; Yates and Lundelius, 2001). In fact, by this definition, large game specialization is a strategy that has never been employed by humans. Even recent caribou hunting societies of the Arctic and bison hunting societies of the Great Plains would not meet this definition since they are and were known to exploit small bodied prey. If anthropologists are fundamentally interested in studying variation in human behavior, then it should be clear that such a strict definition of large game specialist is unworkable since it recognizes no variation whatsoever. While cloaked in the terminology of optimal foraging theory, diet breadth defined in this manner provides no insight into hunter-gatherer economics.

All hunter-gatherers have a diverse set of edible resources available to them, but not all of those resources are regularly exploited. Diet breadth in this sense refers to the actual subsistence choices made in light of the total possible range of choices that could be made based on selectivity. Having the broadest possible diet means regularly exploiting any edible resource upon encounter. Having a narrow diet breadth means often passing up opportunities to exploit certain resources in order to invest greater time and energy into searching for more profitable ones. In this sense, the term "large game specialist" refers to hunter-gatherers who frequently ignore opportunities to go after small prey in favor of searching for larger quarry (Waguespack and Surovell, 2003).1 The distinction between specialist and generalist strategies relates to the extent to which small bodied prey are not exploited. A generalist regularly attacks small prey upon encounter, and a specialist often ignores small prey upon encounter. This definition is preferable because it recognizes the broad diversity of subsistence strategies known to have been used by huntergatherers, and addresses the decision making component of resource procurement. In this framework, the issue is not whether small game was taken by Early Paleoindians but the extent to which it was taken relative to large game.

If large game specialization is defined as regularly ignoring opportunities to take small prey upon encounter, how can it be measured archeologically? After all, the species which humans choose to utilize should produce clear archeological residues, while those not taken should remain absent from the record. There is a fairly straightforward solution to this problem. Strong global relationships exist between body size and population density (Peters, 1986) that can be used to estimate relative encounter frequencies for prey species in any ecosystem, present or past (Fig. 5.1a). Generally speaking, there is a negative power relationship between body size and population density, meaning that, all things being equal, small bodied animals are more common than large ones. Thus, the faunal record produced by a generalist who regularly takes any prey upon encounter should reflect ecological population densities and be dominated by small animals. The faunal record of a large game specialist will be dominated by large bodied mammals,

The degree to which high and low ranked taxa are used is the critical distinction between a hunter's selectivity when choosing prey. Relating prey selectivity to the natural abundance of available prey species creates a simple framework for examining the types of prey utilized by hunter-gatherers of the past and present. The two common strategies, *specialized* and *generalized*, developed here do not make explicit which particular species of prey should be used (Fig. 5.1b). Only general categories of prey based on body size and the relative frequency of their encounter are predicted to be used in different proportions by each strategy. Although the terms generalized and specialized could imply two pure strategies, that is not their intended meaning in this discussion. As used here they refer to ends of an idealized continuum and concern decisions regarding which prey, among those available, a forager will target for predation.

although limited use of small prey may be evident as well.

Because encounter rate is primarily a function of prey population density, estimated population densities based on body size provide a reasonable approximation of prey encounter rates for specific environments. Actual encounter rates are difficult to establish in real world settings and deriving comparable values in prehistoric contexts is exceedingly difficult. Population density must then be considered only a proxy measure of encounter rate. A comparison of actual encounter rates and population densities of eight prey species used by the Ache of Paraguay in the Mbaracayu Reserve shows the disparity between these two measures. In this case, encounter rates equal the number of animals seen in over 2,000 km of transects walked by Ache informants and anthropologists (Hill and Padwe, 2000). Plots of mass and population density and corresponding encounter rates are somewhat different. Importantly, however, the overall trend between body size (Fig. 5.2a) and encounter rate (Fig. 5.2b) is approximated by population density. So although density does not provide an exact measure of encounter rate it does reasonably approximate prey encounters.

#### Prey Utilized by Recent Subsistence Hunters

If prey selection strategies can be characterized as either generalized or specialized based on the size of prey as an indicator of their population density, then clear trends should be apparent in the accumulated prey assemblages of hunting peoples of the past and present. Comprehensive prey species data derived from ethnographic observation were compiled for 12 societies of subsistence hunters from published literature (Table 5.1) (Waguespack, 2003). The data include a range of observation periods from approximately 1 month (Ju/'hoansi [or !Kung San]) to upwards of 2 years (Ache) and includes observations of societies in a diverse array of ecological settings. The sample for each group includes the total number and average weight of each prey species captured during the observation period. We examine the issue with ethnographic data in order to establish a degree of confidence in our application of the modeled relationship between prey size and prey choice decisions to Paleoindian contexts.



FIGURE 5.1a. Generalized relationship between prey size and encounter rate. b. Generalized relationship between body size and number of prey captured for the "large game specialist" and "generalist" prey choice strategies.



FIGURE 5.2a. Body size versus population density for eight prey species commonly taken by Ache hunter-gatherers. b. Body size versus number of prey encountered for Ache hunter-gatherers (Data from Hill and Padwe, 2000.) X- and y-axes are log-scaled, and x-axis is reversed for both graphs.

TABLE 5.1. Summary of prey choice data for recent subsistence hunters.

Group	Location	Sample duration	n people	N kills	Reference
Gidra	New Guinea	80 Days	20+	207	Ohtsuki and Suzuki 1990:42, Table 1
Pume	Venezuela	60+ Days	10+	155	Greaves, 1997:293, Table 2
Yanomamo	Venezuela	30+ Days	10+	171	Hames, 1979:234, Table II
Ye-kwana	Venezuela	30+ Days	10+	716	Hames, 1979:234, Table II
Inujjuamiut	Quebec	1 Year	?	317	Smith, 1991:1997-227
Siriono	Bolivia	1 Year	?	2300	Townsend, 2000:272, Table 13-1
Ju/'hoansi	Botswana	26 Days	5	18	Lee, 1979:266, Table 9.6
Gwi	Botswana	1 Year	50	171	Tanaka, 1980:68, Table 9.6
Yiwara	W. Australia	90 Days	10	468+	Gould, 1980:65, Table 5
	W. Australia	51 Days	40	337+	Gould, 1980:65, Table 6
Bisa	Zambia	1 Year	8	101	Marks, 1976:206, Table 38
Ache	Paraguay	Multiple years	?	3503	Hill and Padwe, 2000:95, Table 5.2
Nunamiut	Alaska	1 Year	20+	745	Binford, 1991:107, Table 39



FIGURE 5.3a. Body size versus kill frequency for eight recent groups of subsistence hunters classified as generalists under the scheme shown in Fig. 1. Data are shown for the three most frequently taken herbivorous terrestrial mammalian prey species and are standardized as percentages. X-axis is reversed and log-scaled. **b**. Same for three groups of subsistence hunters classified as large game specialists.

Based only on the three most frequently utilized terrestrial herbivorous mammalian species, all groups, with three notable exceptions, exhibit a predominately negative trend in the percentage of animals killed relative to animal body size (Fig. 5.3). In the majority of groups, the largest animal hunted contributes the least in terms of the total number of individuals captured (Fig. 5.3a). For these societies, prey assemblages generally conform to the predicted distributions

of an encounter-based or generalized prey selection strategy, an interpretation well supported in the ethnographic literature. Three groups, the Nunamiut, Inujjuamiut, and Bisa appear to utilize large game species more frequently than smaller prey (Fig. 5.3b). Both the Nunamiut and Inujjuamiut occupy arctic environments and their prey frequencies deviate primarily due to the inordinate proportion of caribou in their assemblages. High latitude environments are associated with lower levels of primary productivity (Begon et al., 1996), generally support a lower density and diversity of mammalian species (Andrewartha and Birch, 1961), and often maintain relatively large populations of large-bodied animals than more temperate or tropical ecosystems. While arctic environments may be characterized by a more limited diversity of potential prey, there are small prey species available. Both of the arctic hunting groups are well known ethnographically to purposefully elevate their encounter frequencies with large game, particularly caribou, by maintaining high levels of mobility and concentrating their hunting efforts along ungulate migration routes (Gubser, 1965; Binford, 1978; Smith, 1991). The Bisa are sedentary horticulturalists occupying a tropical dry savannah environment. Hunting is explicitly focused on the procurement of ungulates such as African buffalo, impala, and warthog, and large species are taken more frequently than smaller game. The area is renowned for its density of large mammals which frequent the numerous permanent water sources in the area (Marks, 1976).

While it apparent that within each strategy the relative contribution of the most commonly hunted mammalian species to the total inventory of hunted fauna varies, the distinction between generalists and specialists remains clear. Importantly, specialized large-game predation as defined here does not necessarily imply exclusive hunting of a single species of large prey or only large prey. In zooarcheological contexts assemblage dominance by a single prey species, particularly caribou (e.g., Enloe, 1999; Grayson and Delpech, 2001) and bison (e.g., Todd, 1987; Brugal et al., 1999), is often presented as the only defining characteristic of a specialized hunting economy. While dominance may accurately identify large-game hunting in particular contexts, as it would for the Nunamiut where nearly 70% of the animals taken are caribou, it may not be appropriate for hunting societies which utilize a suite of large species more frequently than smaller taxa. Neither the Bisa's nor Inujjuamiut's total faunal inventories are "dominated" (i.e., show high MNI percent values) by a single large taxon (Marks, 1976; Smith, 1991), but both utilize large game relatively more frequently than would be predicted by a generalist strategy.

