

REPORTS

CLOVIS HUNTING STRATEGIES, OR HOW TO MAKE OUT ON PLENTIFUL RESOURCES

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Traditionally, hunter-gatherers of the Clovis period have been characterized as specialized hunters of large terrestrial mammals. Recent critiques have attempted to upend this position both empirically and theoretically, alternatively favoring a more generalized foraging economy. In this paper, the distinction between subsistence specialists and generalists is framed in terms of forager selectivity with regards to hunted prey, following a behavioral ecological framework. Faunal data are compiled from 33 Clovis sites and used to test the two alternative diet-breadth hypotheses. The data support the older "Clovis as specialist" model, although some use of small game is apparent. Furthermore, data from modern hunter-gatherers are marshaled to support the theoretical plausibility of specialized large-mammal hunting across North America during the Late Pleistocene.

Tradicionalmente, los cazadores-recolectores del período Clovis han sido caracterizados como cazadores especializados en la fauna mayor. Sin embargo, críticas recientes han tratado de cambiar esta posición por una que favorece la economía de recolección generalizada. Este artículo discute la distinción entre la subsistencia generalizada y la especializada en términos de la selectividad del recolector respecto a las presas de caza, desde un punto de vista ecológico conductual. Se utilizan datos faunísticos compilados de 33 sitios Clovis para investigar las dos hipótesis alternas sobre la variedad dietética. Los datos apoyan el modelo tradicional de "especialistas Clovis" aunque aparentemente estos cazadores utilizaron alguna fauna menor. Además, datos provenientes de cazadores-recolectores modernos refuerzan la veracidad teórica de la cacería de fauna mayor a través de Norte América durante el Pleistoceno Tardío.

From the initial finds of Clovis points in association with Late Pleistocene megafauna in the 1930s, Clovis hunter-gatherers have become synonymous with big-game hunting. In fact, the lifestyle of Clovis peoples has frequently, and often solely, been characterized by their unique propensity to prey upon extremely large-bodied animals. As they hunted not only *big game*, but Pleistocene *mammoth-sized game*, the "Clovis as hunter" concept has established itself, depending on one's perspective, as either a proven archaeological fact or as a pervasive and fallacious stereotype. The extent to which Clovis peoples relied upon large game is not just an issue of subsistence. Their alleged economic emphasis on the hunting of Pleistocene megafauna has played an integral role in interpreting their success as colonizers (Kelly and Todd 1988; Surovell 2000), their technological strategy (Frison 1991; Pearson 2001), their mobility regime (Kelly 1996, 1999; Kelly and Todd 1988), the formation of their archaeological sites (Meltzer 1993), and ultimately, the extinction of their

prey (Alroy 2001; Haynes 2002; Martin 1984; Mosimann and Martin 1975).

Revising the long-standing perspective of Clovis peoples by characterizing them as generalized foragers would mark a radical departure from the last 65 years of research regarding Clovis lifeways. Some would applaud this change as a long-overdue revision of an inherently flawed concept (Bryan 1991; Dillehay 2000:15–18; Gero 1995; Meltzer 1989, 1993; Meltzer and Smith 1986). Others might claim it a premature and hasty rejection of an established model (e.g., Haynes 2002). This paper evaluates the theoretical and archaeological implications of the emergent "Clovis as generalist" and the traditional "Clovis as specialist" model based on published archaeofaunal assemblages and on comparisons with a sample of ethnographic hunter-gatherers.

Clovis as Big-Game Hunters

In the early- to mid-1900s, the classification of Clovis peoples as specialized hunters was initially

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derived from the discovery of numerous sites across North America containing mammoth remains in association with Clovis projectile points (Cotter 1937; Figgins 1933; Haury 1953; Haury et al. 1959; Howard 1935; Sellards 1952). Once this co-occurrence was firmly established, deposits throughout North America and Mexico containing *any* lithic tools in association with Pleistocene megafaunal remains have often, but not always, been attributed to Clovis hunting activities. The frequently questionable relationship between artifacts and faunal remains at many reported proboscidean localities, such as Boaz (Palmer and Stoltman 1975), McLean (Ray 1942), Deuwall-Nuberry (Steele and Carlson 1989), and Lamb Spring (Stanford 1981), has led many researchers to doubt the consistency with which Clovis technology is universally found in association with megafauna. However, it must be acknowledged that nearly all generally accepted Clovis sites containing well-preserved faunal remains include in their assemblages large-bodied species such as mammoth, mastodon, camel, and/or bison (e.g., Frison and Todd 1986; Haury 1953; Haynes 1993; Johnson 1987; Laub et al. 1988; Leonhardy 1966; Lundelius 1972). Unfortunately, lingering doubts regarding the cultural association with numerous megafauna deposits render the quantification and comparison of Clovis kill site faunal assemblages difficult. Despite the many ambiguous associations, the fact that Clovis projectile points are not consistently found in archaeological deposits associated *only* with medium-to-small prey has convinced many archaeologists that Clovis peoples were big-game specialists.

In addition to the faunal record, the interpretation of Clovis peoples as big-game hunters has been inferred from ancillary evidence. First, the age of Clovis is roughly coincident with the extinction of over 35 genera of large mammals, although the exact timing of extinction of numerous taxa remains questionable (Meltzer and Mead 1985). Although only a handful of these taxa have been recovered from Clovis sites in clear association with artifacts (Grayson 1984), some researchers accept this temporal coincidence as evidence that the Pleistocene megafaunal extinction was due to overharvesting by Clovis populations (Alroy 1998, 2001; Martin 1984; Mosimann and Martin 1975). Second, the defining characteristic of Clovis lithic technology is the manufacture of large bifacial projectile points. Actualistic studies

have established that these weapons are capable of wounding/killing large prey such as modern elephants (Frison 1989). The extensive use of exotic lithic raw materials and an emphasis on biface production (Goodyear 1989; Kelly and Todd 1988) have been interpreted as evidence of Clovis peoples' high mobility, a strategy congruent with the pursuit of large game.

Clovis as Generalists

Critiques of Clovis people as big-game hunters have ranged from accusations that Clovis hunting behaviors provide a medium for perpetuating androcentric bias (Gero 1995; Hudecek-Cuffe 1998), to theoretical concerns as to whether big-game hunting could have been an economically feasible strategy for Clovis peoples (Meltzer 1993; Meltzer and Smith 1986). Some authors note little or no evidence for large-game hunting in regions such as the Great Basin (Heizer and Baumhoff 1970) or eastern North America (Meltzer 1988). The majority of critics acknowledge that Clovis peoples killed large game at least occasionally, but argue that the bulk of their diet was comprised of small game and plant resources. The most common points of contention between the two positions are the presumed ubiquity of Clovis point/megafauna associations and the viability of big-game hunting as a reliable subsistence strategy for a colonizing population in Pleistocene North America. It is argued that the archaeological record of Clovis suffers from unsystematic sampling, with an overwhelming bias toward the discovery of large-game kill sites, usually attributed to the greater archaeological visibility of large faunal remains:

Most sites were initially paleontological discoveries—the bones of megafauna are visible more readily than artifacts—and the attention to the bone-bearing deposits led to the artifacts and, thus to a Paleoindian record largely comprised of kill or scavenging sites [Meltzer 1989:477].

This argument implies that if more campsites, or at least “nonkill” sites are discovered, they would likely present evidence attesting to the consistent utilization of a diversity of faunal and floral species (Gero 1995; Johnson 1977; Meltzer 1988, 1993, 1995).

A related issue is the reliability of mammoth/Clovis associations. Studies of elephant populations in Africa have led to some troubling observations concerning archaeological associations between proboscideans and humans (Haynes 1988, 1991, 1995).

