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Journal of Archaeological Science 32 (2005) 1624–1640

Journal of Archaeological SCIENCE

http://www.elsevier.com/locate/jas

Should we expect large game specialization in the late Pleistocene? An optimal foraging perspective on early Paleoindian prey choice

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Received 29 January 2005; received in revised form 26 April 2005; accepted 4 May 2005

Abstract

Several recent studies employ foraging theory to model early Paleoindians as big game specialists who focused on hunting large bodied, high-return animals such as mammoths. In this paper, we evaluate the specialist model by identifying the range of handling times and encounter rates within which mammoth (*Mammuthus columbi*) specialization would occur. We continue by using allometric relationships between body size and population density in mammals to estimate encounter rates for mammoth and other North American species. Combining these two pieces of information allows for the construction of an optimal diet curve representative of late Pleistocene prey choice, given the inclusion of mammoth. Our results seriously question the model of early Paleoindians as megafaunal specialists and suggest that foragers should have pursued a wide array of taxa including not only mammoth, but the full range of ungulates and some smaller game as well. These results accord well with empirical data on prey choice from late Pleistocene archaeological contexts from across North America.

Keywords: Mammoth hunting; Prey model; Optimal foraging theory; Early Paleoindian; Clovis; Encounter rates

1. Introduction

Several recent papers appeal to foraging theory in support of the view that early Paleoindians were big game specialists whose subsistence focused on hunting large bodied, high-return animals such as mammoths (*Mammuthus columbi*), mastodonts (*Mammut americanum*) and bison (*Bison antiquus*) (e.g. Refs. [44,45,106]). The importance of fully understanding the place of proboscideans and other large game in the late Pleistocene diet cannot be overstated. If mammoths and other Pleistocene megafauna played a dominant role in shaping early Paleoindian prey choice, then subsistence patterns focused on these extinct animals may have important implications for questions ranging from late Pleistocene extinctions to early Paleoindian mobility and the pace and tempo of the colonization of the New World [27,28,44,45,60,61,69,70,98]. To better understand the interplay between late Pleistocene fauna and human foragers, we employ the prey choice model [68,95] as a framework to evaluate the potential for these extinct taxa to have shaped early Paleoindian subsistence patterns.

Here we address two questions crucial to any discussion of optimal foraging models and megafaunal specialization: what were the likely on-encounter return rates for prey such as mammoths, and how often must

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doi:10.1016/j.jas.2005.05.003

they have been taken to exclude smaller animals from the diet? Most discussions assume that the large size and caloric value of mammoths and other megafauna would have made them highly attractive, yet numerous studies of both human and non-human foragers have demonstrated that prey choice decisions are structured not only by the energetic value of prey, but by their worth relative to acquisition costs once encountered (e.g. Refs. [35,68,90,91]). Unfortunately, current models of early Paleoindian foraging lack the energetic and time investment data critical to evaluating the assumption that proboscideans were the highest ranked prey on the Late Pleistocene landscape. Furthermore, arguments in favor of big game specialization also identify the importance of being able to acquire large prey regularly [59,74,106]. From an optimal foraging perspective, overall return rates and diet breadth depend on encounter rates with higher ranked resources, with returns declining and additional prey being added to the diet as high ranked resources are found less frequently. Thus the issue of specialization depends on demonstrating that 1) animals such as mammoths are higher ranked than other potential prey taxa and, 2) that they could be found frequently enough to make searching for them more attractive than taking smaller animals when encountered.

To answer these important questions, we use anatomical data from African elephants (*Loxodonta africana*) to estimate the caloric yield from a mammoth. These data provide a framework for identifying the range of handling times and encounter rates within which mammoth specialization might occur. We continue by estimating encounter rates for mammoths and other North American species using allometric relationships between body size and population density in mammals. By combining these two pieces of information, we construct an optimal diet curve and evaluate just how narrow the late Pleistocene diet might have been. Our results suggest that a specialized diet focused on large game such as mammoth or extinct bison would be profitable within a very narrow range of circumstances where such prey were extremely abundant, easily procured, and could be processed at minimal time cost. Given the data presented below, we suspect such instances were uncommon at best. Instead, our results challenge the view of early Paleoindians as megafaunal specialists and suggest that these forages would have pursued a wide array of taxa including megafauna, the full range of ungulates and smaller game as well.

2. The meat utility of a mammoth

Estimating return rates for mammoths requires a basic knowledge of the edible components of proboscidean carcasses. Table 1 presents the weight of various organs, bones, and muscle tissue from the necropsies of four adult male *L. africana*. Marrow is not included here because there are no data on the amount of marrow in an elephant carcass and because evidence for marrow extraction at sites showing unambiguous early Paleoindian associations is rare [43]. Carcasses average 38 percent muscle tissue by weight with little variation. Including other portions such as the brain, heart, liver, tongue, and trunk raises the edible mass to 42 percent of total weight, exceeding the 25–35 percent edible portion suggested by Frison and Todd [22]. Because our estimate is more generous, we use this value in subsequent calculations to approximate the edible tissue in a mammoth.

Although African elephants and late Pleistocene mammoths overlap in stature [43], they likely differed in average body mass. Mammoth long bone diameters are often greater relative to their length when compared to those of *L. africana*, which suggests mammoths were more massive for their height [13,88]. Based on an allometric relationship between longbone size and body mass, Christiansen [13] estimates *M. columbi* averaged 6560 kg. This number is the product of measurements from two specimens, one a humerus and the other a tibia. In a more comprehensive analysis focused on North American mammoths, Shipman [88] uses data collected from 28 sets of remains in combination with an allometric relationship between body mass and the circumference of femora and humeri to suggests that *M. columbi* were in some cases 2–2.5 times as large as *L. africana*. In this sample, body mass estimates range from 3838 kg to 14,930 kg with an average of 7368 kg. Here we use the round figure of 7500 kg in our model and given the sexual dimorphism of proboscideans [43,64], suggest this value would be consistent with a female mammoth. Combining this mass estimate with the edible portion data, the average mammoth would have yielded 3150 kg of edible tissue, or slightly more than 1.5 metric tons. We are by no means married to this estimate and simply note that smaller size estimates will broaden diet breadth as developed below.

While the weights of elephant organs and meat are well documented, the nutritional value of the tissue are not. In fact, we were unable to locate any food composition data for elephant. To compensate for the lack of nutritional information, we consider an array of values shared by other game species (Table 2). At the low end, we calculate the caloric yield for raw edible tissue at 1000 kcal/kg, comparable to lean ungulate species such as water buffalo [103]. In this case, a mammoth would have offered ~3.15 million calories (7500 kg*42% edible*1000 kcal/kg). An estimate assuming 1250 kcal/kg, similar to fattier ungulates such as deer and caribou, would provide ~3.94 million kilocalories. Finally, we calculate an upper boundary at 1670 kcal/kg. This number represents the value for beluga whale, a fat-rich arctic marine mammal [91]. A mammoth with similar

Table 1
Weight of various body portions from four adult male *Loxodonta africana*