As specialization is defined here, it assumes that smaller prey species are available but are relatively underutilized. It is difficult to establish whether the three groups identified as specialists are regularly passing up the opportunity to capture smaller animals. But there is evidence to suggest the Nunamiut and Inujjuamiut do deliberately forego small game:

#### Nunamiut

"The Nunamiut had little to say about red squirrels. They know the animal occurs in the timber, but apparently have never utilized them" (Gubser, 1965:263).

"The snowshoe hare occurs rarely in the Brooks Range...The arctic hare is perhaps a bit more common. Nunamiut have reported the presence of both hares...in occasional years...Neither hare is significant as a food source" (Gubser, 1965:276).

"The marmot occurs throughout the Brooks Range, usually in small, localized colonies...Summer may be a hungry time, and the fat meat of marmots is a welcome supplement...They are easy to catch as far as skill is concerned but difficult in the amount of labor required..." (Gubser, 1965:279)

#### Inujjuamiut

"Although the expressed purpose of the hunts was to locate and capture caribou...While hunting inland potential prey included fox, ptarmigan, and lake trout; the fish were never pursued, but the first two prey types were taken on occasion...In the case of ptarmigan, it appears they were sometimes ignored when encountered...The matter of fox trapping is more complicated. For one thing, foxes are harvested primarily for their pelts, which have exchange-value (as trade items) and use-value (as parka ruffs); food consumption is incidental to this...It is probably enough to say that the small loss in foraging efficiency entailed by trapping effort on these hunts was more than offset by the monetary return..." (Smith, 1991:220–2).

With regard to the Nunamiut, Gubser's anecdotal observations suggest that some small prey species are ignored in favor of caribou. For the Inujjuamiut, it seems clear that ptarmigan are overlooked in favor of larger mammals. And the occasional capture of foxes is, at least in part, a direct result of the hunting in exchange for money rather than for food. In both cases there is at least limited evidence to suggest that smaller prey are encountered more frequently then they are pursued and/or captured.

#### Specialization Past and Present

Outside of arctic environments and the unique case of Bisa farmers, none of the societies sampled express a prey selectivity strategy biased towards exceptionally large game. Why not? Assuming that a specialized strategy is viable only when large game are available in sufficient quantities, the environmental conditions present in the majority of ethnographic contexts examined may not be capable of supporting a selective strategy. Subsistence hunters documented in the modern era occupy ecosystems that have been inhabited by humans for thousands of years, and human populations likely exist at relatively high density levels. Also, most recent subsistence hunters occupy primarily "marginal" environments; consequently their subsistence options are likely more constrained than those of hunter-gatherers of the past. In some non-arctic contexts that are no longer represented in the ethnographic record large mammals may have been much more predictable and/or relatively easy to procure. For instance, the risks associated with hunting could be minimal when large prey are abundant relative to human population sizes and/or are naïve to human predation. These prey characteristics are not present in the majority of modern foraging environments, but may have contributed to prey selection criteria among prehistoric foragers. Importantly, comparison of prey use frequency relative to body size and the predicted relationships outlined here provides a method for evaluating prehistoric prey use strategies. Analysis of ethnographically documented subsistence hunters establishes the validity of the more general expectations about specialized and generalized hunting strategies and their faunal assemblage attributes.

## Building a Paleoindian Dataset

In an ideal world, our archeological sample of Early Paleoindian subsistence choices would be large, unbiased, and well-studied. In the real world, it is not large, it is likely biased, and it is not well-studied. There are less than 50 sites from the entirety of North America that are likely to tell us something about Early Paleoindian subsistence choices (Waguespack and Surovell, 2003; Cannon and Meltzer, 2004) (Fig. 5.4, Table 5.2). Potential biases related to discovery, excavation, and research may be skewing our view of Early Paleoindian behavior (Grayson, 1988; Meltzer, 1989, 1993; Grayson and Meltzer, 2002; Waguespack and Surovell, 2003; Cannon and Meltzer, 2004; Byers and Ugan, 2005). Finally, standards of excavation, analysis, and reporting vary widely (Waguespack and Surovell, 2003; Cannon and Meltzer, 2004). In combination, these issues not only make it difficult to determine what people were killing and eating in the late Pleistocene of North America, but also they serve as fodder for debate.

One of the fundamental issues that must be dealt with is how one should go about building a database of Paleoindian subsistence choices from a series of faunal remains reported in archeological monographs and papers. Taphonomy must be considered, but performing a taphonomic analysis on actual specimens is not the same as doing what we call "textual taphonomy," or the evaluation of taphonomic factors on the basis of published text and images. Textual taphonomy has a long tradition in Paleoindian archeology (e.g., Grayson, 1984; Haynes and Stanford, 1984) but remains problematic in that it can be extremely difficult to evaluate evidence for subsistence use on the basis of published accounts which vary widely in quality.

Haynes and Stanford (1984:217–222) provide a useful framework for evaluating subsistence use in terms of levels of association. The weakest evidence for subsistence use they term "contemporaneity," meaning evidence which simply demonstrates spatio-temporal association. Contemporaneity is established solely on the basis of stratigraphic association



FIGURE 5.4. Map of sites included the Surovell and Waguespack and Cannon and Meltzer (2004) Early Paleoindian faunal datasets: 1. Manis, 2. Charlie Lake Cave, 3. Wally's Beach, 4. Colby, 5. Murray Springs, Lehner, Naco, Escapule, and Leikem, 6. Sheaman, 7. Dent, 8. Lange-Ferguson, 9. Jake Bluff, 10. Domebo, 11. Miami, 12. Blackwater Draw, 13. Lubbock Lake, 14. McLean, 15. Kincaid, 16. Gault, 17. Aubrey and Lewisville, 18. Wacissa River, 19. Little Salt Spring, 20. Kimmswick, 21. Boaz, 22. Schaefer and Hebior, 23. Martin's Creek, 24. Shawnee-Minisink, 25. Hiscock, 26. Udora, 27. Whipple, 28. Bull Brook, 29. Guest, 30. Holcombe Beach.

TABLE 5.2	. Sites ι	used in	this stu	udy for	analyses	of	Clovis	diet breadth.
				2	2			

Site (state/prov.)	Region	Hearths? <sup>a</sup>	Kill site?	References
Aubrey (TX)	Central	Y	N	Ferring, 2001; Yates and Lundelius, 2001
Blackwater Draw (NM)	Central	Y	Y	Lundelius, 1972
Charlie Lake Cave (BC)	Central	_	Ν	Driver, 1999; Fladmark et al., 1988
Boaz Mastodon (WI)	East	Ν	Y	Palmer and Stoltman, 1975
Bull Brook (MA)	East	Y	Ν	Byers, 1955; Spiess et al., 1985
Colby (WY)	Central	Ν	Y	Frison and Todd, 1986; Walker and Frison, 1980
Dent (CO)	Central	Ν	Y	Figgins, 1933; Brunswig and Fisher, 1993
Domebo (OK)	Central	Ν	Y	Leonhardy, 1966; Slaughter, 1966; Leonhardy and Anderson, 1966
Escapule (AZ)	West	Ν	Y	Hemmings and Haynes, 1969; Saunders, n.d.
Gault (TX)	Central	Ν	Ν	Collins, 1999
Guest (FL)	East	Ν	Y	Hoffman, 1983; Rayl, 1974
Hebior (WI)	East	Ν	Y	Overstreet, 1996; Overstreet et al., 1995; Overstreet and Stafford, 1997
Hiscock (NY)	East	Ν	Y?	Laub et al., 1988; Tankersley et al., 1998; Steadman, 1988
Holcombe Beach (MI)	East	-	Ν	Cleland, 1965; Fitting et al., 1966; Spiess et al., 1985
Jake Bluff (OK)	Central	Ν	N?	Bement and Carter, 2003 as cited by Cannon and Meltzer, 2004
Kimmswick (MO)	Central	Ν	Y	Graham et al., 1981; Graham and Kay, 1988
Kincaid Shelter (TX)	Central	Ν	Ν	Collins et al., 1989
Lange-Ferguson (SD)	Central	Ν	Y	Hannus, 1989, 1990; J. Martin, 1984
Lehner (AZ)	West	Y	Y	Haury et al., 1959; Haynes and Haury, 1982; Lance, 1959; Saunders, n.d.
Leikem (AZ)	West	Ν	Y	Saunders, 1980; Saunders, n.d
Lewisville (TX)	Central	Y	Ν	Crook and Harris, 1957, 1958
Little Salt Spring (FL)	East	Ν	Ν	Clausen et al., 1979
Lubbock Lake (TX)	Central	Ν	Y?	Johnson, 1987
Manis (WA)	West	Ν	Y	Gustafson et al., 1979
Martin's Creek (OH)	East	Ν	Y	Brush and Smith, 1994; Brush et al., 1994
McLean (TX)	Central	Ν	Y	Ray, 1930, 1942; Ray and Bryan, 1938
Miami (TX)	Central	Ν	Y	Sellards, 1952; Holliday et al., 1994
Murray Springs (AZ)	West	Y	Y	Haynes, 1993; Saunders, 1980; Saunders, n.d.
Naco (AZ)	West	Ν	Y	Haury, 1953; Lance, 1959; Saunders, n.d.
Schaefer (WI)	East	Ν	Y	Overstreet, 1996; Overstreet et al., 1995; Overstreet and Stafford, 1997
Shawnee-Minnisink (PN)	East	Y	Ν	Eisenberg, 1978; Dent and Kauffman, 1985
Sheaman (WY)	Central	Ν	Ν	Frison, 1982
Udora (ON)	East	Y	Ν	Storck and Spiess, 1994
Wacissa River (FL)	East	Ν	Y	Webb et al., 1984
Wally's Beach (AB)	Central	-	Y?	Kooyman et al., 2001, 2006
Whipple (NH)	East	Y	Ν	Spiess et al., 1985