Notably, African elephants tend to die near sources of water, particularly during drought years when catastrophic die-offs can occur. As many Clovis sites are located in or near springs, draws and playas, the potential for fortuitous associations between mammoths and artifacts is high. Also, age and sex profiles of catastrophic elephant die-offs at water holes can mimic those of mass kills (Haynes 1988, 1995). The few Clovis kill sites with age and sex data for mammoths show various patterns, as both catastrophic and isolated individual males, females, juveniles and adult kills are represented (Haynes 1991; Saunders 1977, 1980, 1992). Finally, observations of weak and dying elephants during drought years have led to the conclusion that Clovis elephant hunting activities may have been "moribund scavenging" (Fisher 1986), the killing of animals severely weakened by drought or illness, rather than specialized selection of healthy animals.

There is evidence from a number of sites that Clovis hunter-gatherers did include a diverse set of resources in their diet, utilizing plants, small mammals, birds, fish, and reptiles (e.g., Ferring 1995; Graham and Kay 1988; Haynes and Hauray 1982; Johnson 1987; McNett et al. 1977). For example, in addition to the large game found at the Lehner site, the assemblage contained various small game, including jackrabbit, tortoise, and snake (Haynes and Hauray 1982). The Aubrey site also produced a range of small animals, including abundant evidence for the exploitation of tortoises (Ferring 1995). Other sites such as Blackwater Draw (Lundelius 1972) and Lubbock Lake (Johnson 1987) contain small-game faunal assemblages. The presence of small game has led some researchers to conclude that "Paleoindian subsistence data indicate an economic system rooted in general foraging" (Dixon 1999:255), and "Opportunistic hunting appears as a broad-spectrum meat-related subsistence base, utilizing a variety of animal food from a wide array of vertebrates both large and small" (Johnson 1991:229). Although critics of the Clovis-as-specialists model are quick to point out that the presence of megafauna does not necessarily imply selective hunting (Bryan 1991; Dillehay 2000:28-34; Dixon 1999:247-250; Johnson 1991; Meltzer 1988, 1989, 1993; Meltzer and Smith 1986), it seems reasonable to also question whether the presence of small game alone provides an adequate indicator of a generalized foraging strategy.

Exclusively theoretical arguments against Clovis

as big-game specialists are based primarily on ecological models and ethnographically known hunter-gatherer subsistence behaviors. Three general points regarding the likelihood and potential success of a specialized hunting strategy during Clovis times are consistently cited as reasons against a big-game hunting focus. Presented as foraging constraints, the following statements have been used to suggest that big-game specialization is not only unlikely, but theoretically impossible:

1. Big-game hunting specialization is ethnographically rare and can only be expected to occur among foraging peoples in restricted, homogeneous, low biodiversity environments (Hayden 1981; Kornfeld 1988; Lee 1968; Meltzer 1993; Meltzer and Smith 1986).
2. Big-game hunting specialization is a sustainable subsistence strategy only when the targeted prey is large/abundant and has high renewal rates (Cleland 1976; Jochim 1981; Meltzer 1988, 1993).
3. The diverse environments present during Clovis times and occupied by Clovis peoples would have favored a generalized resource acquisition strategy (Bryan 1991; Dixon 1999; Johnson 1977, 1991; Meltzer 1993).

The most straightforward critiques point to the fact that few historically known and extant foraging groups prey exclusively upon big game outside of arctic environments (Johnson 1977; Meltzer 1988, 1993; Meltzer and Smith 1986). From this perspective, large-game specialization is expected to occur only in environmental contexts without other foraging options. This position runs contrary to the predicted use of resources under optimal foraging models. Formal diet-breadth models (Stephens and Krebs 1986) would predict, assuming that large game could successfully be captured and reliably fulfill resource needs, that large-body-sized animals would be extremely high-ranked prey in any environmental context in which they are available (Hawkes et al. 1982; Hill et al. 1987; Kelly 1996; Winterhalder 1986, 1987).

The argument that specialized big-game hunting would not have provided a sustainable or reliable strategy for Clovis peoples assumes that the large game were rare and/or potentially dangerous to their human hunters, rendering them a poor choice for predation (Meltzer 1993). Large-body-sized animals are consistently rare compared to the population densities of smaller co-resident species in any given envi-

ronment (Colinvaux 1978; Peters 1983). However, what is most important from a human subsistence perspective is the ratio of large-body-sized animals to hunters/consumers. Without reliable estimates of Pleistocene megafauna and Clovis population densities, critics argue that large game were too infrequently encountered by Clovis peoples to provide a reliable nutritional source. Certainly smaller mammals would have been more abundant in environments occupied by Clovis peoples, but it is an empirical issue if large-game populations were at densities too low to be consistently preyed upon. Another possibility is that Pleistocene megafauna such as mammoths and mastodons posed such a threat to human life that they would be hunted only when chance favored humans. Although there are ethnographically documented examples of hunters being wounded (occasionally mortally) by elephants, this does not appear to have deterred modern hunter-gatherers from pursuing them (Duffy 1984; Marks 1976).

The widespread distribution of Clovis points throughout North America indicates that Clovis peoples occupied an environmentally diverse territory. Meltzer and Smith (1986) have argued that in such circumstances, a generalized foraging strategy would be favored over specialized hunting. They suggest that large-game hunting is successful only in specific ecological niches and that generalized foraging is inherently more "adaptable" to a diverse range of environments:

Specialists are more efficient and more productive on their own ground and are thus in some sense "stable" so long as the rules of the game are unchanged. Climatic and biotic changes give specialized systems a long-term evolutionary liability . . . [Meltzer and Smith 1986:8].

Clovis big-game hunting is then construed as a nonviable subsistence strategy for a colonizing population, too inflexible to cope with the environmental diversity encountered. They argue that a generalized "take what you can" subsistence approach facilitated the rapid expansion of migrating Clovis populations into new landscapes. Contrary to this position, Kelly and Todd (1988) argue that large-game hunting is one way foragers *can* successfully cross-cut environments.

What means of adapting to local resource stress would be available if Paleoindians could not have depended on another group's knowledge

of the features of a new region because that other group did not exist? Entering an unpopulated continent, early Paleoindians needed a system which allowed them to utilize unoccupied, "unmapped" tracts of land. A lifeway suitable for this task is one that placed primary reliance on faunal rather than plant resources. . . . Unlike much information on plant resources, an understanding of animal behavior, though by no means perfectly transferable, can be generalized and accommodated to new territories [Kelly and Todd 1988:234].

In sum, opponents of the Clovis-as-specialized-big-game-hunter interpretation base their arguments on (1) the presence of small game in archaeological assemblages; (2) negative evidence, which they suggest would attest to the frequent exploitation of small game, and (3) theoretical concerns regarding the plausibility of a specialized hunting strategy. Appeals to negative evidence, although compelling, can only be resolved if the many "missing" Clovis sites with abundant small game are found. The faunal assemblages of known Clovis sites and the conditions that permit specialized hunting strategies can be addressed with the currently available evidence.

Generalized vs. Specialized Hunting

To adequately address the issue of subsistence specialization requires defining the terms "specialist" and "generalist." Although the terms often 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. On the whole, generalists should utilize a broad range of species, while specialists should exploit a more narrow range. More important, however, is the relative degree to which these taxa are exploited when encountered. In this light, the most critical variable is *selectivity*, i.e., the degree to which certain taxa are *not* exploited upon discovery. Ultimately, generalists as defined here tend to use, or at least attempt to utilize, a broad range of taxa when encountered, while specialists tend to ignore many of the species they encounter in favor of pursuing a more limited high-ranked suite.