Carcass portion	Mass in kg[a]	Mass in kg[b]	Mass in kg[b]	Mass in kg[b]	Mean (kg)
Bodily fluids	534.50	596.20	533.60	565.40	557.43
Brain	n/a	n/a	n/a	4.00	4.00
Cranium/mandible (excluding brain)	180.50	188.10	179.90	158.10	176.65
Ears	42.50	50.20	42.10	43.90	44.68
Heart	25.00	n/a	24.80	n/a	24.90
Innominate	91.00	98.30	90.70	71.90	87.98
Kidneys	8.00	8.50	8.10	9.00	8.40
Leg elements (all legs, includes feet)	303.50	413.60	302.90	358.20	344.55
Liver	77.50	83.30	77.40	73.40	77.90
Lungs	29.50	32.10	29.40	27.60	29.65
Meat	1936.00	2327.20	1931.60	1945.80	2035.15
Penis	51.00	57.40	50.70	53.40	53.13
Ribs, vertebrae and scapulae	383.50	460.70	378.20	381.30	400.93
Skin	414.00	500.60	413.10	412.20	434.98
Spleen	18.00	19.90	18.10	18.50	18.63
Stomach and intestines (empty)	302.00	304.20	301.50	n/a	302.57
Stomach and intestines (with contents)	n/a	n/a	n/a	886.50	n/a
Stomach contents	539.50	625.20	538.10	n/a	567.60
Tail	11.50	7.60	11.20	9.00	9.83
Testicles	5.50	6.30	5.40	6.30	5.88
Tongue	12.50	14.00	12.60	13.00	13.03
Trunk	113.50	127.30	117.90	95.60	113.58
Tusk nerves	12.00	9.90	12.10	n/a	11.33
Tusks	69.50	72.90	69.20	41.20	63.20
Total	5160.50	6003.50	5148.60	5174.30	5385.93
Percent meat	0.38	0.39	0.38	0.38	0.38
Total edible tissue[c]	2182.00	2602.00	2181.60	2171.70	2284.33
Percent edible tissue	0.42	0.43	0.42	0.41	0.42

[a] Data from Wilson (in Ref. [30]).

[b] Data from Robertson-Bullock [80].

[c] Includes brain, heart, liver, meat, tongue, trunk.

body composition would provide ~5.26 million kilocalories. Given that these values encompass game species varying from very lean to fat-rich, we see no reason to expect that the caloric yield of mammoth meat would not fall somewhere within this range.

Table 2
kcals/1000 grams of edible portion for selected prey species

Species	Common name	kcals/kg
Bubalus bubalis	Water buffalo	990
Alces alces	Moose	1020
Cervus elaphus	Elk	1110
Antilocapra americana	Pronghorn	1140
Sylvilagus sp.	Cottontail	1140
Odocoileus sp.	Deer	1200
Sciuridae sp.	Squirrel	1200
Bison bison	Bison	1220
Sus scrofa	Wild boar	1220
Rangifer sp.	Caribou	1270
Equus caballus	Horse	1330
Castor canadensis	Beaver	1460
Ursus arctos	Bear	1610
Ondatra zibethicus	Muskrat	1620
Delphinapterus leucas[a]	Beluga whale	1670

All values from USDA [103] unless otherwise noted.

[a] Value from Smith [91].

3. Handling time and on-encounter return rates

While a mammoth would have offered a bonanza of calories, elephant meat comes at a cost in pursuit and handling. We emphasize that in order for a group of early Paleoindians to have specialized in mammoth hunting, procuring these animals must have provided on-encounter return rates greater than other potential prey available in the late Pleistocene environment. This observation leads us to evaluate the handling time thresholds for mammoth specialization relative to the return rates from other game species.

3.1. Handling time and return rates

Table 3 identifies the minimum handling times required to provide return rates of 10,000, 20,000, and 30,000 kcals/hr given a 7500 kg mammoth of varying caloric value. It is important to note that unless post-encounter returns for a mammoth exceed ~30,000 kcals/hr, early Paleoindians would have found proboscideans no more attractive than a variety of medium sized artiodactyls such as deer (*Odocoileus* sp.), mountain sheep (*Ovis canadensis*) and pronghorn (*Antilocapra*

Table 3
Handling time thresholds

kcal/hr	1000 kcal/kg	1250 kcal/kg	1670 kcal/kg
10,000	315.0	393.8	527.6
20,000	157.5	196.9	263.8
30,000	105.0	131.3	175.9

americana) (Table 4). Prehistoric hunters would have been indifferent to which of these taxon they exploited *regardless of how many mammoths were encountered*, and diets would have been correspondingly broad as a result. Returns of 10,000 kcals/hr carry similar implications for the incorporation of lagomorphs, beaver, and other small to medium-sized mammals. With this in mind, fat-rich mammoths (1670 kcals/kg) need to be pursued, killed and processed in less than 175 hours in order for mammoth hunting to provide on-encounter returns exceeding those for medium artiodactyls. Comparatively leaner mammoths would require even shorter handling times to maintain the required threshold, ranging from 131 total hours at 1250 kcal/kg to 105 hours for fat poor animals in the 1000 kcal/kg range.

3.2. Ethnographic estimates of handling time

Although specific time allocation data on elephant hunting and processing are unavailable, ethnographic accounts suggest that proboscidean hunting comes at a substantial time cost. Several ethnographic records of recent elephant butchery events illustrate this point. While conducting ethnographic research with the Efe and Lese in the Ituri Forest of Zaire, Bailey [3, personal communication 2004] observed two elephant butchery events. In these instances, parties ranging from 40 to 120 people moved from the local village to the kill site and made camp. Approximately ten men defleshed an elephant carcass in about 2.5 hours, while subsequent processing of the meat, cutting it into strips, building drying racks and fires and tending the meat while it dried, occupied up to 30 people for an additional 24 hours. The Efe and Lese also processed the carcasses with metal knives, machetes, and axes, all implements that likely reduced handling times relative to the use of stone tools. If everyone in the group performed some task related to processing the carcass for just the time spent on butchery, then handling time would vary from 100 to 300 hours, depending on group size. If we include the effort spent drying the meat, then the butchery and processing of an animal the size of an African elephant could take as many as 745 person-hours, not including the time to get the processing party to the kill site.

Fisher [21] provides complementary evidence from three additional Efe and Lese butchery events. Here, groups of 25 to 35 adults spent 3 to 5 hours defleshing the elephants, setting up temporary habitation shelters, and building meat drying racks. No estimates were given for the time spent processing the meat, and we assume that metal tools were again the norm. Given that the smaller group took longer, this amounts to 105–125 hours of handling time excluding costs associated with drying the meat.

3.3. Actualistic data and handling time

Actualistic experiments involving elephant carcasses also point to the substantial numbers of people and subsequent investments in man-hours inherent in elephant processing. Huckell [52] recounts that simply processing the intestines of a female Asian elephant required almost 3 1/2 hours. Moreover, a group of seven people was unable to flip the carcass to access the meat on its downside, even after it had been gutted, limbs and ribs removed, and head disarticulated from the body. In this instance, Huckell finally resorted to a pick-up truck and tow chain to roll the carcass. Laub [63] also notes the difficulty of flipping an elephant carcass and his crew of eight ultimately resorted to using a back-hoe to access the meat on the downside of the body. Finally, in their accounts of elephant culls, Frison [22] documents that it took 15 individuals to flip the carcass of a large male African elephant once the upside had been butchered and Haynes [43] observed that this task took 10 to 12 individuals.