<sup>a</sup> Data taken directly from Cannon and Meltzer (2004: Table 6). Cell values left blank represent those sites not considered by Cannon and Meltzer (2004)

of archeological and faunal specimens. Of greater reliability is "association" referring to spatio-temporal contemporaneity of artifacts and animal remains demonstrably discarded by humans in a single event, such as during occupation of a campsite. Finally, "utilization" shows not only spatiotemporal contemporaneity but also clear evidence of subsistence use, whether derived through hunting or scavenging. Utilization can be established by tight spatial association between artifacts and faunal remains that display human modifications, usually cut marks and/or impact fractures. The most conservative approach to building a database of subsistence choices would be to rely on utilization evidence only, but as Haynes and Stanford (1984:222) caution, by doing so, "we run the risk of ignoring true archaeological specimens." It is unrealistic to expect that all utilized fauna will present and

retain evidence of butchery. At the other extreme, one could use all evidence established through contemporaneity but risk creating "fictive data" (Haynes, 2002a:182) through the inclusion of specimens that are not archeological. Both approaches have been used and both likely present skewed views of the record. The question is how skewed?

In 2003, we compiled a dataset including 33 late Pleistocene archeological sites from North America (Waguespack and Surovell, 2003) based solely on "contemporaneity" evidence in the Haynes and Stanford (1984) scheme, essentially assuming that that if a species is present, it was used. This assumption is obviously incorrect, and undoubtedly produced a biased sample, a sample which we felt was probably "skewed in favor of small game" (Waguespack and Surovell, 2003: 339). Thus, we knowingly included species which had a very low probability of use, but no preference was given to species with regard to body size. For example, we included bison from the Naco site on the basis of the presence of scattered tooth fragments (Lance, 1959:37), which we were fairly confident had no association with the eight Clovis points scattered throughout the body of the nearby mammoth. Similarly, from the Lange Ferguson mammoth kill in South Dakota (Hannus, 1989, 1990), we included bison, cervids, rabbits, fish, two species of birds, two species of amphibians, ten species of rodents, three species of insectivores, and two species of snakes (J. Martin, 1984).

In contrast, Grayson and Meltzer (2002) and Cannon and Meltzer (2004) attempted to cleanse the data of species which show no evidence of subsistence use. Cannon and Meltzer explicitly criticized us (Waguespack and Surovell, 2003) and Haynes (2002a, b) for the very reason outlined above:

These publications are welcome contributions to the literature, but they unfortunately devote little attention to taphonomic issues that must be addressed before animal remains can be treated as evidence of human subsistence practices (Cannon and Meltzer, 2004:1956).

This is a fair criticism, at least in our case, although it would have been judicious to note that we pointed out this weakness ourselves. It is worth questioning whether Cannon and Meltzer (2004) truly treat all faunal remains equally. It is our contention that they do not, and that by taphonomically vetting the record, they introduce biases as well.

Two sites that figure prominently in the Clovis subsistence debate are Aubrey and Lewisville located in the upper Trinity River basin of North Texas (Crook and Harris, 1957, 1958; Ferring, 1995, 2001; Yates and Lundelius, 2001). Cannon and Meltzer lean heavily on these sites; of the 14 strong cases for use of small game (lagomorphs, rodents, birds, turtles, other reptiles, and fish) that they identify, Aubrey and Lewisville account for ten (Table 5.3). In other words, these sites are critical to making the argument that Early Paleoindians were not large game specialists. A wide array of species have been recovered from the Clovis occupation at Aubrey including mammoth, bison, ground sloth, deer, rodents, turtles and tortoises, snakes, birds, amphibians, and fish.

Regarding the small game from Aubrey, Cannon and Meltzer (2004: Table 5), accept rabbits, rodents, birds, turtles, snakes, and fish as having been exploited by Clovis peoples, based on the association of burned bone with hearths, spatial analysis, and the unlikelihood of natural burning producing observed spatial patterns (Cannon and Meltzer, 2004:1969). Regarding the hearths at the site, Ferring (2001:124) noted: "Despite extremely slow troweling in areas yielding burned material, no hearth or pit outlines of any kind could be found." Instead, hearths were identified on the basis of clusters of burned bone and charcoal (Ferring, 2001:124–125). This is a common practice in Early Paleoindian archeology, and we have done the same thing ourselves (Surovell and Waguespack, 2007). Unfortunately, there is a bit of circular reasoning here. Hearths are presumed

to be cultural on the basis of clustering in burned bone, and burned bone is assumed to be cultural on the basis of association with hearths. Thus, in one fell swoop, we could eliminate all of the evidence for use of small game from Aubrey since it is in large part based on clustering in association with hearths. Furthermore, burned bone occurs at Aubrey in sediments preand post-dating the Clovis occupation (Yates and Lundelius, 2001:115). We point this out not to make the argument that Clovis people at Aubrey did not use small game. They may have, and we included a greater array of small game from Aubrey in our study (Waguespack and Surovell, 2003: Table 2) than did Cannon and Meltzer (2004). Instead, we do this to show how easy it is to eliminate any evidence for subsistence use by careful reading of site reports and the use of clever arguments to exclude things that do not fit our preconceptions.

Turning to the Lewisville site, Cannon and Meltzer (2004:1969–1970) accept evidence for use of horse, deer, carnivores, rabbits, rodents, birds, turtles, and snakes. The Lewisville site was excavated between 1949 and 1951 in conjunction with construction of the Lewisville dam on the Trinity River. A diverse Pleistocene fauna was recovered in association with 21 burned features interpreted to be hearths (Crook and Harris, 1957, 1958). Cannon and Meltzer accept the evidence from Lewisville on the following basis:

[B]ecause the findings at Lewisville have essentially been replicated at nearby Aubrey, a reasonable case can be made for subsistence use of at least those taxa, listed above, for which specimens described as burned have been recovered from hearth contexts (Cannon and Meltzer, 2004:1970–1971).

There are two significant differences between the Aubrey and Lewisville sites. Aubrey has produced just under 10,000 artifacts from the Clovis level (Ferring, 2001: 130). Lewisville has produced only one artifact from buried deposits, a Clovis point, which some felt was intrusive or possibly planted at the site (Sellards, 1960; Krieger, 1962). It is difficult to attribute the lack of artifacts at Lewisville to excavation practices since a wide variety of small animals were recovered (Crook and Harris, 1957).<sup>2</sup> Also, a radiocarbon date on charcoal (some think lignite) from one of the "hearths" produced an infinite age (Crook and Harris, 1958). In other words, there is significant reason to doubt whether the Lewisville site is archeological at all, and yet just like Aubrey it shows clustering in charcoal, burned sediments, and faunal remains interpreted to be "hearths."

Not only does this place further doubt on the cultural nature of hearths and the use of small game at Aubrey, but it also shows how difficult it is to equally apply textual taphonomic criteria to all sites. For example, if we apply the criterion of whether "findings have essentially been replicated" elsewhere to a serious of questionable mammoth and mastodon kills which have been rejected by some (Grayson and Meltzer, 2002; Cannon and Meltzer, 2004), many additional sites might be included in a database of "secure" subsistence associations. These would include the Boaz mastodon (Palmer and Stoltman, 1975), the Manis mastodon (Gustafson et al., 1979), TABLE 5.3. Presence/absence of vertebrate taxa by site for Surovell and Waguespack Early Paleoindian subsistence dataset.