According to the optimal diet-breadth model, a forager can maximize return rates by focusing on taxa whose return rates exceed the average environmental return rate (Charnov 1976; Stephens and Krebs 1986). Taking low-ranked taxa only serves to lower

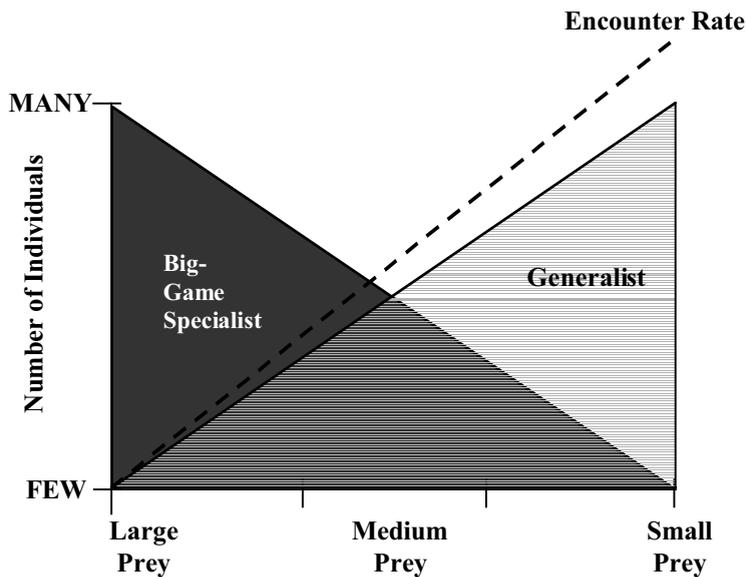


Figure 1. Predicted faunal assemblages for specialist and generalist hunter-gatherers.

overall return rates, an unproductive activity from an evolutionary standpoint. According to the diet-breadth model, specialized subsistence strategies should be present in environments where return rates for highly ranked prey species far exceed those of low-ranked items, and high-ranked taxa are encountered frequently. A generalized strategy would be expected in environments where high-ranked taxa are infrequently encountered, where high-ranked taxa are rarely successfully captured, or where little variability exists in return rates among prey items.

The classic diet-breadth model predicts that a species will either always be taken or always be ignored, the “zero-one rule” (Stephens and Krebs 1986:20–21). However, if environmental and species-specific return rates are allowed to vary, as in a risk-sensitive model (Winterhalder et al. 1999), there would be ample reason to expect that even hunter-gatherers that tend toward a specialist strategy would occasionally take low-ranked prey. For example, if a forager encounters a low-ranked prey item in an unusually favorable circumstance with minimal handling costs, the effective return rate for that animal is enhanced, and it will likely be exploited. Also, if high-ranked items are temporally scarce the average environmental return rate effectively drops, bringing low-ranked prey types into the diet (Haynes 2002). Finally, optimal diet breadth should vary for different segments of a foraging pop-

ulation with respect to age, skill, mobility patterns, and access to hunting technology.

Due to these situational and contextual contingencies, it follows that the number of taxa utilized is not in itself a good measure of subsistence specialization. Therefore, the relative degree to which high- and low-ranked taxa are used is the critical distinction between specialized and generalized strategies. Returning to the issue of selectivity, clear predictions can be made for the archaeological record produced by specialists and generalists. Since generalists will tend to exploit most prey items they encounter, prey frequencies in the archaeological record should be positively correlated with encounter rates (Figure 1). Since encounter rates for prehistoric prey taxa are unknown, a proxy measure must be used. Because encounter rate is primarily a function of prey population density, estimated population densities can provide a reasonable approximation. For specialists, however, there should not be a positive correlation between encounter rates (as estimated by prey population densities) and archaeological abundance. In fact, there would likely be a negative correlation since high-ranked prey are generally large-bodied animals that also tend to have low population densities and therefore low encounter rates. Consequently, if Clovis foragers behaved as specialists, high-ranked, but relatively rare, large game would dominate their faunal assemblages. This does

not, however, necessarily predict that small game would not have been utilized, only that these resources would be hunted less frequently than expected in relation to encounter rate.

Relating prey selectivity to the natural abundance of available prey species creates a methodological framework for examining diet breadth zooarchaeologically. Unlike measures that rely primarily on the relationship between assemblage size, species diversity, and evenness, which have effectively documented temporal trends in the diet breadth of prehistoric foragers (Broughton and Grayson 1993; Grayson and Delpech 1998, 2001; Grayson et al. 2001), the methodology used here is designed to evaluate the selectivity expressed in prey choice decisions among roughly contemporaneous foragers and their faunal assemblages.

Estimating Prey Population Densities

Although seemingly we have substituted one unknown (encounter rate) for another (prehistoric prey population densities), it is argued here that it is possible to roughly estimate *relative* animal population densities for any ecosystem in the past using basic ecological principles and global relationships between prey body size and population density. A global sample of body size and population density data for 36 primarily herbivorous mammalian taxa was taken from *Walker's Mammals of the World*, 6th edition (Nowak 1999). The sample includes forest, desert, and grassland species, which range in body size from 30 g (Common Dormouse) to 5,000 kg (African Elephant). The data demonstrate a clear relationship between body size and population density (Table 1, Figure 2). Peters (1983:164–183) reports similar relationships for a broader array of taxa. This correlation results from the simple fact that for animals with similar metabolic processes (e.g., homeotherms), existing at the same trophic level (e.g., herbivores), equal amounts of biomass can be consumed by many individuals of a small body size or fewer large-bodied individuals. There are many intervening variables that serve to muddle this relationship. For example, carnivores exist at lower population densities than herbivores of comparable body size, due to inevitable energy losses that occur at higher trophic levels (Colinvaux 1978).

Although precise quantitative estimates of the population densities of late Pleistocene mammals are not possible, it is reasonable to assume that body

size can serve as an inverse proxy measure of population density and therefore encounter rates. For example, in relation to Clovis, it is abundantly clear that proboscideans would be expected to exist at far lower densities than small-game species, such as rabbits and rodents, and this general relationship should exist independent of environment (e.g., it should be equally applicable for the Great Basin, Great Plains, and Eastern Woodlands). Foraging encounter rates can then be expected to vary consistently with regard to prey size based on population densities. Thus, the more specialized foragers are, the more likely their prey assemblages will deviate from the natural abundance of each species hunted.

Estimating Clovis Diet Breadth

As discussed above, assuming that a highly selective subsistence strategy favoring the use of large terrestrial game was the basis of Clovis subsistence economy, it is predicted that either a negative correlation or no correlation will exist between archaeological species abundance and natural abundance based on body size. If Clovis hunter-gatherers were generalists, the archaeological abundance of prey taxa should be positively correlated with natural abundance. Although some have argued that the record is unduly biased by an overrepresentation of megafauna kill sites, the archaeological record is the only direct source of information regarding Clovis hunting behaviors.

To this end, the faunal assemblages of 33 archaeological sites were tabulated by species presence/absence and when possible minimum number of individuals (MNI) (Figure 3, Table 2). Sites were included in the sample if they contained Clovis diagnostics, or in a few cases, lack fluted points, but show evidence of human interaction with extinct fauna. Due to inconsistencies in the literature with regards to the quantification of fauna, reliable MNI values for all taxa present could only be obtained for 15 site assemblages, and even the data from some of these sites are problematic. For example, MNIs are sometimes reported for some taxa, while only presence is noted for others. In these cases, our MNIs are based on the number of species present within a given taxonomic grouping. Faunal data for the remaining sites were recorded simply as present/absent for each taxon. For simplicity, certain species were aggregated into general taxonomic groupings (e.g., mammoth/mastodon, lagomorphs, rodents, turtles/

Table 1. Animal Body Mass and Population Density.