In the only instance that speaks directly to total butchery time, Laub [63] observes that his crew of eight

Table 4
Return rates for various prey species

Animal	Taxa	Hunting method	Return rate		Reference
			Low	High	
Bison	*Bison bison*	Encounter hunting	32,400	32,400	[47]
Pronghorn	*Antilocapra americana*	Encounter hunting	15,725	31,450	[90]
Mtn. sheep	*Ovis canadensis*	Encounter hunting	17,971	31,450	[90]
Mule deer	*Odocoileus hemionus*	Encounter hunting	17,971	31,450	[90]
Bearded seal	*Erignathus barbatus*	Encounter hunting	15,000	25,680	[91]
Caribou	*Rangifer tarandus*	Encounter hunting	25,370	25,370	[91]
Jackrabbit	*Lepus californicus*	Encounter hunting	13,475	15,400	[90]
Snowshoe hare	*Lepus americanus*	Trapping	8260	15,220	[108]

took 10.5 hours to deflesh an already eviscerated carcass, including the examination of anatomy and note taking. He suggests that if his team had systematically butchered the animal without stopping they could have accomplished the task in 1/2 to 2/3 the time. This translates into 42 to 56 person-hours of butchering time, omitting the cost of removing the internal organs. Finally, we note that although these experiments were in part designed to evaluate the use of stone tools, both Laub [63] and Huckell [52] used modern tools including knives, crowbars, and chainsaws while processing their carcasses.

While none of these examples can be used as direct analogs for early Paleoindians, who may have been much more adept at elephant processing than anyone today, they do suggest that the costs associated with elephant hunting are far from trivial. Indeed, mammoth processing would have required a substantial number of people, especially considering that the animals studied in both the ethnographic examples and the actualistic experiments were likely much smaller than their late Pleistocene counterparts. Given the data available, 50 to 125 hours appears to be a reasonable range for elephant handling times, excluding costs associated with pursuit time, moving camps, and drying meat. We note that pursuit time might add significantly to the total cost of exploiting proboscideans and that by excluding it we increase the returns from mammoth hunting. We also note that spoilage would have been an issue throughout most of the year even in the late Pleistocene and that ignoring partial processing also inflates return rates; partial processing of the carcasses to avoid the problem comes at the cost of lower overall returns as discussed later. Assuming that the ethnographic times are for 5000 kg animals and that we use a mass for mammoths that is 50% larger, handling times for mammoths would range from 75 to 187.5 hours.

Using this range of handling times translates into post encounter return rates of 16,800 to 70,140 kcal/hr (minimum energy, maximum time to maximum energy, minimum time). Since actualistic butchering experiments suggest elephants lack large packets of subcutaneous fat [52,63], we are skeptical of the proposition that the caloric value of mammoths approached that of marine mammals like beluga whale. We are equally skeptical that they were as lean as water buffalo. If we take 1250 kcal/kg as a reasonable middle ground, then on-encounter return rates for mammoths would vary from 21,028–52,500 kcal/hr with a midpoint return of 30,029 kcal/hr at 131.125 hours of handling (Fig. 1). A return rate of 30,000 kcal/hr is greater than that for almost all other small and medium bodied animals common to North America [90]. This implies that big-game specialization in the terminal Pleistocene may have been sustainable *provided that* 1) we are not being overly generous in our estimates of handling time and, 2) that mammoths and other large animals were encountered frequently enough. If encounter rates with megafauna were low, then the addition of search time will cause overall return rates to drop and make smaller animals attractive on encounter.

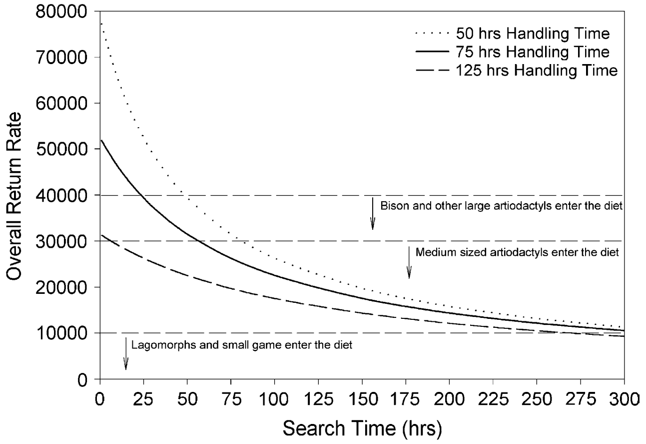

Fig. 1. Relationship between overall return rate and search time for a mammoth only diet. Overall returns are plotted for three different handling times.

4. Prey densities and search time

Whether a predator pursues only one or a range of prey types depends not only on energetic returns for the animals once encountered, but also on how often they are found. Table 5 presents data for encounter rates and overall returns for both moderate (1250 kcal/kg) and fat rich (1670 kcal/kg) mammoths. Areas marked in bold indicate where overall return rates are high enough to favor mammoth specialization and the exclusion of most small mammals and medium sized artiodactyls from the diet. In both cases, overall returns decline as time invested in either search or handling increase. Because we are interested in "best case" scenarios, we omit the 1000 kcal/kg example discussed above. Lowering the caloric value into this range simply requires much lower handling times and much higher encounter rates in order to maintain high overall returns.

While it might appear that mammoth specialization was sustainable, several important observations merit further discussion. First, the 50 hour handling time estimate is provided for completeness and represents best case handling times associated with modern elephants weighing less than 5000 kg. This estimate is almost certainly too low when modeling the 7500 kg mammoth used here. Second, the more favorable case for specialization makes the problematic assumption that mammoths are the caloric equivalent of beluga whales. Focusing on the more probable middle ground estimates of 1250 kcal/kg and 125 hours handling time,

Table 5
Overall return rates for mammoth hunting

Hours Search	Encounter rate		Handling time in hours					
	Ind/hr	Kg/hr	50	75	100	125	150	175
1250 kcal/kg								
1	1.0000	3150	**77,206**	**51,809**	**38,985**	**31,250**	26,076	22,372
10	0.1000	315	**65,625**	**46,324**	**35,795**	29,167	24,609	21,284
20	0.0500	158	**56,250**	**41,447**	**32,813**	27,155	23,162	20,192
30	0.0333	105	**49,219**	**37,500**	**30,288**	25,403	21,875	19,207
40	0.0250	79	**43,750**	**34,239**	28,125	23,864	20,724	18,314
50	0.0200	63	**39,375**	**31,500**	26,250	22,500	19,688	17,500
70	0.0143	45	**32,813**	27,155	23,162	20,192	17,898	16,071
100	0.0100	32	26,250	22,500	19,688	17,500	15,750	14,318
150	0.0067	21	19,688	17,500	15,750	14,318	13,125	12,115
200	0.0050	16	15,750	14,318	13,125	12,115	11,250	10,500
250	0.0040	13	13,125	12,115	11,250	10,500	9844	9265
300	0.0033	11	11,250	10,500	9844	9265	8750	8289
1670 kcal/kg								
1	1.0000	3150	**10,3147**	**69,217**	**52,084**	**41,750**	**34,838**	29,889
10	0.1000	315	**87,675**	**61,888**	**47,823**	**38,967**	**32,878**	28,435
20	0.0500	158	**75,150**	**55,374**	**43,838**	**36,279**	**30,944**	26,977
30	0.0333	105	**65,756**	**50,100**	**40,465**	**33,939**	29,225	25,661
40	0.0250	79	**58,450**	**45,743**	**37,575**	**31,882**	27,687	24,467
50	0.0200	63	**52,605**	**42,084**	**35,070**	**30,060**	26,303	23,380
70	0.0143	45	**43,838**	**36,279**	**30,944**	26,977	23,911	21,471
100	0.0100	32	**35,070**	**30,060**	26,303	23,380	21,042	19,129
150	0.0067	21	26,303	23,380	21,042	19,129	17,535	16,186
200	0.0050	16	21,042	19,129	17,535	16,186	15,030	14,028
250	0.0040	13	17,535	16,186	15,030	14,028	13,151	12,378
300	0.0033	11	15,030	14,028	13,151	12,378	11,690	11,075

Data reflect a 7500 kg mammoth and a 42 percent edible portion (3150 kg). Here returns rates are ‘‘overall’’ returns rather than those achieved on-encounter and incorporate the cost of searching for as well as handling the animal. Search time is presented in terms of raw hours. Encounter rates with mammoth are expressed as both individuals per hour and kilograms of meat per hour. Regions highlighted in bold provide more than 30,000 kcal/hr and would be sufficient to exclude most small and medium sized animals from the diet.

early Paleoindians would have needed to take mammoth once per hour of search to exclude medium artiodactyls (> 30,000 kcal/hr) from the diet and once every 150 hours to exclude jackrabbits (> 10,000 kcal/hr; Table 5, upper panel; Fig. 1).