Kincaid Shelter (TX)			1	+	ı	ı	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	+	I	I	I	I	I	I	I	I	I	I	I	I	I	I	+	I	I	I	I	I	I	1	+
Kimmswick (MO)			I	I	I	I	I	I	I	+	+	+	I	I	I	I	I	+	+	+	+	+	I	+	+	I	I	+	I	I	I	+	+	I	I	I	I	I	I	I	I	I	I	I	I	I	+	+	I	I
(OK) Jake Bluff			I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	+	I	I	I	I	I	I
Holcombe Beach (MI)			I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	+	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I
Hiscock (NY)			I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	+	I	I	I	+	I	I	I	I	I	I	I	I ·	+	I	I
(IW) Tebior			I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	1	+
Guest (FL)			I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	+	I	I	I	I	I	I	I	I	I	I	I	+	I	I	I	I	1	+
Gault (TX)			I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	+	I	+	I	I	I	I	1	+
Escapule) Excapule			I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	+	I	I	I	I	I	I	1	+
Domebo (OK)	[		1	+	I	I	I	I	I	+	+	I	I	I	I	+	I	I	I	+	I	I	I	+	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	+	I	I	I	I	1	+
Dent (CO)			I	I	I	I	I	I	Ι	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	1	+
(YW) voloy			I	I	I	I	I	I	Ι	I	Ι	I	I	I	I	I	I	I	I	I	I	I	I	I	I	+	I	I	I	I	+	I	I	I	I	I	I	I	I	I	I	+	I	+	+	I	I	I	1 -	+
Mastodon (WI) Bull Brook (AM)			1	1	1	1	1	1	1	1	I	I I	1	1	I I	1	1	1	1	1	1	1	I	T	T	1	1	1	1	+	1	1	1	1	+	1	1	1	1	1	1	1	1	1	I	1	I	+	I	1
Cave (BC)																																																		
Charlie Lake			I	I	I	I	I	I	I	I	+	+	I	I	I	I	I	I	I	I	+	+	I	+	I	+	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	+	I	I	I	I	I	I
Blackwater Blackwater			I	I	I	I	I	I	Ι	I	+	I	I	I	I	I	I	I	I	I	I	I	+	+	I	+	I	I	I	I	+	+	I	I	I	+	+	I	+	I	I	+	I	+	+	I	I	I	1	+
Aubrey (TX)			1	+	+	+	I	I	Ι	+	+	+	+	I	+	+	I	I	+	+	+	I	I	+	+	+	I	I	I	I	I	+	I	I	I	I	I	I	I	I	I	+	I	+	I	I	+	I	+	I
Body Size Class		-		_, ,	-	1	-	-	-	1	1	1		-			_	-	-	1	1	1	0	0	0	0	0	0	0	61	e	m (	n o	n c	n d	n c	n o	<b>.</b> .	4 .	4 .	4	4	4	4	4.	4.	4 r	ŝ	n u	n
لاق) Body mass		2000	0.000	0.01	0.01	0.01	0.02	0.025	0.03	0.03	0.05	0.05	0.06	0.08	0.1	0.15	0.15	0.19	0.2	0.24	0.3	0.52	1	1.15	1.42	ŝ	4.2	5.4	12.5	22	46	55	<u>د</u>	200	80	011	110	120	218	250	323	400	600	006	006	1100	1587	4500	5750	000/
Taxonomic eroun	Herbivorous mammals	Commenter of the second s	Sorex	Perognathus	Reithrodontomys	Family Soricidae	Clethrionomys	Zapus	Onychomys	Synaptomys	Microtus	Peromyscus	Oryzomys	Eutamias	Scalopus	Sigmodon	Thomomys	Blarina	Neotoma	Geomys	Spermophilus	Sciurus	Cynomys	Ondatra	Sylvilagus	Lepus	Dasypus	Marmota	Capromeryx	Castor	Antilocapra	Odocoileus	Mylohyus	Palaeolama	Kangijer	Hemiauchenia	Platygonus	Family Cervidae	Cervus	Holmesina	Tapirus	Equus	Megalonyx	Bison	Camelops	Glyptotherium	Glossotherium	Mammut	Order Proboscidea	Mammuthus

(continued)

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axonomic group	(kg) Body mass	Body Size Class	Lange- Ferguson (SD)	(ZA) rəndəJ	(ZA) тэйэЛ	JelivsiwaJ (XT)	Spring (FL)	(TX) Manis (WA) Luddock Lake	Martins Creek (OH)	McLean (TX)	(XT) imniM	Varray (SA) sgningS	(ZA) 03611	Schawnee-	Mininink (AG) Armandz	(WY) Udora (ON)	Wacissa River (FL)	Wally's Beach (AB)	(HN) əlqqıd
Herbivorous mammals																			
orex	0.006	1	+	I	I	I	I	I I	I	I	I	I	I	I	I	I I	I	I	I
Perognathus	0.01	1	I	+	I	I	I	י +	I	I	I	I	I	I	I	I	I	I	I
Reithrodontomys	0.01	-	+	I	I	I	I	۱ +	I	I	I	I	I	I	I	ı I	I	I	I
<sup>7</sup> amily Soricidae	0.01	-	I	I	I	I	I	1	I	I	I	I	I	I	I	1	I	I	I
<b>Clethrionomys</b>	0.02		+	I	I	I	I	 	I	I	I	I	I	I	I	1	I	I	I
Zapus	0.025		+	I	I	I	I	 	I	I	I	I	I	I	I	1	I	I	I
Dnychomys	0.03		+	I	I	I	I	۱ +	I	I	I	I	I	I	I	1	I	I	I
synaptomys	0.03		I	I	I	I	I	 	I	I	I	I	I	I	I	1	I	I	I
Aicrotus	0.05		+	+	I	+	I	۱ +	I	I	I	+	I	I	I	1	I	I	I
Peromyscus	0.05		+	I	I	+	I	۱ +	I	I	I	I	I	I	I	1	I	I	I
Dryzomys	0.06		I	I	I	I	I	 	I	I	I	I	I	I	I	1	I	I	I
Tutamias	0.08	-	+	I	I	I	I	I I	I	I	I	I	I	I	I	I	I	I	I
calopus	0.1	1	ı	I	I	+	I	 	I	I	ı	I	ı	I	I	1	I	I	ı
ligmodon	0.15	1	I	I	I	I	I	I I	I	I	I	I	ı	I	I	1	I	I	I
Thomomys	0.15	-	+	+	I	I	I	۱ +	I	I	I	I	ı	I	I	1	I	I	I
<i>Slarina</i>	0.19	-	+	I	I	I	I	۱ +	I	I	I	I	ı	I	I	1	I	I	I
Veotoma	0.2	1	I	I	I	+	I	۱ +	I	I	I	+	I	I	I	I	I	I	I
Jeomvs	0.24		ı	I	I	1	I	+	I	I	I	- 1	I	ı	I	1	I	I	I
aermophilus	0.3	-	+	I	I	+	I	+	I	I	I	I	I	I	I	1	I	I	I
ciurus	0.52	-	1	I	ı	+	ı	1	I	I	I	I	I	ı	I	1	I	I	I
Synomys	1	0	I	I	I	+	I	۱ +	I	I	I	I	I	I	I	1	I	I	I
)ndatra	1.15	6	+	+	I	I	I	++	I	I	I	I	I	I	I	1	I	I	I
Sylvilagus	1.42	0	I	+	I	+	+	I I	I	I	ı	I	ı	I	I	1	I	ı	I
sndar	m	0	+	+	I	+	I	۱ +	I	I	ı	I	ı	I	I	+	I	ı	I
Dasypus	4.2	0	I	I	I	ı	I	I I	I	I	ı	I	ı	I	I	1	I	ı	I
Aarmota	5.4	0	I	I	I	I	I	I I	I	I	I	I	I	I	I	1	I	I	I
Japromeryx	12.5	0	I	I	I	I	I	۱ +	I	I	I	I	I	I	I	1	I	I	I
Castor	22	0	I	I	I	I	I	1	I	I	I	I	I	I	I	1	I	I	I
Antilocarpa	46	ŝ	I	I	I	I	I	 	I	I	I	I	I	I	I	۱ +	I	I	I
<i>Ddocoileus</i>	55	ŝ	I	I	I	+	+	I I	+	I	I	I	I	I	I	1	+	I	I
Aylohyus	75	ŝ	I	I	I	I	I	I I	I	I	I	I	I	I	I	I I	I	I	I
Palaeolama	80	m	I	I	I	I	I	I I	I	I	I	I	I	I	I	 	+	I	I
Rangifer	86	n	I	I	I	I	I	 	I	I	I	I	I	I	I	+	I	I	+
Hemiauchenia	110	ŝ	I	I	I	I	I	۱ +	I	I	I	I	I	I	I	1	+	I	I
olatygonus	110	Э	I	I	I	+	I	۱ +	I	I	I	+	I	I	I	I	I	I	I
<sup>a</sup> mily Cervidae	120	ŝ	+	I	I	I	I	 	I	I	ı	I	ı	I	I	1	I	I	ı
Cervus	218	4	ı	I	I	I	I	 	I	I	ı	I	ı	I	I	1	I	I	ı
Holmesina	250	4	ı	I	I	I	I	۱ +	I	I	ı	I	ı	I	I	1	I	I	I
rapirus	323	4	I	+	I	I	I	 	I	I	I	I	I	I	I	1	I	I	I
īguus	400	4	I	+	I	+	I	۱ +	I	I	I	+	I	ı	I	1	+	+	I
Megalonyx	600	4	ı	I	I	I	+	I I	I	I	ı	I	ı	I	I	1	I	I	I
Bison	006	4	+	+	I	+	+	+	I	I	I	+	+	I	I	۱ +	+	I	I
Jamelops	006	4	I	+	I	+	ı	י +	I	I	I	+	I	I	I	1	I	I	I
Jlyptotherium	1100	4	I	I	I	+	I	1 1	I	I	I	I	I	I	I	1	I	I	I

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I	I	I	I		I	I	I	I	I	I	I	I	I	I	I		I	11	I	
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1587	4500	5750	7000		4	100	3.2	3.45	720	32	27	0.42	400	7.1						
Glossotherium	Mammut	Order Proboscidea	Mammuthus	Carnivorous mammals	Procyon	Ursús	Vulpes	Alópex	Arctodus	Canis	Mephitis	Müstela	Smilodon	Taxidea	Order Carnivora	Non-mammalian taxa	Class Reptilia	Class Aves Class Osteichthves	Class Amphibia	

the Leikem mammoth (Saunders, 1980, n.d.), the McLean mammoth (Ray, 1930, 1942; Ray and Bryan, 1938), and the Martin's Creek mastodon (Brush and Smith, 1994; Brush et al., 1994). Though questions of association remain unanswered, at all of these sites artifacts have reportedly been recovered in spatial association with proboscidean remains, a pattern which has been repeated at numerous sites, including Aubrey itself.