Common Name	Scientific Name	Page #	Mass (kg)	Pop. Density (animals/km ²)
<i>Order Rodentia</i>				
Common Dormouse	Genus <i>Muscardinus</i>	1628–1629	.03	180
Genus <i>Abrothrix</i>	Genus <i>Abrothrix</i>	1390–1391	.04	600
African Bush Squirrels	Genus <i>Paraxerus</i>	1279–1281	.05	350
Northern Pygmy Gerbils	Genus <i>Gerbillus</i>	1446–1448	.07	375
Coney Rat	Genus <i>Reithrodon</i>	1409–1410	.09	69
Red Squirrels	Genus <i>Tamiasciurus</i>	1271–1275	.23	475
Plains Visacha	<i>Lagostomus maximus</i>	1659–1660	5.63	475
North American Porcupine	<i>Erethizon dorsatum</i>	1656–1659	5.25	7.5
Capybara	<i>Hydrochaeris hydrochaeris</i>	1672–1674	53	9.8
<i>Order Lagomorpha</i>				
Cottontail Rabbits	Genus <i>Sylvilagus</i>	1726–1729	1.15	963.3
Bushman Rabbit	<i>Bunolagus monticularis</i>	1722–1723	1.25	115.0
Jack Rabbits (Hares)	Genus <i>Lepus</i>	1733–1738	4.18	93.3
<i>Order Artiodactyla</i>				
Dik-diks	Genus <i>Madoqua</i>	1191–1192	5	24
Water Chevrotain	<i>Hyemoschus aquaticus</i>	1081–1082	11	17.9
Javelina	<i>Pecari tajacu</i>	1065–1066	22	5
Gazelles	Genus <i>Gazella</i>	1199–1202	48.5	16
Vicuña	<i>Vicugna vicugna</i>	1077–1078	50	50
Impala	<i>Aepyceros melampus</i>	1194–1196	52.5	2.5
Pronghorn	<i>Antilocapra americana</i>	1132–1134	53	16.4
Reedbuck	Genus <i>Redunca</i>	1170–1172	57	17.5
Blue Sheep	Genus <i>Pseudois</i>	1228–1229	57.5	9.9
Axis Deer	Genus <i>Axis</i>	1100–1102	68.5	23
Ibex	<i>Capra Ibex</i>	1222–1224	92.5	3.8
White-Tailed Deer	<i>Odocoileus virginianus</i>	1114–1118	100	37.5
Wart Hogs	Genus <i>Phacochoerus</i>	1060–1062	100	10
Gemsbok	Genus <i>Oryx</i>	1175–1178	155	1.4
Hartebeest	<i>Alcelaphus buselaphus</i>	1181–1183	162.5	1.4
Wapiti	<i>Cervus elaphus</i>	1110–1113	245	5
Greater Kudu	<i>Tragelaphus strepsiceros</i>	1137–1140	250	2.6
Moose	<i>Alces alces</i>	1126–1128	512.5	0.6
African Buffalo	<i>Syncerus caffer</i>	1151–1153	600	9.1
<i>Order Perissodactyla</i>				
Burchell's Zebra	<i>Equus burchelli</i>	1021–1024	280	10
Black Rhinoceros	<i>Diceros bicornis</i>	1034–1037	1100	2.9
<i>Order Proboscidea</i>				
Indian Elephant	<i>Elephas maximus</i>	994–998	4,060	0.6
African Elephant	<i>Loxodonta africana</i>	998–1004	5,000	1.3

Note: Data from Walker's *Mammals of the World*, 6th ed. (Nowak 1999).

tortoises, and carnivores; see Table 2 for all groupings). To maximize the number of sites and by using an extremely lenient measure of cultural association—simple presence in the assemblage—the quantity of *all* taxa in each assemblage was tabulated. Although the inclusion of both the presence and MNI data of species with undoubtedly questionable cultural association skews the distribution of taxa, no

preference was given to the recording of large- or small-body-sized animals. In fact, by counting the presence of numerous small species that are less likely to have been utilized as food sources (e.g., amphibians, rodents, and insectivores), the sample is probably preferentially skewed in favor of small game.

The presence/absence of taxa across all 33 sites

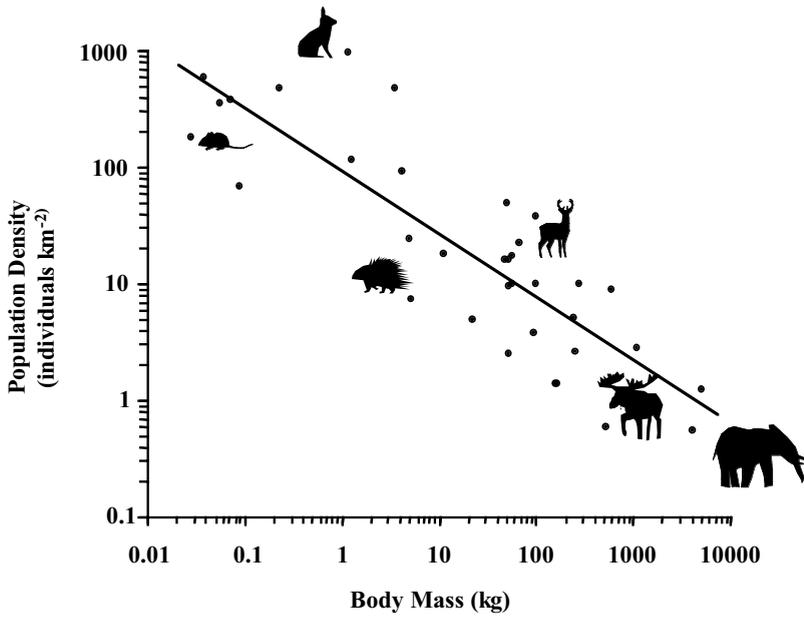


Figure 2. Animal population density versus body mass. Both axes are log-scaled. Regression line: $\log_{10}(\text{Population Density}) = 1.962 + -.536 \times \log_{10}(\text{Body Mass})$ (data from Nowak 1999).

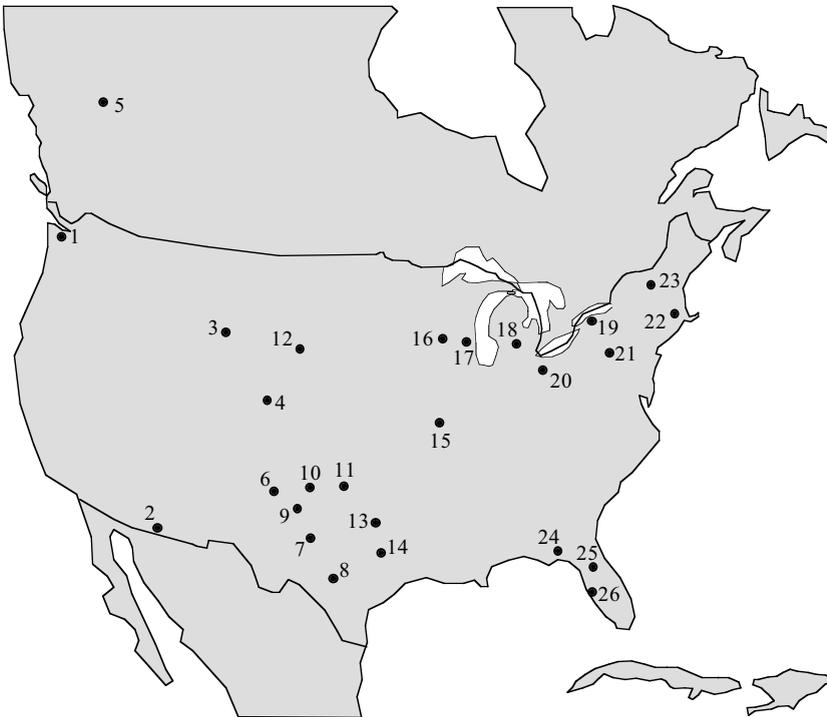


Figure 3. Map of sites included in this study. (1) Mannis; (2) Murray Springs, Lehner, Naco, Escapule, Leikem; (3) Colby; (4) Dent; (5) Charlie Lake Cave; (6) Blackwater Draw; (7) McLean; (8) Kincaid; (9) Lubbock Lake; (10) Miami; (11) Domebo; (12) Lange Ferguson; (13) Aubrey, Lewisville; (14) Gault; (15) Kimmswick; (16) Boaz; (17) Schaefer, Hebior; (18) Holcombe Beach; (19) Hiscock; (20) Martins Creek; (21) Shawnee-Minnisink; (22) Bull Brook; (23) Whipple; (24) Wacissa River; (25) Guest; (26) Little Salt Spring.

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Table 2. Summary of Clovis Site Faunal Data.