This encounter rate threshold points directly to a third issue, namely the need to understand large game abundances on the late Pleistocene landscape. Recent ethnographic data underscore this point. Modern hunter-gatherers such as the Hadza regularly pursue a variety of large bodied animals, yet successful encounters with *any* of them occur only once every 30 hunter-days [77]. If early Paleoindians enjoyed comparable success rates, then mammoth specialization would be indefensible regardless of their caloric value or associated handling times. Even if one argues that early Paleoindians enjoyed higher success rates than the Hadza because Hadza territory had been depleted of most of its big game, some estimate of how much higher is still in order. A mammoth every 150 hours of hunting, for example, implies an encounter rate of 21 kg of meat per hour. By way of comparison, Simms' [90] estimates suggest that prehistoric hunters in the North American Great Basin would have acquired 1.4 kg of meat per hour from deer, mountain sheep, and pronghorn combined, *assuming all taxa were encountered at the maximum rate*. This striking contrast raises questions about the kinds of prey densities which might have been sustained during the late Pleistocene. There is a temptation to view late Pleistocene North America as a landscape teeming with large game prior to the arrival of Paleoindian hunters (e.g. Refs. [61,106]), but quantitative estimates of actual prey densities are generally lacking.

Some arguments in favor of megafaunal specialization appeal to paleoenvironmental reconstructions which suggest patchy resource distributions associated with drought conditions during the early Paleoindian period (11,200 to 10,900 ^{14}C yr. BP) (e.g. Refs. [44,45,93]). C.V. Haynes [39–42] for example, interprets the presence of wells at sites such as Murray Springs and Blackwater Draw, in combination with stratigraphic evidence, as indicating a period of drought coincident with the timing of the initial Paleoindian occupation of the American Southwest. If important water sources were widely distributed across the terminal Pleistocene landscape, then megafauna would have been concentrated at these oasis water-holes. Early Paleoindians would have been aware of the patchy distribution of mammoth and such knowledge in combination with well worn and highly visible elephant trails would have resulted in decreased search time and locally elevated encounter rates such that the diet narrowed to the exclusion of medium artiodactyls and other smaller taxa.

Three points need to be made, however. First, even if true this scenario would only apply around the proposed late Pleistocene oases. Densities of mammoth and other megafauna across much of the rest of continent would be lower and diets broader. Even within such oases, the fundamental questions continue to be how often do we think mammoth were encountered and how quickly must they have been pursued and processed in order to exclude smaller animals. Second, more recent geoarchaeological treatments of the early Paleoindian period find little evidence for the severe and wide-spread drought necessary to restructure the environment in this way [48,49]. In fact, Holliday [48,49] argues that this time was more likely cool and wet, especially when compared to the environmental conditions that would immediately follow. Finally, there is no strong evidence to date for intensive megafauna hunting at oasis water holes as predicted by the oasis hunting model [76]. Here we focus exclusively on this first issue: how often must mammoth and other megafauna been encountered to exclude smaller game.

5. Modeling early Paleoindian prey choice

5.1. Model assumptions

We turn to building a diet breadth model for early Paleoindian hunters using two pieces of data to reconstruct late Pleistocene encounter rates. The first is a body of biological literature concerning the allometric relationship between population density and body size in plants and animals [7,8,18,20,58,82,109]. For this study, we use data from Damuth [15,16], who demonstrates that population densities among mammalian primary consumers ($n = 368$) scale at $-3/4$ the power of body mass[1]. Absolute densities vary geographically and by habitat type [16, Table 3], and are generally higher in non-tropical environments. We use the intercept for all North American taxa ($b_0 = 4.33$) as the baseline for our study such that log (density) = 4.33−0.75*log (mass). This allows us to reconstruct mean population densities for prey that prehistoric foragers were likely to have encountered, including now extinct taxa such as mammoths (for a similar approach to reconstructing fish communities, see Ref. [56]).

Table 6
Population density and encounter rates

Density (Ind/km^2)	Encounter Rate (Ind/hr)	Source
0.000	0.000	No animals, no encounters
0.502	0.010	[57]
1.930	0.012	[104]
3.860	0.018	[104]
7.722	0.060	[104]
11.583	0.096	[51]

The second data set derives from several studies describing the relationship between population densities and artiodactyl encounter rates cited in Simms [90] (Table 6). Here encounter rates and population density for a sample of deer and bighorn sheep hunts are tightly and linearly correlated ($b = 0.007$; $r = 0.98$; $P < 0.01$). We use the slope of this regression line as a "scale factor" in order to translate density estimates into encounter rates. By extending the linear relationship to larger and smaller taxa and combining it with the allometric data from Damuth [16], we can estimate encounter rates for a range of potential resources and model diet breadth accordingly. Body size dictates prey density, the scale factor translates density into prey encounter rates, and prey encounter rates coupled with our knowledge of post-encounter return rates predicts diet breadth.

5.2. Potential sources of error

Whether either of these two relationships provide a valid basis for comparison is certainly a reasonable question. In their defense, we make the following observations. In terms of prey abundances during the late Pleistocene, the use of modern North American density data will only be inappropriate if late Pleistocene landscapes supported substantially higher numbers of primary consumers than the modern densities on which Damuth's estimates are based. Several considerations make this unlikely. First, late Pleistocene herbivores supported a large predator guild. These predators would have helped keep prey densities low even in the absence of human hunters. Second, several studies suggest that many of the large herbivores such as horse (*Equus caballus/ferrus*, Fig. 2) and bison (*Bison* sp.) were in decline before Clovis hunters made an appearance [29, supplemental; 86]. These paleontological studies provide reason to expect that prehistoric prey densities may not have been substantially greater than we would expect today for animals of their size. Finally, our model results

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[1] There is substantial debate about the nature of the relationship between animal density and body mass, including the appropriateness of −0.75 as a slope. We evaluated Silva et al.'s [89] alternative derivation for terrestrial herbivores, which is log(density) = 1.43−.68*log(mass). Proboscidean densities are comparable to those predicted using Damuth's [16] derivation, but encounters with smaller animals drop off sharply. Using this formula would substantially depress overall return rates and increase diet breadth compared to Damuth. We feel Damuth's relationship provides more reasonable estimates, especially for small and medium sized animals, and use it instead.