The two approaches discussed above each offer varying degrees of "security" and reliability in the Early Paleoindian faunal record. We included all species on the basis of spatial and stratigraphic association, whether there was strong evidence for subsistence use or not (Waguespack and Surovell, 2003). Using this approach, we can be confident that our dataset includes all species recovered that were used by Early Paleoindians, but it does so by the inclusion of many species that were likely not used. In contrast, Cannon and Meltzer (2004) included only those species which they felt could be securely linked to human subsistence behavior. This approach produces a much smaller sample, but one that might be a better reflection of past subsistence choices, although there is a much greater likelihood of eliminating taxa that were actually used. The downside of this approach, we argue, is that it is difficult to equally apply such criteria to all sites, and as such, one is likely to introduce additional research bias into the data.

#### What Does the Record Tell Us?

In Tables 5.2 and 5.3, we present our original dataset (Waguespack and Surovell, 2003) with the addition of three new sites: Udora (Storck and Spiess, 1994), Jake Bluff (Bement and Carter, 2003 as cited by Cannon and Meltzer, 2004), and Wally's Beach (Kooyman et al., 2001, 2006) (Fig. 5.4). The addition of these sites does not significantly change any patterns we previously identified. We have reformatted the data to facilitate comparison with the Cannon and Meltzer dataset. Mammalian data are presented as presence/absence values by genus, family, or order. Data for non-mammals are presented as present/absent by class. In Table 5.4, we present the Cannon and Meltzer (2004) dataset. The largest difference between the two datasets is sample size. Our dataset includes a minimum of 241 occurrences of animals (Table 5.3), and the Cannon and Meltzer dataset includes a minimum of 46 occurrences (Table 5.4). The total number of associations, however, is not as critical to the diet breadth debate as relative species representation. Does species representation differ significantly between the two datasets?

To perform this analysis, we grouped herbivorous mammalian genera into five body-size classes, as shown in Table 5.3. From Class 5 to 1 respectively, these are roughly mammoth-, bison-, deer-, rabbit-, and small rodent-sized animals. Body size estimates for extinct and extant species were derived from Smith et al. (2003). Body size classes were further compressed for the purpose of performing chi-square tests, which are sensitive to small cell values. Two chi-square tests were performed, one based on the number of sites showing the presence or absence of each taxonomic group (Table 5.5), and one based on the total number of occurrences of each taxonomic group in each dataset (Table 5.6). Looking at the relative frequencies of sites showing each taxonomic group (Table 5.5, Fig. 5.5a), there are no significant differences between the two datasets  $(X^2 = 1.46, df = 4, p = 0.83)$ .

When viewed this way, the same result in terms of taxonomic representation is obtained whether a taphonomic filter is applied to the data or not. The total number of occurrences of each taxonomic group (Table 5.6, Fig. 5.5b) does, however, differ significantly ( $X^2 = 17.9$ , df = 4, p = 0.001). Large mammals (Body Size Classes 3–5) are overrepresented in the Cannon and Meltzer dataset, and small mammals (Body Size Classes 1 & 2) are overrepresented in our dataset. This finding supports our hypothesis that by including all species present within an assemblage, whether there is clear evidence for subsistence use or not, we disproportionately included larger frequencies of small fauna.

What the preceding analysis demonstrates is quite clear. Although arguments have been made to the contrary, the debate is not about relative species representation. If this was the crux of the debate, the conclusions of these two studies should have been reversed or perhaps identical (Fig. 5.5). Instead, the argument is in large part about what we should label the subsistence strategy that produced this faunal record and the extent to which the current faunal record reflects Early Paleoindian subsistence choices.

The issue of semantics aside, regarding prey choice and its relationship to Pleistocene extinctions, the more important question is whether either or both datasets show evidence of selective hunting of large-bodied animals. Because the ecological relationship between body size and population density is dependent upon metabolism and trophic level (Peters, 1986), we limit this analysis to herbivorous mammals, but increasing the taxonomic scope would not change the outcome. To control for variation in taxonomic diversity within each body size class, we divide the total number of occurrences by the number of genera represented within each body size class (Table 5.7). For both datasets, there is a significant positive correlation between body size and archeological abundance (Cannon and Meltzer, Spearman's  $\rho = 0.975$ , p = 0.005; Surovell and Waguespack, Spearman's  $\rho = 1.00$ , p < 0.001) (Fig. 5.6).

In other words, whether the data are taphonomically vetted or not, the largest and rarest mammalian herbivores in late Pleistocene landscapes are the most frequent species to occur in Early Paleoindian faunal assemblages. This pattern is robust and occurs even within our dataset which includes 93 occurrences of small mammal fauna. In fact, large game is apparently more abundant when taphonomic considerations are used in dataset construction. This finding provides strong support for the large game specialist hypothesis. If Early Paleoindians regularly took small game upon encounter, small animals such as hares should vastly outnumber mammoths and bison in the archeological record. They do not (Fig. 5.6).

	(HN) (HN)		I	I	I	+	I	I	I	I	I	I		T	I	I
	(NO) arobU		I	+	I	+	Ι	I	I	I	T	+		I	I	I
dataset	Wacissa River (FL)		T	I	I	I	I	I	+	I	I	I		I	I	I
bsistence	Shawnee- Minisink (A9)		I	I	I	I	I	I	I	I	I	I		I	I	+
lian su	Pleasant Lake (MI)		I	I	I	I	Ι	Ι	I	+	I	I		I	I	I
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a with "	Bull Brook (AM)		+	I	I	+	I	I	I	I	I	I		I	I	I
rate taxa	Blackwater Draw (NM)		I	I	I	I	+	I	+	I	+	I		I	+	I
f verteb	Aubrey (TX)		+	+	+	I	I	I	+	I	I	I		+	+	+
sence of	Body Size Class		1&2	0	б	3	4	4	4	5	5	I		I	I	I
ABLE 5.4. Presence/abs	axonomic group	lerbivorous mammals	rder Rodentia	amily Leporidae	amily Cervidae	angifer	sunp	amelops	ison	lammut	1 ammuthus	<b>Jarnivorous Mammals</b> htder Carnivora	on-mammalian taxa	lass Aves	lass Reptilia	lass Osteichthyes

TABLE 5.5. Chi-square test comparing the number of sites showing the presence or use of all taxonomic groups present in the Surovell and Waguespack and Cannon and Meltzer datasets.

	Numbe	er of sites
Body Size Class	S&W	C&M
HMBS 5	26 (28.5)	14 (11.5)
HMBS 3&4	28 (27.8)	11 (11.2)
HMBS 1&2	15 (13.6)	4 (5.4)
Carnivores	9 (8.6)	3 (3.4)
Nonmammals	14 (13.6)	5 (5.4)
$X^2 = 1.46, df = 4, p = 0.834$		

Expected values shown in parentheses. Cells for which observed values exceed expected values are shown in bold.

TABLE 5.6. Chi-square test comparing the number of occurrences of all taxonomic groups present in the Surovell and Waguespack and Cannon and Meltzer datasets.

	Number of o	occurrences
Body Size Class	S&W	C&M
HMBS 5	26 (33.5)	14 (6.5)
HMBS 3&4	70 (71.2)	15 (13.8)
HMBS 1&2	90 (80.5)	6 (15.5)
Carnivores	18 (17.6)	3 (3.4)
Nonmammals	34 (35.2)	6 (6.8)



FIGURE 5.5a. Percent of sites showing the presence of prey taxa for the Surovell and Waguespack and Cannon and Meltzer (2004) datasets. **b**. Percent of occurrences of mammalian prey taxa for both datasets.

 $X^2 = 17.9$ , df = 4, p = 0.001Expected values shown in parentheses. Cells for which observed values exceed expected values are shown in bold.

	Ca	nnon and M	Ieltzer	Wagu	espack and	Surovell
Body Size Class	Occurrences	Genera	Occurrences per genus	Occurrences	Genera	Occurrences per genus
5	14	2	7.00	26	2	13.00
4	9	3	3.00	44	9	4.89
3	6	2	3.00	26	7	3.71
2	4	3 <sup>a</sup>	1.33	30	8	3.75
1	2	2 <sup>b</sup>	1.00	63	19	3.32

TABLE 5.7. Number of occurrences of herbivorous mammals standardized to taxonomic diversity by body class for the Surovell and Waguespack and Cannon and Meltzer datasets.