Site (State or Province)	Proboscidean	Bison	Equid	Camelid	Tapir	Peccary	Other Ungulate	Sloth	Glyptodont	Bear	Other Carnivore	Lagomorphs	Armadillo	Muskrat	Other Rodent	Insectivore	Turtle/Tortoise	Snake	Alligator	Fish	Bird	Amphibian	References	
Aubrey (TX)	✓	16	15	15		3	2	✓		4	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	Fearing 1995	
Blackwater Draw (NM)	✓	15	✓																				Lundelius 1972	
Charlie Lake Cave (BC)																							Driver 1995; Fladmark et al. 1988	
Boaz Mastodon (WI)	1																						Palmer and Stollman 1975	
Bull Brook (MA)	7	3	1	1			✓				✓												Byers 1955; Spiess et al. 1985	
Colby (WY)	13						1					1											Frison and Todd 1986; Walker and Frison 1980	
Dent (CO)	1	1									5												Frison 1980	
Domebo (OK)	1										1												Figginis 1933; Brunswig and Fisher 1993	
Escapule (AZ)	1		✓																				Force 1997; Leonhardt 1966; Leonhardt and Anderson 1966; Slaughter 1966	
Gault (TX)	✓	✓	✓																				Hemmings and Haynes 1969; Saunders 2000b	
Guest (FL)	2	1																					Collins 1999	
Hebior (WI) †	1						1																Hoffman 1983; Rayl 1974	
Hiscock (NY)	8						2				✓												Overstreet 1946; Overstreet and Stafrford 1997; Overstreet et al. 1995	
Holcombe Beach (MI)	✓						✓																Laub et al. 1988; Steadman 1988; Tankersley et al. 1998	
Kimmswick (MO)	✓					✓	✓																Overstreet 1996; Overstreet and Stafrford 1997; Overstreet et al. 1995	
Kincaid Shelter (TX)	✓		✓				✓																Laub et al. 1988; Steadman 1988; Tankersley et al. 1998	
Lange-Ferguson (SD)	2	✓					✓																Cleland 1965; Fritting et al. 1966; Spiess et al. 1985	
Lehner (AZ)	13	4	2	4	1		✓																Overstreet 1996; Overstreet and Stafrford 1997; Overstreet et al. 1995	
Leikem (AZ)	2																						Overstreet 1996; Overstreet and Stafrford 1997; Overstreet et al. 1995	
Lewisville (TX)	2	2	8	2		1	9	1	1	1	9	13	1										Overstreet 1996; Overstreet and Stafrford 1997; Overstreet et al. 1995	
Little Salt Spring (FL) †	1	1						1															Overstreet 1996; Overstreet and Stafrford 1997; Overstreet et al. 1995	
Lubbock Lake (TX)	3	1	2	2		1	1																Overstreet 1996; Overstreet and Stafrford 1997; Overstreet et al. 1995	
Mantis (WA) †	1	✓					✓																Overstreet 1996; Overstreet and Stafrford 1997; Overstreet et al. 1995	
Martins Creek (OH) †	1						✓																Overstreet 1996; Overstreet and Stafrford 1997; Overstreet et al. 1995	
McLean (TX)	1																						Overstreet 1996; Overstreet and Stafrford 1997; Overstreet et al. 1995	
Miami (TX)	5																						Overstreet 1996; Overstreet and Stafrford 1997; Overstreet et al. 1995	
Murray Springs (AZ)	4	11	3	2		1																	Overstreet 1996; Overstreet and Stafrford 1997; Overstreet et al. 1995	
Naco (AZ)	1	✓																					Overstreet 1996; Overstreet and Stafrford 1997; Overstreet et al. 1995	
Schaefer (WI) †	1																						Overstreet 1996; Overstreet and Stafrford 1997; Overstreet et al. 1995	
Shawnee-Minnisink (PN)		2																					Overstreet 1996; Overstreet and Stafrford 1997; Overstreet et al. 1995	
Sheaman (WY)		1		2																			Overstreet 1996; Overstreet and Stafrford 1997; Overstreet et al. 1995	
Wacissa River (FL) *																							Overstreet 1996; Overstreet and Stafrford 1997; Overstreet et al. 1995	
Whipple (NH)																							Overstreet 1996; Overstreet and Stafrford 1997; Overstreet et al. 1995	
TOTAL SITES	26	17	9	7	1	5	15	3	1	3	7	8	3	9	13	4	10	6	2	8	10	6		
TOTAL MNI	91	48	34	28	1	7	25	3	1	5	25	22	3	10	77	6	67	26	2	14	30	19		

Notes: ✓ = Taxa present; † Sites lacking fluted points; * Site contains a projectile point of uncertain typology.

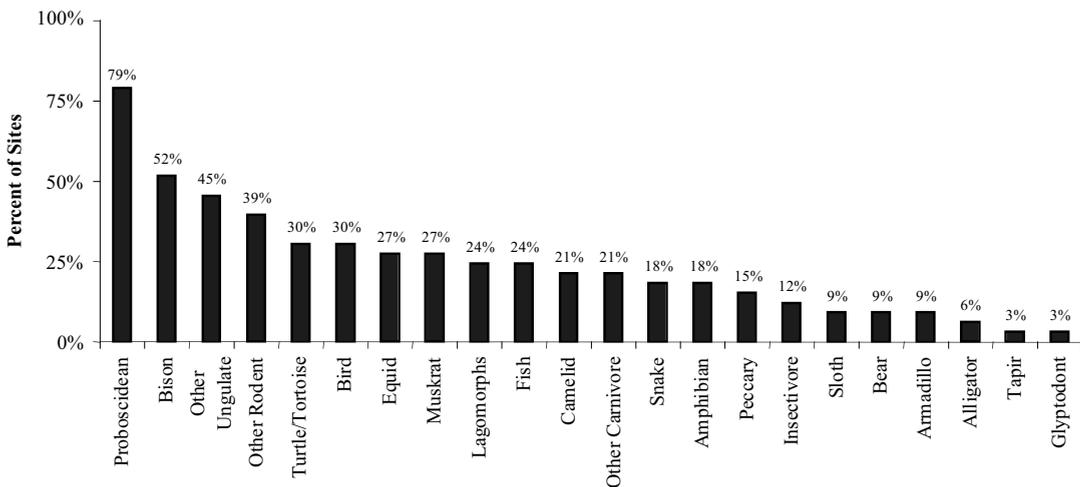


Figure 4. Percentage of Clovis sites (n = 33) containing each taxonomic grouping.

(Figure 4) shows that mammoth and mastodon are the most frequently occurring species, present in 79 percent of all assemblages. Bison occur in 52 percent of bone-bearing sites, followed by other ungulates (45 percent), other rodents, turtle/tortoise and birds (30 percent), and equids, muskrats, and lagomorphs (27 percent). Rare species include sloth, glyptodont, tapir, and alligator. Either mammoth/mastodon or bison are found in 88 percent of assemblages, and 42 percent of sites contain both. The relatively high frequency of rodents and carnivores is likely artificial since little clear evidence of their use as a food source has been documented for Clovis peoples.

Based on presence/absence data alone, two general conclusions can be drawn. First, the most consistent component of Clovis faunal assemblages is the presence of mammoth/mastodon (Figure 4). Second, when small-game species are present in an assemblage, which they are in most but not all cases, a broad diversity of species is present (Table 2, Figure 4). Alongside typical mammalian faunas, birds, fish, and reptiles are not uncommon constituents of Clovis sites. These findings are mimicked by MNI data (Figure 5). Mammoths and mastodon are most common, represented by at least 91 individuals. Interestingly, "other rodents" (MNI = 77) and turtles and tortoises (MNI = 67) are the next most common taxa, followed by bison, equids, birds, and camelids, respectively.

In order to analyze the data with regard to prey specialization and diet breadth, categories of taxa were further aggregated by general body-size classes. Excluding all non-mammalian species (birds, fish,

amphibians, and reptiles) and carnivores, the following categories ranked from largest to smallest were created: Proboscideans (Size Class 1), Bison/Equid/Camelid (Size Class 2), Other ungulates, sloths, and glyptodonts (Size Class 3), Lagomorphs and Armadillos (Size Class 4), and Rodents and Insectivores (Size Class 5) (see Table 3). Both the number of sites in which species of each of these five categories are represented and total MNI values were tabulated. In order to include the presence/absence data for analysis, the presence of a species was assigned an arbitrary MNI value of one. To standardize for varying numbers of taxa in each category, the total MNI for each taxonomic grouping was divided by the total number of species included in each size class (Table 3).