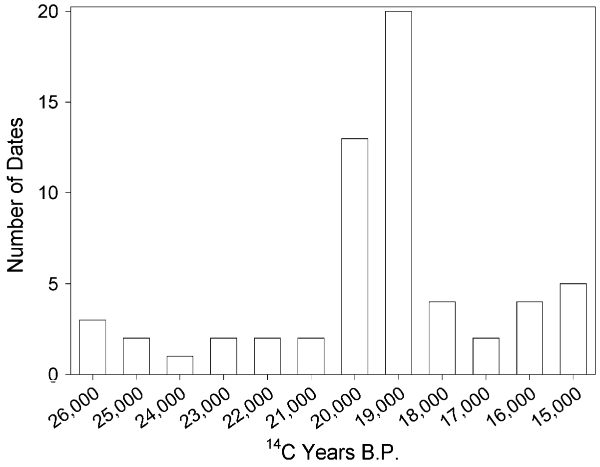

Fig. 2. Frequency of radiocarbon dates for Alaskan *Equus caballus/ferrus*. *Equus* is most common during the last glacial maximum but declines in numbers substantially thereafter. Raw data from Guthrie [29, supplemental].

remain consistent even using the largest intercept identified by Damuth ($b_0 = 4.62$). That intercept implies carrying capacities and prey densities twice those of modern N. American herbivore taxa ($n = 84$), a value that is almost surely too high.

The relationship between prey density and encounter rates also poses problems. First, whether trends identified for medium artiodactyls can be reliably extended to very large animals such as mammoth or smaller game such as rabbits, hares, and gophers is unclear. Doing so implies that the larger and smaller animals are distributed in the same fashion as the artiodactyls, which is unlikely. Jetz et al. [58, supplemental] note a significant relationship between body size and group size, suggesting that larger animals not only occur at lower densities but are more patchily distributed. If female and juvenile mammoths tended to form herds in the same way as modern elephants, their effective density would be even lower than predicted. Scaling encounters in a linear fashion will overestimate encounter rates unless increased group size makes mammoth easier to locate, thereby offsetting the additional search associated with a more patchy distribution. Encounters with small animals, which are likely to be more evenly distributed, will show the reverse pattern. Scaling up and down as we do may therefore favor rather than diminish encounters with the larger animals, though this is by no means proven.

A second problem revolves around the appropriateness of the linear model itself. The estimate of 0.007 encounters/animal/km^2 derives from a very small sample. While it appears linear, a larger sample might exhibit a sigmoidal response (c.f. Ref. [50]), with low encounter rates at low densities, higher than expected encounters at intermediate densities, and a leveling off as density and encounter rates become saturated. We are unaware of any study which addresses this issue and cannot evaluate the possibility directly. If we consider encounters with all organisms, however, then the effect of such a response would be higher encounters with intermediate sized animals. Megafauna densities would remain low and the potential impacts on megafaunal specialization would be small.

5.3. Model results

While empirical measurements of encounters with large game at varying densities would be preferable to our indirect estimates, quantification of any sort for late Pleistocene environments is lacking. We recognize the potential problems inherent in our approach and encourage due caution, but we feel it is still sufficiently robust to be constructive. Using this relationship between body size, population density, and encounter rates allows us to reconstruct overall returns associated with taking any of a hypothetical suite of taxa. Table 7 shows the results of such a model. All fauna are ranked from high to low on the basis of their post-encounter returns. The taxa chosen loosely reflect the kinds of animals one might encounter in prehistoric western North America. They include a range of small mammals, birds, and medium artiodactyls that would have been typical of many late Pleistocene environments, plus bison and mammoth. Late Pleistocene bison (*B. antiquus*) are modeled by increasing size and handling time estimates for modern bison (after Ref. [47]) by 50%. This scales extant bison into a size range generally consistent with that demonstrated by the mean difference in horn core measurements between early and late Holocene specimens [107]. The data for mammoths assume 7500 kg per mammoth, a 42 percent edible portion, 1250 kcal/kg, and 75 hours of handling time. By using the low-end estimate for handling time, mammoths become the largest and highest-ranked resource available and provide 52,500 kcal/hr on encounter. Bison rank only slightly lower and encounter rates with the two megafauna in term of kilograms of meat per hour are 37 percent greater than the next three taxa combined.

The rightmost three columns in Table 7 show the overall return rates enjoyed by adding successive, lower-ranked, prey taxa to the diet. The first of these columns computes returns assuming that encounters with mammalian prey scale at 0.007 times prey density (scale factor (SF) = 0.007, Table 6). This is the density/encounter rate relationship derived from Simms data and given this value, the optimal diet yields 6503 kcal/hr and includes megafauna, medium artiodactyls, and lagomorphs (Fig. 3). A single forager enjoying these encounter rates could acquire a little over half a metric ton of edible meat per month working just three hours

Table 7
Optimal diet breadth

Resource	Scientific name	Energy (kcal/kg)[a]	Live weight (kg/ind)	Edible fraction	Edible weight (kg/ind)	Total (kcal)	Handling time (hr)[c]	Handling time (hr/kg)	Encounter rate (ind/hr)[d,e]	Encounter rate (kg/hr)	Return rate on-encounter (kcal/hr)	Overall return rate (kcal/hr @1*SF)[f]	Overall return rate (kcal/hr @1/2*SF)	Overall return rate (kcal/hr @2*SF)
Mammoth	*Mammuthus columbi*	1250	7500.00	0.42	3150.00	3937500	75.000	0.0238	0.00066	2.0778	52500	2475	1267	4727
Bison[b]	*Bison antiquus*	1090	900.00	0.60	540.00	588600	14.609	0.0271	0.00324	1.7470	40291	4105	2147	7544
Deer	*Odocoileus hemionus*	1200	85.00	0.60	51.00	61200	2.517	0.0493	0.01899	0.9685	24318	4949	2641	8787
Mtn sheep	*Ovis candensis*	1200	75.00	0.60	45.00	54000	2.517	0.0559	0.02086	0.9387	21457	5673	3091	9742
Pronghorn	*Antilocapra americana*	1140	56.50	0.60	33.90	38646	2.017	0.0595	0.02580	0.8745	19163	6234	3462	10,396
Hare	*Lepus* sp.	1140	2.42	0.60	1.45	1655	0.125	0.0861	0.27399	0.3978	13242	6421	3609	10,520
Cottontail	*Sylvilagus* sp.	1140	1.10	0.60	0.66	752	0.083	0.1263	0.49494	0.3267	9029	6503	3705	10,446
Gopher	*Thomomys* sp.	1200	0.25	0.85	0.21	255	0.042	0.1961	1.50362	0.3195	6120	6485	3769	10,140
Lg Squirrel	*Spermophilus* sp.	1200	0.35	0.85	0.30	357	0.058	0.1961	1.16827	0.3476	6120	6468	3834	9854
Sage grouse	*Centrocercus urophasianus*	1340	1.50	0.70	1.05	1407	0.258	0.2460	0.81250	0.8531	5446	6339	3961	9060
Sm Squirrel	*S. tridecemlineatus*	1200	0.20	0.85	0.17	204	0.042	0.2451	1.77755	0.3022	4896	6278	3986	8811
Ducks	*Anas* sp.	1230	1.00	0.70	0.70	861	0.258	0.3690	0.81250	0.5688	3333	5961	3940	8017

[a] Caloric values are taken from USDA Poultry Products; Lamb, Veal, & Game; Ethnic Foods [103].

[b] Bison weights and handling times are from Henrikson [47] and scaled up 50% to reflect the larger size of *B. antiquus*.

[c] All other handling times were computed using median times from Simms [90]; sage grouse use estimated times for ducks.

[d] Encounter rates for rodents, rabbits, hares, and ungulates use data from Damuth [16] and Simms [90]. Log density in individuals per square kilometer is 4.33-.75∗log(mass in kg). Encounter rates are computed as (density∗ScaleFactor).

[e] Encounter rates for birds use the data from Simms [90]. Because they cannot use the same allometric equations as mammals, these values are adjusted up or down to reflect changes in encounter rate relative to a base scale factor of .0035.