<sup>a</sup> Cannon and Meltzer (2004) do not specify which genera are included in this body size class. We can infer at least two genera from their data: *Castor* and at least one genus of lagomorph. We assume three genera to be represented: *Castor*, *Lepus*, and *Sylvilagus*. If only two genera are assumed, it does not change the outcome of the analysis.

<sup>b</sup> Two rodent genera are assumed. Cannon and Meltzer identify three reliable associations with rodents, one of which is beaver at Bull Brook, which falls within our Body Size Class 2. We assume the other two associations to be small rodents (Body Size Class 1), and that two genera are represented.

The data also provide an opportunity to directly test the Byers and Ugan (2005) Early Paleoindian diet breadth model. They argued that Early Paleoindian diets should have consistently included animals down to the size of hares, and possibly even smaller mammals depending upon estimated encounter rates (Byers and Ugan, 2005:1633). In other words, they predicted all animals roughly 2 kg or larger would have always been taken upon encounter. Therefore, one would expect prey frequencies in Paleoindian faunal assemblages to be directly proportional to their estimated relative encounter rates (Byers and Ugan, 2005: Table 5.7)<sup>3</sup>. In Table 5.8, we show the predicted number of occurrences of each body size class stand-



FIGURE 5.6a. Body size class versus archeological abundance standardized to taxonomic diversity for all sites in the Surovell and Waguespack database. **b**. Same for Cannon and Meltzer (2004) dataset.

TABLE 5.8. Predicted relative archeological frequency by body size class for herbivorous mammals estimated using the Byers and Ugan (2005) model.

Body Size Class	Predicted Relative Archeological Frequency <sup>a</sup>	
5	1.0	
4	7.6	
3	25.7	
2	630.6	
1	15737.4	

aPredicted relative archeological frequency was calculated using the equation relating body mass (kg) to population density (indiv.\*km<sup>-2</sup>) in Byers and Ugan (2005:Table 7): density = 4.33 - 0.75\*log(mass). Population density for each Body Size Class was based on a weighted average of density by body size class for genera listed in Table 5.3. To calculate predicted archeological relative frequency, population densities for each body size class were standardized to that of Body Size Class 5 (proboscideans) assuming that encounter and capture rate are directly proportional to population density following Byers and Ugan (2005). These values assume constant taxonomic diversity for each Body Size Class.

ardized to proboscideans, which according to their model should be least frequently encountered and therefore least abundant in Early Paleoindian faunal assemblages. In short, the Byers and Ugan model predicts that for every mammoth or mastodon present in Early Paleoindian faunal assemblages, there should be approximately 7 bison-, 26 deer-, and 630 hare-sized mammals. If small rodents are included in the diet, there should be approximately 15,737 of these animals per mammoth or mastodon. Obviously, these predictions are easily falsified, but it should also be noted that the predicted encounter rates shown in Table 5.8 assume constant taxonomic diversity for each body size class. Because taxonomic diversity is generally inversely correlated with body size, these numbers are dramatic underestimates. Furthermore, because there are at least 14 known secure associations with mammoth and/or mastodon from Clovis contexts (Grayson

and Meltzer, 2002; Cannon and Meltzer, 2004), the actual number of associations with non-proboscidean fauna predicted by the Byers and Ugan (2005) for our current sample of sites is much greater (e.g., 106 bison, 360 deer, 15,120 hares, 15,120 rabbits, etc).

Thus, the Byers and Ugan model does not appear to be a very good predictor of Paleoindian subsistence behavior. In contrast to the strong negative correlation between body size and archeological abundance predicted by their model, a strong positive correlation is seen. In order to stress this point, we repeat it: The largest and the least common animals on Pleistocene landscapes are the most abundant and the most regular constituents of Paleoindian faunal assemblages. Why does the Byers and Ugan (2005) model fail? There are three possible reasons. First, it may be built upon faulty assumptions such that estimated encounter and/or return rates are highly inaccurate. Second, the model may not be a good reflection of Paleoindian subsistence decisions. For example, post-encounter return rates may not have been the sole currency upon which the decision to kill or not to kill was made. Finally, it is possible that their model is a good representation of Paleoindian behavior, but that the archeological record of Paleoindian prey choice is extremely biased.

#### Is the Record Biased?

The simplest answer to this question is: probably, but it is difficult to know with certainty. Although numerous studies have discussed the possibility of bias in the Early Paleoindian faunal record (Grayson, 1988; Meltzer, 1989; Waguespack and Surovell, 2003; Cannon and Meltzer, 2004; Byers and Ugan, 2005), it is extremely difficult to directly test hypotheses about sample bias. Bias occurs when certain portions of populations have a greater or lesser likelihood of being sampled. Without knowing the distribution of the sampled population, the only way to directly test a hypothesis about sample bias is to have a theoretical or empirical model of what the underlying population should look like.

In the case of the Early Paleoindian faunal record, we have no clear basis for developing such null models. Here is an example. Hypothesis: Large game kill sites are overrepresented in the Early Paleoindian archeological record because they are more easily discovered than campsites (Grayson, 1988; Meltzer, 1989; Cannon and Meltzer, 2004). Thus, large game are overrepresented in the Paleoindian archeological record. To directly test this hypothesis, one would need some way to determine the expected relative frequencies of kill and non-kill sites in the case of no bias (the relative frequencies in the population). A theoretical or empirical null model, in theory, could be used. For example, one could examine huntergatherer ethnography to determine approximately how many large game kill sites are expected to occur per campsite and compare this to the archeological record, but this approach is problematic because it rests upon a tenuous uniformitarian assumption that the selected ethnographic case or cases are suitable analogies for the Paleoindian case. In other words, if the Paleoindian dataset is found to differ significantly from the null model, is it because the sample is biased or because the null model is inappropriate?

Despite these considerations, Cannon and Meltzer (2004:1974–1978) claim to have tested this and other hypotheses concerning bias. For example, they compare taxonomic richness and species representation between sites which were discovered on the basis of large mammal bones and those that were not. Not surprisingly, they find that sites which were discovered due to the presence of large mammal bones tend to contain greater proportions of large mammals in their assemblages (Cannon and Meltzer, 2004:1978). It is not difficult to show that this does not tell us one way or another whether the record is biased. To do so would require demonstrating that our method for sampling the archeological record produces a faunal record that actually differs from Paleoindian subsistence choices. They conduct a similar test with regard to kill sites versus campsites showing that large game kill sites tend to have lower taxonomic diversity and greater relative frequencies of large game (Cannon and Meltzer, 2004:1980– 1981). From this analysis, one could argue that if campsites are overrepresented in our current sample of Paleoindian subsistence, then small game would be overrepresented as well, but it is unclear if our sample of kill and campsites differs significantly from the underlying population.

Nonetheless, we suspect that the record is biased and that large game are overrepresented (Waguespack and Surovell, 2003; Surovell and Waguespack, 2008). It seems very unlikely to us that more than one-half of the bone-bearing sites produced by Early Paleoindians were mammoth or mastodon kills, something which the record at face value would suggest (Table 5.2). This contention admittedly is not based on a theoretical or empirical null model per se but is instead a hunch. More importantly, it is worth asking whether excavating more campsites would really change our conclusion that Early Paleoindians preferentially targeted large mammals. Specifically, if we were to limit our analysis to sites that are not kills, would we come to a different conclusion about Paleoindian prey choice?

Again, we perform this analysis for both datasets. Cannon and Meltzer (2004) used the presence or absence of hearths to make the distinction between camp and kill sites. In contrast, for our dataset, to identify kill sites we use the criterion of whether artifacts are found in direct association with the carcasses of individual animals, or in the case of the Wacissa River site, a projectile point embedded in bone. Thus, certain sites which Cannon and Meltzer (2004) considered campsites due to the presence of hearths, such as Murray Springs, Lehner, and Blackwater Draw, we do not include in our non-kill site sample, and Jake Bluff, which Cannon and Meltzer consider to be a kill site, we include in our non-kill sample. This reduces our sample to 14 sites, and the Cannon and Meltzer sample to nine sites. It may be surprising to discover that when the sample is limited to non-kill sites, the same pattern of large game specialization persists (Fig. 5.7, Table 5.9). For both datasets, there is a significant positive



FIGURE 5.7a. Body size class versus archeological abundance standardized to taxonomic diversity for non-kill sites in the Surovell and Waguespack database. **b** Same for Cannon and Meltzer (2004) dataset.

TABLE 5.9. Number of occurrences of herbivorous mammals standardized to taxonomic diversity by body class for non-kill sites (campsites and processing sites) in the Surovell and Waguespack and Cannon and Meltzer (2004) datasets.

		Cannon and	Meltzer	Wa	guespack and	d Surovell
Body Size Class	Occurrences	Genera	Occurrences per genus	Occurrences	Genera	Occurrences per genus
5	3	1	3.00	6	2‡	3.00
4	7	3	2.33	16	6	2.67
3	5	2	2.50	10	4	2.50
2	4	3 <sup>a</sup>	1.33	12	6	2.00
1	2	2 <sup>b</sup>	1.00	23	12	1.92

For the Cannon and Meltzer (2004) dataset, sites with hearths were included in this analysis (see Table 5.2). For our dataset, we included those sites labeled "N" in the Table 5.2 "Kill Site" column.