On average, the largest species occur in the greatest numbers (Figure 6a, Table 3). Three species of proboscideans, the largest size group, are represented by an average of 30.3 individuals each. This is followed by an average of 12.2 individuals for 9 species of bison, equids, and camelids. Four species of lagomorphs and armadillos are represented by an average of 6.3 individuals. Other ungulates, sloths, and glyptodonts are represented by 4.1 individuals per species. Least abundant are the remaining size classes of rodents and insectivores with 3.1 individuals per species. The relationship between body size class and MNI value shows a strong, statistically significant negative correlation (*Spearman's* $\rho = -.9$; two-tailed significance, $p = .037$) providing strong support for the Clovis-as-large-game-specialist model.

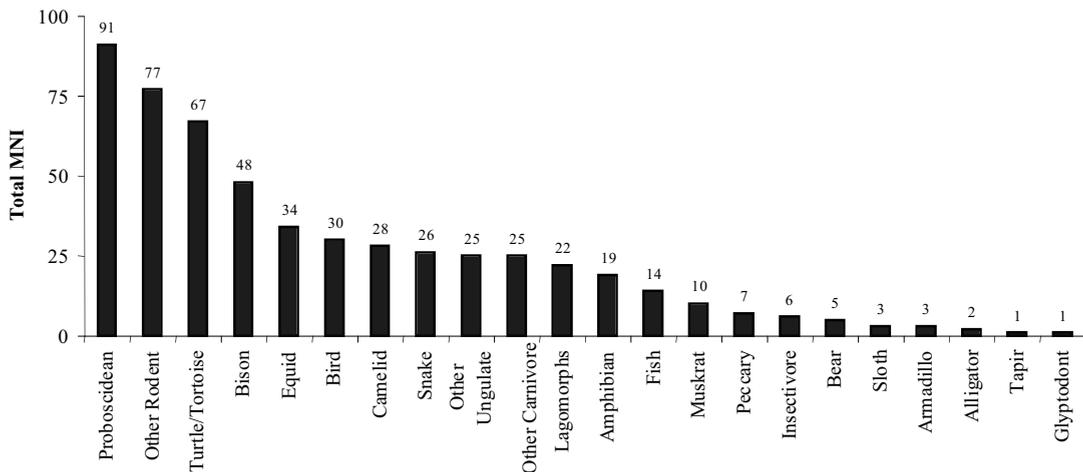


Figure 5. Total MNI by taxonomic group for 33 Clovis sites.

To investigate the relationship between body size and taxa presence and absence, a slightly different approach was taken to avoid problems of autocorrelation. For each size class, the expected number of sites in which each group should be present was calculated, assuming a generalist “take what you encounter” strategy (Table 3). The expected value for each size class was standardized to the most taxonomically abundant group (rodents and insectivores, $n = 30$ species), as groups with more taxa should have more opportunities to enter archaeological sites. The expected value for rodents and insectivores was set to 33 sites (the total sample), and the expected values for the remaining taxa were set proportionately. For example, for proboscideans, consisting of three species, or one-tenth the diversity of rodents and insectivores, the expected value is 3.3 sites. Since this method only takes into account numbers of species and not numbers of individuals in each taxonomic grouping, it is biased toward smaller, more abundant species. Comparison of the observed and expected number of sites shows that the largest taxa are overrepresented in Clovis sites (Table 3, Figure 6b). Proboscideans appear in 22.7 more sites than expected, bison, equids, and camelids appear in 9.1 more sites than expected, and other ungulates, sloths, and glyptodonts are present in 8.1 more sites than expected. Lagomorphs and armadillos are present in 4.6 more sites than expected, while rodents and insectivores are present in 19 fewer sites than expected. Using a Spearman’s rho correlation ($\rho = -1.0$; $p = 0$), this pattern is statistically highly significant. Therefore, the pres-

ence/absence data also provide strong support for the Clovis-as-specialist model since a strong negative correlation between body size and presence in Clovis assemblages is suggested, and the largest, least diverse, and least abundant taxa are the most consistent members of Clovis faunal assemblages.

One of the nonmammalian small-game categories not examined in relation to natural abundance is turtles and tortoises, for which there is clear evidence of Clovis utilization (e.g., Lubbock Lake, Aubrey, and Lehner). In our sample, a minimum of 67 individual turtles or tortoises is represented. In other archaeological contexts high frequencies of chelonians have been used as evidence of harvesting behaviors of human groups with low population densities (Stiner et al. 2000). Since turtles and tortoises are easily captured with low handling costs, they are likely to be high-ranked resources, despite relatively small body size. Interestingly, turtles and tortoises share many life history traits with proboscideans. Both taxa are characterized by low reproductive rates resulting from delayed reproductive maturation (Haynes 1991; Shine and Iverson 1995), making both chelonians and proboscideans especially susceptible to overharvesting and extinction (Mithen 1993; Stiner et al. 2000). While elephants postpone reproduction by investing energy early in life into growth to reach a large-body size, turtles and tortoises do the same by directing energy into the growth of bony shells. These are essentially predation avoidance mechanisms since both adult turtles, tortoises, and elephants have few natural predators. If an invasive

Table 3. Clovis Assemblage Data Summarized by Body Size.

	Proboscideans	Bison, equids, and camelids	Other ungulates, sloths, and glyptodonts	Lagomorphs and armadillos	Rodents and insectivores
Size Class	1	2	3	4	5
N Taxa	3	9	9	4	30
Total MNI	91	110	37	25	93
<i>MNI per taxon</i>	30.3	12.2	4.1	6.3	3.1
Expected <i>n</i> sites [†]	3.3	9.9	9.9	4.4	33
Actual <i>n</i> sites	26	19	18	9	14
Act. – Exp. <i>n</i> sites	22.7	9.1	8.1	4.6	-19

Note: [†]See text for explanation of calculation.

species, in this case prehistoric humans in Pleistocene North America, is expected to move into a niche with minimal interspecific competition, then the prey duo of elephants and tortoises is not unexpected.

Is Big-Game Hunting Possible?

The Clovis faunal record certainly implies the extensive and selective use of large-bodied prey. Although potentially the result of biased archaeological visibility and recovery, the distribution of Clovis faunal assemblages appears more congruent with a specialized hunting strategy. Some critics, however, claim that specialized hunting was simply not a viable subsistence strategy for Clovis peoples. As previously discussed, theoretical arguments launched against Clovis-as-specialists frequently point to the fact that ethnographically known examples of foragers with specialized hunting economies are geographically limited to arctic and grassland environments (Meltzer 1988, 1993; Meltzer and Smith 1986).

The ethnographic record does evidence that a strong relationship exists between the proportion of subsistence resources derived from hunted game and environmental context (Keeley 1988; Kelly 1995; Murdock 1981). With few exceptions, hunter-gatherer groups who derive more than 50 percent of their food resources from hunting generally occupy environments with low mean effective temperatures (i.e., arctic ecosystems), in areas in which the bulk of primary biomass cannot be consumed by humans but is accessible to herbivores (i.e., grasslands and tundra), and less commonly, in tropical ecosystems where foragers trade meat for plant products with local, nonforaging, peoples (reviewed in Kelly 1995:66–73). But these patterns are drawn from modern and historically known hunting and gathering groups, and do not necessarily reflect the range of possible subsistence behaviors of the past. Since

most recent foraging populations occupy primarily “marginal” environments and must coexist with neighboring nonforaging societies, their subsistence options are perhaps significantly more limited than the constraints on hunter-gatherers of the past. Also, hunter-gatherers documented in the modern era occupy ecosystems that have been inhabited by humans for thousands of years and they likely exist at relatively high population densities (as compared to Clovis). For Clovis populations living in late Pleistocene North America, land-use options would have had few limits since population densities would have been extremely low. In such a situation of relatively few people and abundant big-game availability, hunting specialization may have been possible in environments where this strategy does not and could not exist today. In most contemporary environments, large-game specialization is simply not possible because there are too many people and/or too few large animals, a situation that has existed for perhaps thousands of years.