[f] Overall return rates are computed using encounter rate scale factors of .007, .0035, and .014. The first estimate uses the raw scale factor computed from the regression in Table 6. Given the second value, encounter rates with all medium artiodactyls (in kg/hr) are equivalent to the maximum levels estimated by Simms [90]. The third value is twice that estimated by the regression equation. Although encounters with mammoth and bison are much higher, the optimal diet continues to include medium artiodactyls and lagomorphs.

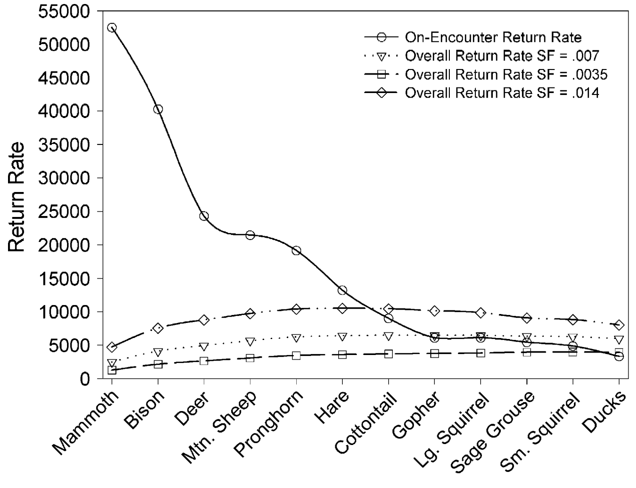

Fig. 3. A diet breadth model for early Paleoindians. Overall returns are plotted for the encounter rate scaling factors of SF = 0.007, SF = 0.0035, and SF = 0.014.

per day (100 hrs total). About 60 percent of that would come from megafauna, and the workload would include searching for, pursuing, and processing the animal. As a comparison, these rates are four to five times greater than those reported for the Hadza of Tanzania, who are specialized big-game hunters with access to a wide variety of species including elephant, giraffe, and other megaherbivores [37,38].

The second to last column in Table 7 assumes encounters scale at one-half the derived value (0.0035) and is provided as an additional basis for comparison. Here the optimal diet provides 3986 kcal/hr and includes not only the megafauna, artiodactyls, and lagomorphs, but also all small animals except the ducks. At this level, encounters with the deer, bighorn sheep, and antelope total 1.4 kg/hr, corresponding to the maximum estimate provided by Simms [90][2]. The appropriateness of using this measure depends on how accurately Simms' maximum estimated encounter rates for Holocene hunters captures prey availability in the Pleistocene. Unless early Paleoindian hunters regularly encountered game at densities higher than Holocene maxima, diets would have been quite broad. This is true even after including megafauna in the list of potential prey. Even if encounters with all taxa were twice as high as those predicted by the derived scaling factor (SF = 0.014), hares remain firmly in the diet with cottontails on the cusp (last column, Table 7). Such observations provide reason to question whether Paleoindian subsistence would ever have been narrow and highly specialized as some have contended [44,45,60,106].

6. Modeling returns from partial carcass utilization

Up to this point, we have only considered a scenario where an entire mammoth was procured and then completely processed. As a result, we have presented one extreme of a continuum of processing intensity that would have varied not only in the proportion of the edible products harvested but also in the handling times needed to do so. In fact, the early Paleoindian faunal record suggests that partial carcass utilization may indeed have been the norm [43]. If so, our model overestimates both total caloric yields and handling times. Accordingly, we evaluate the impact of partial carcass utilization on both on-encounter returns and the average return rate earned by a group of early Paleoindians.

Partially processing likely offered much higher return rates than would be gained by using an entire animal. When a resource provides diminishing returns with handling, a hunter should leave off processing as soon as the marginal returns for the resource at hand fall below the average returns for the environment as a whole [95: 31–33]. If completely processing a mammoth provides substantially higher returns than the overall environment, as we suggest here, then partial processing is a sub-optimal choice. Even though the chosen part of the carcass provides extremely high returns, lucrative pieces still go to waste and the animal is underutilized. Large mammals contribute less to the overall diet than they should given their size and diets actually broaden. While energetically sub-optimal, such partial processing decisions may have been common where spoilage, transport constraints, band size or mobility decisions limited the amount of flesh a group of early Paleoindians could effectively use.

To illustrate this point consider a case where a forager takes one third of a mammoth's edible tissue (0.14 total weight) in 1/15 of our 75 hr handling time estimate (5 hrs). Also assume encounters scale at the higher rate (SF = 0.007). In this instance, on-encounter returns increase from 52,500 kcal/hr to 262,500 kcal/hr. Because only part of the carcass was used, however, the maximum overall return rate drops from 6503 kcal/hr to 5451 kcal/hr and a range of small animals including gophers, large squirrels and sage grouse enter the diet. Scavenging partial carcasses would result in similar outcomes. On-encounter returns increase dramatically while maximum overall returns fall and diets widen. Because we are interested in showing that a wider range of animals may have been favored even under very auspicious circumstances, we chose to focus on complete rather than partial carcass utilization.

To summarize, megafauna may well have been the highest ranked prey on the late Pleistocene landscape. In terms of kg/hr of edible tissue, they were probably encountered more frequently than other prey. Based on

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[2] The specific encounter rates used in Table 7 differ slightly from Simms [90] because here they vary with body weight. Encounters with deer and antelope are more frequent than reconstructed by Simms, bighorn sheep a bit less frequent.

these results however, we simply question whether early Paleoindians encountered mammoth and other megafauna taxa often enough to support a specialized hunting economy.

7. The importance of encounter rates

Prey encounter rates are the fundamental reason why diets are broad in this model. As a matter of empirical fact, one could reduce handling times for completely processing a mammoth from 75 to 50 hours (making them worth 78,750 kcal/hr on-encounter) or increase them to 150 hours (reducing returns to 26,250 kcal/hr). Neither would alter the optimal diet. Likewise, if we assume partial butchering of a carcass in a relatively short time, the model still predicts a wide diet. This is because overall returns from exploiting high ranked resources tend to be much more sensitive to search time than processing [36]; high-ranked animals require relatively little time to process by definition. Moreover, whether or not a forager ignores small game should be a function of encounters with all of the larger, higher ranked taxa, to include the medium artiodactyls.

We recognize that attention to Paleoindian diets has focused on whether they were specialized big-game hunters, not mammoth hunters per se (e.g. Ref. [106]), which is part of the reason bison were added to the list of potential prey. Adding multiple, high-ranked taxa serves to increase overall returns and substantially narrow the diet in much the same way as increasing encounter rates with mammoth or bison. If we were to drop bison entirely, overall returns would fall to the point where sage grouse become attractive, even while using the higher encounter rate scaling. Conversely, adding additional large taxa such as giant ground sloth (*Megatherium* sp.), mastodont and horse to the diet would cause it to narrow further. Consequently, one might ask whether our results are simply a function of failing to consider the full range of megafauna available to early Paleoindian hunters.

While we acknowledge this latter possibility, there are four issues to consider. The first is niche overlap, how many different large taxa can be supported within a particular area, and the degree to which there is partial competitive exclusion ([2,6: 247–290, 670–699, 67,72,84]; for specific examples for herbivores similar to those used here see Refs. [23,54,73,85]). Here we included mammoth and bison, both grazers, a suite of smaller ungulate browsers, and a variety of birds and small mammals representative of similar animals found in almost any habitat. Making a case for big game specialization in the Pleistocene must start by identifying a larger set of megafauna sufficiently differentiated to coexist and that early Paleoindians might have encountered frequently enough to drive small animals from the diet. While such subsets may exist for particular ecosystems, we are skeptical about their ubiquity on a continental scale. Even if we wish to concede that such high-density patches existed, it seems premature to talk about "megafuanal specialization" if it only occurs in certain favorable but potentially rare circumstances. The late Pleistocene Great Basin provides a case in point, since there is clear evidence of Paleoindian occupation along pluvial lakes throughout the region yet no evidence for the use of extinct megafauna [5,25,46].