<sup>a,b</sup>See notes in Table 6

<sup>b</sup>Only mammoth has been identified from these sites, but at Little Salt Springs and Aubrey, proboscideans were only identified to Order. We assume two genera here, but assuming only one genus may be more realistic.

correlation between body size and archeological abundance (C&M, Spearman's  $\rho = 0.90$ , p = 0.037; S&W, Spearman's  $\rho = 1.00$ , p < 0.001). Therefore, using only the campsite sample, again the largest and rarest species are the most common in Paleoindian faunal assemblages. This analysis suggests that if our current sample had a greater proportion of campsites, Early Paleoindians subsistence would still appear to have been focused upon large game.

Finally, we address what we call "geographic bias." To this point, we have only examined the record at a continental scale. Some have argued that the bulk of sites informing us about Paleoindian subsistence occur in the mid-continent, particularly the Western Great Plains and Southwest, and that we cannot and should not extrapolate subsistence patterns from these areas to far eastern or western North America (Meltzer and Smith, 1986; Grayson, 1988; Meltzer, 1989, 1993; Cannon and Meltzer, 2004). Thus, the appearance of large game specialization may be due to a record biased toward regions where large game hunting was more prevalent. It is true that there are large swaths of the continent where we know little or nothing about Early Paleoindian subsistence (Fig. 5.4), the Great Basin being one obvious example. Any discussion of Early Paleoindian subsistence in the Great Basin, therefore, must by necessity be based on indirect evidence because there is little direct evidence to speak of (e.g., Heizer and Baumhoff, 1970; Grayson, 1993; Beck and Jones, 1997). There are two important points to be made here. First, in areas where we have no evidence of Early Paleoindian subsistence, we simply do not know what people were killing and eating. Second, arguments about geographic bias implicitly argue that if we had more sites in the far east or possibly far west, they would attest to a more generalized subsistence pattern. The available data allow us to begin to explore this idea.

One last time, we turn to both datasets. We divided each dataset into three regions: Eastern North America (east of the Mississippi River), Western North America (west of the Continental Divide), and Central North America (east of the Continental Divide and west of the Mississippi River) as shown in Table 5.2. For each dataset and region, we once again examined body size vs. archeological abundance among herbivorous mammals (Table 5.10). Central North America accounts for the majority of associations in both datasets representing 57% of occurrences in the Cannon and Meltzer sample, and 72% of our sample. The remaining occurrences are equally divided between eastern and western North America for both datasets, but these samples are both problematic. The sample for western North America is comprised exclusively of large game kill sites by our definition, and the sample for eastern North America contains a series of very poorly preserved faunal assemblages.

In our dataset, for all regions, there are positive though not statistically significant correlations between body size and archeological abundance (Fig. 5.8). In the Cannon and Meltzer dataset, Western and Central North America show similar correlations. For Eastern North America, however, there is a nonsignificant but negative correlation between body size and archeological abundance. This analysis again suggests that across the continent, with the possible exception of Eastern North America, late Pleistocene huntergatherers preferentially targeted large-bodied prey. Because Eastern North America stands out and because it has been argued that large game specialization might not be expected for this region (e.g., Meltzer and Smith, 1986; Meltzer, 1988), it is worth taking a closer look at this record. The Cannon and Meltzer dataset includes a total of eight occurrences of herbivorous mammalian fauna: one mammoth, one mastodon, one bison, three caribou, one hare, and one beaver. While this might suggest a generalized foraging pattern for eastern North America, of the eight secure associations identified by Cannon and Meltzer (2004), six are with megafauna, using the traditional definition of animals weighing more than 40-45 kg (Martin, 1984; Martin and Steadman, 1999; Stuart, 1999; Barnosky et al., 2004; Koch and Barnosky, 2006). Thus, large game occur at significantly higher frequencies than small game based upon relative encounter frequencies.

TABLE 5.10. Number of	occurrences of herbivorous	mammals standardized	to taxonomic	diversity by	body class	s for by	geographic
region for the Surovell a	and Waguespack and Canno	n and Meltzer (2004) da	atasets.				

Body Size Class	Region: West			Region: Central			Region: East		
	Occurrences	Genera	Occ/gen	Occurrences	Genera	Occ/gen	Occurrences	Genera	Occ/gen
Cannon and M	Ieltzer								
5 4 3 2 1	4 3 0 0 0		4.00 1.50 _ _	8 5 3 2 2	2 2 1 2 2	4.00 2.50 3.00 1.00 1.00	2 1 3 2 0		1.00 1.00 3.00 1.00
Surovell and V 5 4 3 2 1	Vaguespack 6 10 1 4 5	2 4 1 3 4	3.00 2.50 1.00 1.33 1.25	13 28 14 23 58	3 7 5 7 19	4.33 4.00 2.80 3.29 3.05	7 6 11 3 0	2 4 4 3 0	3.50 1.50 2.75 1.00



FIGURE 5.8. Body size class versus archeological abundance standardized to taxonomic diversity by geographic region for the Surovell and Waguespack and Cannon and Meltzer (2004) datasets.

Aside from sample size, there are other reasons why the record from eastern North America may differ. There is certainly no shortage of fluted point sites in eastern North America (Anderson and Faught, 2000), but there is a lack of

bone from those sites, or in some cases a lack of clear associations (e.g, Dunbar, 1991; Fisher, 1984). The humid and acidic soils of the east dramatically reduce the probability of survival of late Pleistocene bone. Of Cannon and Meltzer's eight associations with herbivorous mammals, five are preserved due only to burning and calcination. These include the five smallest animals of the sample, all three caribou, the hare, and the beaver. In other words, the bulk of the record from eastern North America is based on an extremely limited sample of burned bones recovered from possible hearth contexts, which again raises the red flag of bias. While it is not a simple matter to test the hypothesis that the faunal record of eastern North America is biased, it is interesting to note that virtually all the small game associations that are accepted by Cannon and Meltzer for all regions are accepted on the basis of burning, while very few of the large game associations are based on this criterion. Nonetheless, even for the small and problematic sample known from eastern North America, megafauna regularly occur and dominate faunal assemblages, and when criteria for association are relaxed, the pattern for eastern North America mimics that of the remainder of the continent.

# Paleoindian Prey Choice and North American Megafaunal Extinctions

Do the analyses above support the hypothesis that human hunting directly or indirectly caused the extinction of >30 genera of North American megafauna? In a general sense, we believe the answer is yes. Globally or locally extinct fauna regularly occur in Early Paleoindian faunal assemblages. In fact, extinct fauna occur in 83% to 97% of the sites used in this study (Table 5.3) depending upon how one defines "extinct". The high estimate includes Bison antiquus (ancestral to B. bison and locally extinct in parts of North America) and Rangifer tarandus (locally extinct in parts of North America) as extinct species; the low estimate does not. Including both species, only one site, Shawnee-Minisink, lacks evidence of hunting of extinct megafauna. Even if one only uses "secure" subsistence associations (Table 5.4), extinct megafauna still occur in 68% to 95% of Early Paleoindian faunal assemblages using the same criteria. Furthermore, as we have argued, there is clear evidence that Paleoindians not only hunted but preferentially hunted large-bodied prey. Because late Pleistocene extinctions in North America were similarly size-selective (Martin, 1984; Alroy, 1999; Lyons et al., 2004), large game specialization by Early Paleoindians provides circumstantial support for the Overkill hypothesis.

Selective targeting of the largest available animals would have meant that all potential prey would not have been subject to equal predation pressures. Generally speaking the ability of animal populations to sustain viable populations under predation pressure is negatively correlated with body size (Alroy, 2001), but there are exceptions to this pattern, such as turtles and tortoises (Stiner et al., 1999, 2000; Surovell, 1999). As a group, these animals are usually not largebodied. Importantly however, they also suffered extinctions in the Pleistocene (Martin, 1984) and occur in a number of Early Paleoindian faunal assemblages (Waguespack and Surovell, 2003). Preferential human hunting of large, slowly reproducing species is thus one clear mechanism for producing the pattern of size bias in Pleistocene extinctions seen in North America and worldwide (Alroy, 1999, 2001; Lyons et al., 2004).

At best, this evidence must be seen as circumstantial because there are very few "secure" subsistence associations with the vast majority of extinct Pleistocene genera (Grayson and Meltzer, 2002, 2003; Cannon and Meltzer, 2004). Of globally extinct North American megafauna, according to Cannon and Meltzer (2004) only Mammuthus, Mammut, Equus, and Camelops can be shown to have been utilized by Early Paleoindians for subsistence purposes. Of these genera, Mammuthus accounts for the vast majority of "secure" associations (Table 5.4). For extinctions in the Order Proboscidea, we think a strong argument can be made for human causation for two reasons. First, over three continents and 800,000 years, evidence of human subsistence use of proboscideans is limited to the edges of human global colonization, suggesting that for Europe, Asia, North America, and South America local extinctions among the proboscidea coincided directly with human incursions into uninhabited regions (Surovell et al., 2005). Second, although 14 "secure" associations with mammoths and mastodons may not seem like a large number in the absolute sense (Dixon, 1999:216; Adovasio and Page, 2002:127; Grayson and Meltzer, 2002:248), it is a huge number of proboscidean kills when compared to similar evidence from other parts of the world (Haynes, 2002b:183; Surovell and Waguespack, 2008; Surovell et al., 2005). Strong evidence for hunting of mammoths and mastodons, however, is not easily translated into an argument that humans also hunted other extinct taxa for which there are few or no subsistence associations.