If big-game hunting specialization is a viable strategy in any environment as long as human population densities are low relative to available game, then there is little reason to presume that Clovis peoples could not have been specialists simply because they occupied an ecologically diverse environment. To examine the relationship between reliance on hunting, environment, and population density, a sample of 92 foraging groups was examined. Populations of hunter-gatherers that derive all of their subsistence resources from foraging were collected from the *Atlas of World Cultures* (Murdock 1981). The percent of the diet comprised of plant/small terrestrial fauna and larger game resources was tallied. In addition, the environment occupied and population density for each group was recorded (data from Kelly 1995: Table 6–4).

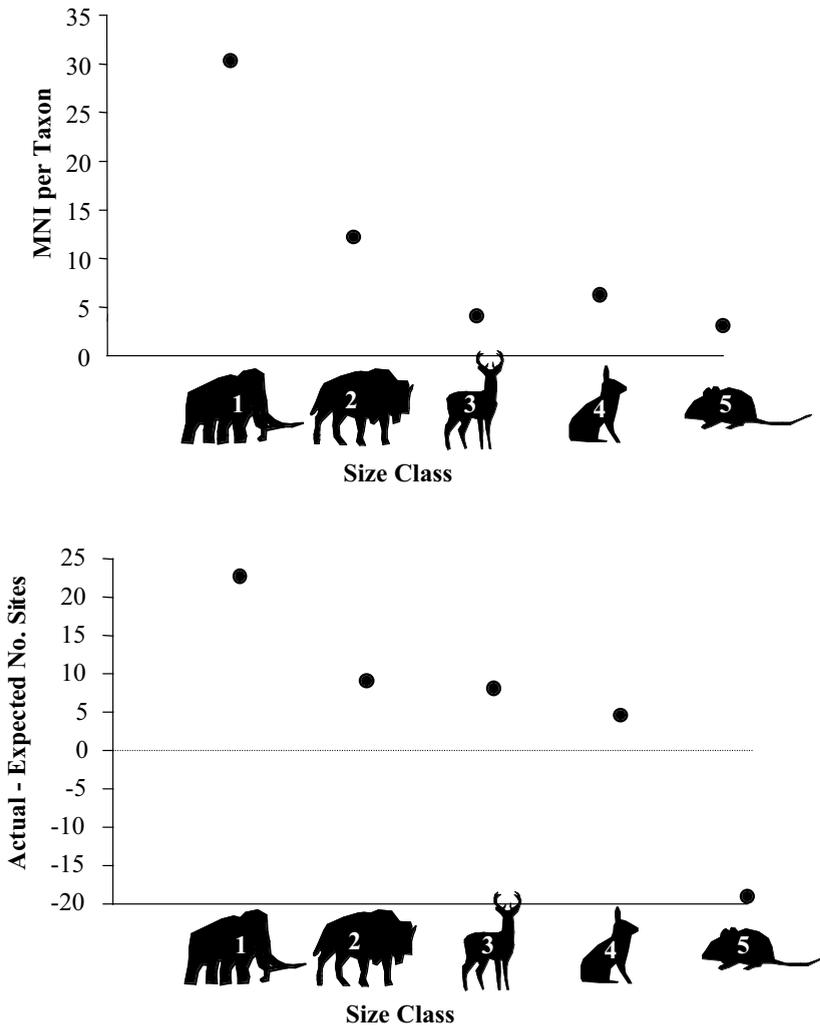


Figure 6. (a) (top) Prey size class versus total MNI per species, calculated as the sum of MNIs for all taxa in each size-class grouping, divided by the total number of species in that group (two-tailed Spearman's $\rho = -.9$; $p = .037$); (b) (bottom) Prey-size class vs. the actual minus the expected number of sites per taxonomic grouping, assuming a generalist subsistence strategy (two-tailed Spearman's $\rho = -1$; $p = 0$).

Plots of log population density (people per 100 km²) for the sampled hunter-gatherer groups and their reliance on both plants/small fauna and large game are presented in Figure 7a and 7b. Not surprisingly, dependence on plants and small fauna increases with population density and is statistically significant (Spearman's $\rho = .397$, $p < .001$). The average dependence on larger game decreases with greater population density for all environments (Spearman's $\rho = -.68$, $p < .001$), the only exceptions being the Mbuti and groups of the North American Great Plains who both tend to depend more on hunt-

ing than would be predicted by their population densities. Hunters of the Great Plains are an interesting exception because, as noted by Meltzer (1993), they were armed with rifles and had the use of the horse. As predicted by the diet-breadth model, the introduction of the horse and gun should have caused a contraction of diet breadth because greater mobility would have increased encounter rates with large mammals, notably bison, and rifles would have decreased handling costs. A similar effect was observed with the introduction of the snowmobile to the Cree (Winterhalder 1981).

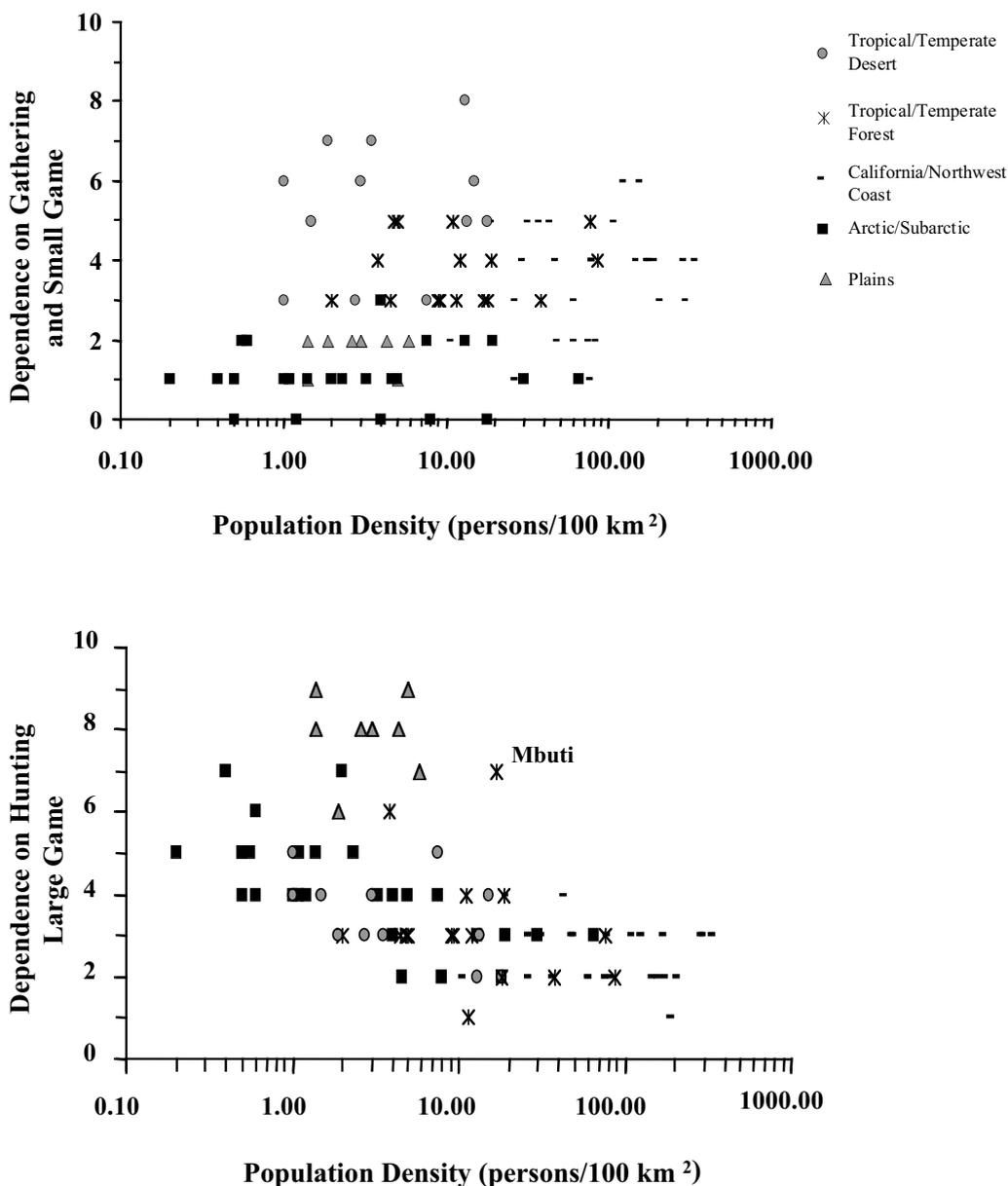


Figure 7. (a) (top) Proportion of plants in the diet vs. population density for a global sample of hunter-gatherers ($n = 92$, Spearman's $\rho = .397, p < .001$); (b) (bottom) proportion of large game in the diet vs. population density for the same groups (Spearman's $\rho = -.68, p < .001$).