Second, it is highly unlikely that any subset of taxa would ever lead foragers to exclude the medium artiodactyls (i.e. pure megafaunal specialization). Doing so would require either mammoth encounter rates 15 times greater than those predicted by the body mass allometry data, encounters with 30 different taxa similar in size and post-encounter returns to *Bison antiquus*, or overall encounter rates with bison 30 times higher than suggested here. Although any of these options would raise overall returns enough to exclude "average" artiodactyls (providing 21,000 kcal/hr or so, Table 7), none seems likely. Given that the upper limit for medium artiodactyl returns is ca. 30,000 kcal/hr [90], excluding them entirely would require even greater megafauna densities.

Third, there is the empirical observation that bison and mammoth are the only megafauna taxa regularly identified in firm association with early Paleoindian artifacts [12,27,28]. We include them in our list of potential prey for this reason. If Paleoindians were capable of regularly taking animals the size of mammoths and mastodonts, smaller animals such as horse, capybara (*Hydrochaeris hydrochaeris*), giant ground sloth, camel (*Camelops hesternus*) and the many other now extinct late Pleistocene herbivores would seem obvious targets. That neither these nor a host of other large mammals show signs of being actively hunted suggests they may have been rare or extinct by the early Paleoindian period and as a result are omitted from this discussion. Any evidence of their use would obviously deserve reconsideration, though doing so will likely have little effect on the overall results for the reasons just discussed.

Fourth, and perhaps most importantly, our discussion so far has been decidedly androcentric. There is substantial evidence that men, women, and children differ in foraging ability and foraging goals [9,19,31,32, 34,53,66, and others]. Women or children may have participated in the production and maintenance of hunting technologies and household goods and also in processing animals once acquired. At the same time, each of these groups could also be expected to provision themselves, especially to the degree that large game exploitation is risky and highly variable in terms of success rates [31–33]. Such variability is often at odds with needs of mothers and young children, requiring both groups to exploit lower-ranked, more readily and reliably acquired resources including both plants and smaller game animals. Since the Paleoindian subsistence record should reflect the contributions of all participants, the presence of a variety of small game should come as no surprise even where the overall encounter rate with megafauna was quite high and men were able to focus exclusively on their exploitation.

8. Proboscideans and prey choice: prehistoric and recent subsistence records

Our model predicts that megafaunal specialization would have rarely provided an optimal foraging solution for early Paleoindians. An optimal prey set would almost certainly have included both megafauna and medium artiodactyls, while rabbits would have been pursued often and we would not be surprised to see larger rodents in some contexts as well. We arrive at this conclusion even though the model parameters we chose were biased in favor of the specialist model whenever possible. The overall returns earned by early Paleoindians would surely have been better than many Holocene foragers would later experience (e.g. Ref. [11]), but never sufficient to exclude prey such as deer and pronghorn at any set of megafauna encounter rates. We proceed by comparing these expectations against not only the early Paleoindian faunal record, but also data from a range of Old World prehistoric and recent ethnographic contexts offering encounters with proboscideans.

8.1. Variability in the early Paleoindian subsistence record

The expectation that early Paleoindians exploited a broad range of taxa does not imply that every faunal assemblage should contain every prey item in the diet. In fact, we expect the faunal record to be highly variable in the numbers and types of taxa identified in any given assemblage, particularly if sites represent short term, non-redundant occupations across a range of different environments. In this case, it is important to recognize a central prediction of the prey model: foragers always take high ranked animals upon encounter. Consequently large game kill/processing sites simply demonstrate that, as expected, early Paleoindians took large animals such as mammoth whenever possible.

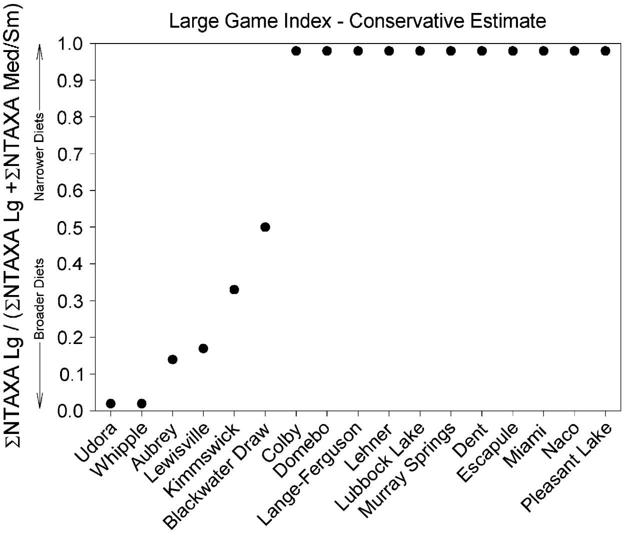

Fig. 4. Large game index, conservative estimate, plotted as point values. Values closer to 1 indicate assemblages limited mainly to megafauna. Values closer to 0 document assemblages containing a wide range of prey. Raw data from Cannon and Meltzer [12].

To underscore this point, we use information compiled by Cannon and Meltzer [12, references therein, Tables 3 and 4, pp. 7–10], to illustrate the variability in early Paleoindian prey choice. Fig. 4 shows the proportion of the total number of taxa (NTAXA) represented by large game (> 500 kg) at 17 early Paleoindian sites. This sample provides a conservative estimate that only employs taxa demonstrating strong evidence for subsistence use. While mammoths dominate at eleven of the sites, the faunal remains at Lewisville and Aubrey include artiodactyls, lagomorphs and small rodents, not to mention birds, snakes, turtles, fishes, snails and fresh water mussel. Importantly, many of these species represent small bodied prey not considered in our analysis and document diets even wider than our simulation might suggest. Likewise, the assemblages from Whipple and Udora are limited to medium and small bodied species such as caribou (*Rangifer* sp.), beaver (*Castor* sp.) and hares (*Lepus* sp.).

Because the conservative approach potentially obscures the variability in early Paleoindian diet breadth and because our model predicts a wide range of prey choice, we construct a second, inclusive index (Fig. 5) using all taxa identified at these 17 sites (c.f. Ref. [106]). Thirteen of the assemblages include a wide variety of large, medium and small bodied prey. We note that in both the conservative and inclusive examples, several of the assemblages consistently suggest diets focused on prey other than megafauna, while a number of others contain only the remains of proboscideans. The range of species identified in the remaining assemblages varies depending on whether or not one opts for a conservative or inclusive estimate. In these cases, we suspect that the actual number of prey species lies in between the two sets of values. Given the ambiguity of much of the available data however, we simply note that the record appears more variable than a big game specialist model would predict.