However, one must ask whether this absence of evidence is truly meaningful given our current sample of late Pleistocene archeological sites. At the start of 1926, the first year of excavations at the Folsom site in New Mexico, no one would have considered it odd that there were no recognized "secure" subsistence associations between Early Paleoindian artifacts and extinct fauna because so few sites relevant to the question had been investigated. Now, 80 years later, the sample has increased, but we still struggle to interpret what the numerous extinct fauna absent from the subsistence record means for Overkill. How large of an archeological sample is necessary to demonstrate that this absence of evidence is truly meaningful? Consider the "secure" subsistence associations identified by Cannon and Meltzer (2004) shown in Table 5.4. It is well known that there is a strong relationship between sample size and taxonomic diversity in faunal assemblages (Grayson and Delpech, 1998, 2001, 2002; Grayson, et al., 2001), and one could ask what is the probability of discovering >30 extinct genera represented in sufficient quantities to support Overkill from a total of 42 "secure" subsistence associations? Obviously, the probability is extremely low and it would require that virtually every association be taxonomically unique. In other words, this particular absence of evidence need not be evidence of absence.

From a brief examination of the set of sites which do tell us something about what Early Paleoindians hunted (Tables 5.3 and 5.4), it is not difficult to again make the argument that this absence may not be meaningful. First, one must ask in which sites we might expect to reliably see evidence of hunting of non-proboscidean extinct fauna? Of the 22 sites that Cannon and Meltzer (2004) consider to contain reliable evidence of Paleoindian subsistence behavior, 15 are in whole or in part mammoth, mastodon, or bison kills (Tables 5.2 and 5.4). While other utilized fauna do occasionally occur in these sites, particularly those with hearths such as Lehner and Blackwater Draw (Table 5.4), generally speaking we do not see taxonomically diverse subsistence associations at such sites (Cannon and Meltzer, 2004), and thus the absence of secure evidence for subsistence use of other extinct Pleistocene fauna at these large mammal kill sites may not be meaningful. Of the remaining six sites, four (Bull Brook, Shawnee-Minisink, Udora, and Whipple) have very small (NISP<20), very poorly preserved faunal assemblages, where the only skeletal elements preserved are those which happened to become calcined in hearths. Again, the absence of extinct Pleistocene fauna in these sites may not be meaningful.

This leaves us with three sites in the Cannon and Meltzer (2004) sample where one might reasonably expect to see evidence of the use of the remaining 29 genera of extinct Pleistocene fauna, for which we have little evidence of human hunting: Aubrey, Jake Bluff, and Lewisville. Cannon and Meltzer (2004) classify Jake Bluff as a kill site, and there are serious reasons to doubt whether Lewisville is an archeological site at all (see above). Thus, one could argue that the only site currently published in sufficient detail to evaluate taphonomically and likely to show evidence of use of the remaining extinct fauna is Aubrey. We do not consider the absence of evidence for hunting of 29 genera of extinct fauna at Aubrey to be meaningful.

Over 20 years ago, Donald Grayson made a similar argument and concluded that "the lack of human associations with certain extinct taxa may well be a function of the structure of the record as we happen to know it" (Grayson, 1984:220). Since that time Grayson seems to have firmed up his opinion on the matter and decided that the record is sufficient to address the Overkill question (Grayson, 2001; Grayson and Meltzer, 2002, 2003). But we feel the point is still valid. Given our prior arguments about bias, it should be clear we are not arguing that if we were to dig a number of well-preserved Early Paleoindian campsites from across North America, they would necessarily provide evidence for hunting of all extinct Pleistocene megafauna. It is tempting to invoke such negative evidence, but ultimately it is nothing more than speculation. Instead, we wish to make the point that although 80 years have passed since the Folsom discovery, our archeological sample of Early Paleoindian subsistence still may be inadequate for answering the question of whether

this particular absence of evidence is truly problematic for the Overkill hypothesis. Clearly, we feel that the current sample is adequate for addressing general trends of prey-choice as it relates to body size, but it may not be adequate for addressing the detailed predation histories for most individual taxa that would be required for a true test of the Overkill hypothesis.

# Conclusions

While much ink has been spilled over the issue of dataset construction and as easy as it may be to continue quibbling about the inclusion of various specimens from various sites, the archeological record presents a fairly consistent record of Paleoindian prey choice decisions. From an optimal foraging perspective, there is enormous potential economic and social benefit to hunting the largest prey available. So while mammoth predation may be odd in light of other carnivores and in comparison to the majority of ethnographically documented hunter-gatherer societies, it is a logical and arguably predictable human subsistence activity to occur when large prey is available in sufficient quantities. During the late Pleistocene in North America, and at varying times and places throughout the world, human population densities were undoubtedly extremely low. In such circumstances where large animals are available and encountered frequently enough to meet human subsistence needs, either because humans are few, prey are plentiful or some combination of the two, the option to exercise a specialized predation strategy exists (Waguespack and Surovell, 2003). Further, since specialized hunting economies can provide an efficient means of procuring animal resources, preferential predation of large game was likely far more common in past hunter-gatherer societies than represented in the recent ethnographic record. Importantly, the risks and variance associated with specialized hunting strategies due to lengthy search costs and/or unpredictable, infrequent successes have organizational implications for Paleoindian mobility (e.g., Kelly and Todd, 1988; Anderson and Gillam, 2000; Haynes, 2002a), demography (Anderson, 1995; Surovell, 2000; Marlowe, 2001; Meltzer, 2004), and labor (Waguespack, 2005).

While the case for Overkill is not, from our perspective, definitively settled, our investigation of Paleoindian subsistence provides the following relevant conclusions regarding Pleistocene hunting strategies and its potential impact on Pleistocene prey:

- Specialized large-game predation strategies can provide economic and social benefits to hunter-gatherer populations. While rare ethnographically, when and where ecological conditions provide large-game in sufficient quantities and sociocultural mechanisms are in place to offset costs, a narrow diet-breadth selecting and utilizing prey based on their rank as opposed to encounter rate is the expected strategy.
- 2. Early Paleoindian hunters followed a specialized predation strategy, passing up some opportunities to procure

small prey in favor of larger animal resources. Medium and small sized animals were part of the diet, but were not used as frequently as one would expect based on relative encounter rates. Thus, Early Paleoindian diets included a wide variety of prey species, but large, rare prey remain the most frequently occurring and abundant animals in Early Paleoindian sites and assemblages.

- 3. The Early Paleoindian faunal record is likely biased. The combined effects of taphonomy, site discovery bias, research attention bias, and inconsistent site analysis and recording procedures, render imperfect the archeological record pertaining to Early Paleoindian hunting. Much like the archeological record in other times and regions, or for that matter all times and all places, it is difficult to address the extent of these biases. Our analysis suggests that the cumulative record, compiled from known sites and faunal inventories, presents a consistent pattern of size related hunting preferences that are difficult to dismiss on the basis of chance or deliberate bias.
- 4. The hunting strategy of Early Paleoindian foragers is compatible with the Overkill hypothesis of Pleistocene megafaunal extinction, but due to the lack of secure associations with most extinct genera, support for Overkill can be viewed only as circumstantial. By focusing their predation efforts on the largest available prey, Early Paleoindian foragers also deliberately hunted prey species that were the least able to sustain population growth or maintenance under hunting pressure. Quite simply: (a) Early foraging populations of America hunted really big prey, (b) Really large animals are highly susceptible to the deleterious impacts of predation, and (c) Primarily large animals went extinct. There is currently little evidence attesting to the regular subsistence use of all extinct Pleistocene fauna. Negative evidence is famously difficult to interpret, and as more sites are discovered we are left only to assume that they will either contain more extinct Pleistocene fauna or will contain the long lost plethora of rabbits, rodents, and other small game currently needed to change the archeological patterns identified here.

#### Notes

- 1 We consider the use of plants to be a separate issue. While Paleoindians certainly used plants for subsistence and other purposes, we are concerned solely with the degree to which hunting was selective with respect to prey body size.
- 2 Dennis Stanford conducted additional excavations at the Lewisville site from 1978–1980, but the results of this work have not been published. Microflakes (sand-sized?) were reportedly recovered during this work, possibly supporting the hypothesis that these deposits do represent a late Pleistocene archeological site. This evidence is difficult to evaluate (see also Grayson and Meltzer, 2002), but we do not find it convincing. First, it is unclear if the microflakes are truly artifacts. Also, it is difficult to understand how a group of hunter-gatherers killed, butchered, and cooked dozens of animals involving 21 hearths while leaving behind only one Clovis point and a handful of tiny flakes.

3 This assumes searching in a "fine-grained environment." This is a fundamental assumption of the prey choice model (Stephens and Krebs, 1986) and as such, it is an assumption also made by Byers and Ugan (2005).

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