Dividing the sample into groups who derive more than 46 percent of their subsistence by hunting from those who do not (Figure 8), a two-tailed t -test establishes significant differences between their mean population densities ($p < .001$). The mean population density value for groups with greater than 46 percent reliance on hunting is .25 people per 100 km², and for less than 46 percent it is 37.5 people per 100

km². These findings cannot directly implicate Clovis peoples as big-game hunters, but it does establish that hunting specialization can and frequently does occur at low population densities.

A problem of equifinality arises when these results are compared with the findings of others who have correlated dietary hunting dependence with environmental parameters (Binford 2001; Keeley 1988, 1995;

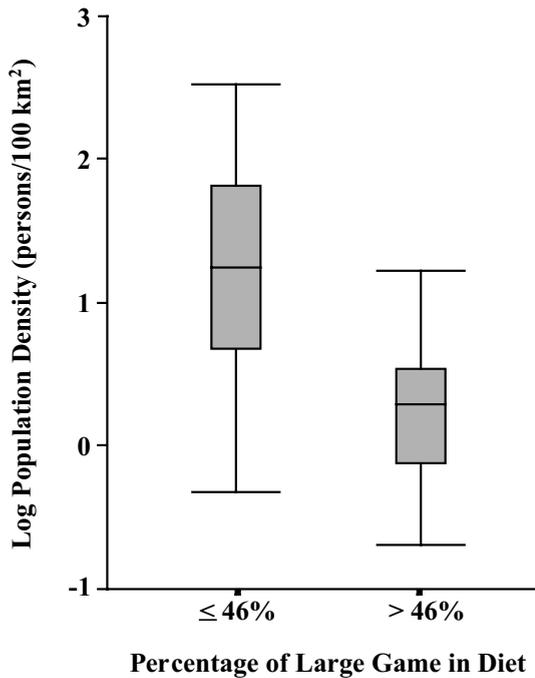


Figure 8. Percentage of large game in the diet vs. population density for a worldwide sample of hunter-gatherers ($n = 92$, two-tailed t -test, $p < .001$). Note Y-axis is the \log_{10} of population density. Data from Kelly (1995: Table 6-4) and Murdock (1981).

Kelly 1995; Meltzer 1993). In other words, three independent variables are collinear (population density, environment, and subsistence), resulting in a sticky problem of establishing causality. An argument could be made that environment is the proximate cause of subsistence practices and population density. We argue above with respect to the diet-breadth model that large-game specialization should result from relatively high encounter rates with large game. Therefore, subsistence should ultimately be a product of the density of prey coupled with the density of human hunters, independent of environmental parameters. Although prey densities will ultimately be controlled by environmental productivity, human population densities can be modified by adjusting "territory" or range size. Absolute numbers of humans, however, should be limited by food supplies, which is ultimately limited by subsistence practices. That is, hunter-gatherers who depend entirely on hunting will exist at far lower densities than those who adopt a more "vegetarian" lifestyle since hunters only exploit a small fraction of the available edible biomass in an ecosystem.

We argue that large-game specialization is only seen in recent times in areas where there are few other subsistence options. The inability to switch subsistence strategies in the arctic, for example, has resulted in one of the very few areas where humans exist at extremely low population densities because they were forced into a very narrow subsistence niche, that of top carnivore. In other biomes where large animals were readily available, humans chose to be large-game specialists early on, but due to increasing numbers of people and decreasing numbers of prey, they moved into a more generalized subsistence strategy, eventually allowing for higher human population densities. Furthermore, although the environments where large-game specialization occurs in recent times are characterized by relatively low primary production, a vast majority of the primary biomass present is accessible to large ungulates (due to the paucity of woody vegetation), allowing these animals to attain and maintain high population densities. These factors, we suggest, have shaped the modern ethnographic record of large-game hunting. Therefore, regardless of the diverse environments they occupied, as long as Clovis peoples maintained low population densities and large game was available and regularly encountered, a hunting-based subsistence economy seems highly plausible.

Conclusions

Although there has been much debate regarding Clovis diet breadth and subsistence strategy, few attempts have been made to quantitatively analyze Clovis faunal assemblages. The zooarchaeological data collected for the current analysis are admittedly imperfect, but provides one important source of evidence for the examination of Clovis prey choice. Many potential biases exist in the dataset. Differential recovery and preservation of animal remains that bias the record toward large animals are possible influences on the Clovis record that currently remain difficult to assess. Nonetheless, for the purposes of this study, while acknowledging the existence of these nonrandom factors influencing the dataset, we are not willing to assume that this bias is so extensive as to reverse our findings.

We have framed the contrast between hunting specialization and generalization on the degree of selectivity expressed in prey choice in a manner consistent with optimal foraging theory. Selectivity has been defined as the relative degree to which certain

taxa are not exploited upon encounter. Specialists tend to bypass numerous potential prey in favor of higher-ranked resources. The quintessential generalist, on the other hand, would exploit all or nearly all prey encountered. Despite their presentation here as alternative strategies, they are intended only to describe two possible extremes of a continuum. Based on the analysis of 33 faunal assemblages it has been argued that Clovis hunting behaviors appear more closely aligned with a specialized, rather than generalized, strategy.

This conclusion is drawn from the relative abundances of a range of taxa represented in Clovis sites. Unlike the expectations for a generalist strategy, the taxa most frequently occurring in sites and occurring in the greatest numbers are those that would have been infrequently encountered by Clovis hunter-gatherers. This does not mean that Clovis existed by mammoth alone. Nor does it imply that Clovis peoples only hunted mammoth, bison, and other large animals. There is clear evidence that they did exploit small mammals and reptiles on occasion. However, based on estimated encounter rates, Clovis hunter-gatherers often ignored opportunities to harvest smaller game species, likely in favor of obtaining a higher-ranked resource. Turtles and tortoises are one clear example of small game taxa that Clovis foragers may have regularly taken upon encounter since handling costs are minimal for such slow-footed prey. Rabbits, rodents, birds, fish, and other small game taxa, however, are not so easily taken since they have evolved sophisticated defense mechanisms to elude numerous predators, and therefore have relatively high handling costs for a relatively small payoff. Therefore, it should come as no surprise that these taxa seem to have only played a minor role in Clovis subsistence. Although we acknowledge the potential for hundreds of missing Clovis sites with thousands of individuals of small-game species, until these sites are discovered, excavated, and published, the Clovis faunal record points to a clear conclusion—large-game specialization.

There is not only empirical evidence that Clovis peoples were specialized predators of large game, but this characterization also receives some theoretical support. Since large-game specialization is only possible when people are few and large animals are many, or at least regularly encountered (to provide sufficient caloric yields), human population density is a critical variable. Data from modern hunter-gath-

ers show a clear increase in hunting of large animals as human population densities decline. Since Clovis represents the colonization of an uninhabited landscape or slightly postdates that event, early Paleoindian population densities were undoubtedly low. Low population densities coupled with frequent residential mobility over large distances provide a context where large-game specialization is not only possible but also likely. Following Kelly and Todd (1988), subsistence emphasizing large-game hunting is not restricted to any particular environment (except those lacking large game), and is perhaps the ultimate strategy for maneuvering among diverse environments.

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