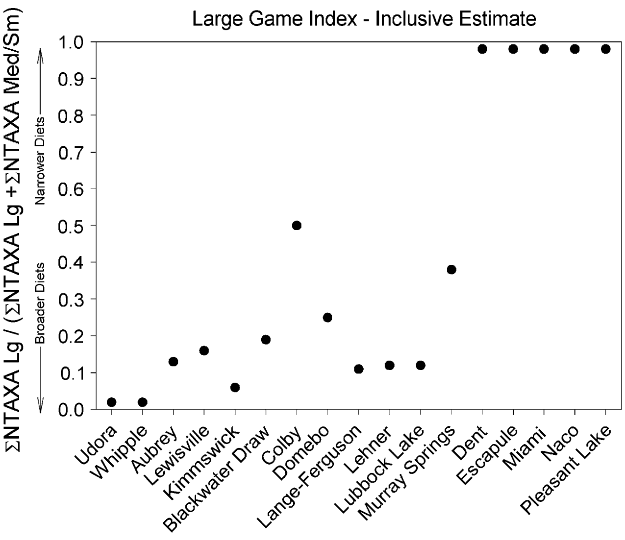

Fig. 5. Large game index, inclusive estimate, plotted as point values. Values closer to 1 indicate assemblages limited mainly to megafauna. Values closer to 0 document assemblages containing a wide range of prey. Raw data from Cannon and Meltzer [12].

8.2. The Old World record and megafauna hunting

Human foragers and megafauna also shared much of the Old World throughout the Pleistocene [43,79] and one might reasonably expect Old World foragers to have specialized on their exploitation under favorable circumstances. Yet faunal assemblages from archaeologically well known areas of the Old World contrast sharply with the view of early Paleoindians as megafaunal specialists and instead suggest the routine exploitation of a broad spectrum of prey dominated by artiodactyls and perrisodactyls. Throughout Eastern Europe, for example, faunal assemblages include red deer (*Cervus elaphus*), reindeer (*Rangifer tarandus*), musk ox (*Ovibos moschatus*), bison (*Bison priscus*), horse (*Equus* sp.), fox (*Vulpes* sp.), wolf (*Canis lupus*), boar (*Sus scrofa*), hares (*Lepus* sp.), fish and birds (e.g. Ref. [10,92]). Across 14 occupational layers at Kosoutsy on the Dnestr River [10], reindeer account for 40 percent ($n = 80$) of the total MNI, followed by Equus (21%, MNI = 38), bison (17%, MNI = 31) and hares (MNI = 13, 7%). In contrast to the abundances of artiodactyls and horses, only two individuals (3%) represent mammoth (*M. primigenius*). Similarly, sites on the Central Russian Plain have produced the remains of substantial numbers of marmots (*Marmota bobac*) as well as the bones of numerous artiodactyls and mammoths, and there is good evidence for the systematic procurement of hares as well [92].

Upper Paleolithic faunal records from Western Europe also document a wide range of species frequently dominated by medium artiodactyls. In 33 Aurignacion assemblages from southern France reviewed by Grayson and Delpech [26], *Rangifer tarandus* occurred in 76 percent of the collections, bison in 13 percent, and mammoth in none. The total number of taxa at these sites ranged from two species to ten, and more than five taxa are recovered in over 80 percent of the cases. Upper Paleolithic sites in Spain demonstrate not only large numbers of medium sized artiodactyl remains, but in several cases lagomorphs appeared to have played a substantial role [101,105]. Within the Aurignacian/Gravettian components of Cova Beneito and Cueva de Malladetes, lagomorph remains are by far the most common taxa with NISPs of 5544 (86%) and 83 (55%) respectively [17,71], and artiodactyls such as ibex (*Capry pyrenacia*) and red deer comprise the bulk of the remaining faunas. We note that in each of the cited instances, all of the assemblages predate the youngest radiocarbon date on mammoth bone for each region [97]. Similarly wide diets from contexts where megafauna are known to have been present include the Levant (e.g. Ref. [96]), Africa (e.g. Ref. [62]), and Australia (e.g. Ref. [1]).

8.3. The prey choice of recent African elephant hunters

The wide range of animal prey taken by recent hunting and gathering groups further underscores our conclusions about the importance of proboscideans to early Paleoindian subsistence. While recent African hunter-gatherers cannot provide direct analogs for late Pleistocene foragers living in North America, they do provide a valuable ethnographic context. Insofar as mammoths can be argued to have provided returns substantial enough to narrow the diet to the exclusion of all but a few other large bodied prey, than there is little reason to view elephants otherwise today. If elephants are highly ranked, then they should regularly be taken on encounter; if they are frequently enough encountered, overall diets should be narrow. This is simply not the case.

While numerous accounts of African hunter-gatherers describe elephant hunting (e.g. Refs. [3,4,14,21,55,81,83,87,94,100,102]), a close look at prey choice reveals that these animals were rarely taken. This observation is nothing new. Roosevelt [81, p. 299] for instance, noted that “very few of the native tribes in Africa hunt the elephant systematically.” Indeed, Bailey’s [3,4] ethnographic accounts of Efe subsistence mention elephant hunting only briefly and mainly within the context of photo captions. Instead of elephants, more than 45 species of smaller prey constitute the bulk of the diet. South African Bantu-speaking groups took a similar range of prey; including not only elephant, but also artiodactyls such as buffalo and eland in addition to monkeys, small game and birds [83,100]. Moreover, elephants are notably absent from subsistence accounts of many other recent African foraging groups, including the !Kung [65] of southern Africa and the Hadza of east Africa [77]. While both groups share environments with elephants, accounts of their pursuit are largely absent and hunters from both groups focus on a wide range of smaller artiodactyls.

In sum, these records appear to support our expectations. In areas with elephants, African foragers pursue these animals but regularly take a variety of other prey ranging from large game to medium and small bodied taxa. Given the lack of ethnographic accounts documenting systematic elephant hunting and the paucity of evidence for the widespread use of similar sized animals in either the New World, Old World (see Ref. [99]), or even Australia, one might question whether hunter-gatherers focused on megafauna anywhere during the Pleistocene.

While both the Old World Pleistocene and ethnographic records are generally consistent with our predictions, proboscidean-only faunas do represent a comparatively large portion of known Paleoindian sites. This empirical observation begs the question of why these animals are so common. One suggestion is that the prevalence of mammoths in the early Paleoindian record may simply be a function of discovery bias [12,24,74,75]. Not only are sites with mammoth remains more likely to be discovered, but excavations often focus spatially on bone beds derived from kill/processing events [12]. As a result, investigations limited to megafauna remains may fail to recover the full range of prey present at a site. Hadza intercept hunting locations, for instance, often document multiple kills representing a range of taxa spread over several thousand square meters [78]. Likewise, transport decisions and the selective deletion of the remains of smaller taxa by scavengers can also bias kill/processing locations in favor of larger bodied animals [78]. This might be especially so in the context of a mammoth kill where the ethnographic record predicts a residential move to the carcass as opposed to the transport of meat back to a residential base. Whatever the case, published excavations appear to have left us with a record skewed towards easily recognizable cultural deposits containing the highly visible bones of mammoths.

9. Conclusions

Our study suggests that early Paleoindians should have pursued a broad range of mammalian prey. Moreover, these results appear very robust. One can vary the model parameters across a wide range of values without changing the outcome to any great degree. Consequently, we expect that megafaunal specialization would have been profitable within a very narrow range of circumstances where large game species were extremely abundant, easily procured, and could be processed at minimal time cost. Given the data presented here, we suspect such instances were uncommon at best.

While we will never know how often early Paleoindians actually encountered megafauna, we suspect that encounter rates never exceeded the levels necessary to exclude medium artiodactyls from the diet and would rarely have been sufficient to exclude lagomorphs. In this respect, the late Pleistocene of North America appears to have been little different from most other terrestrial hunter-gatherer contexts through time and across space. The highest ranked taxa (in this case, megafauna) were taken whenever possible, but were likely never plentiful enough to result in the sort of narrow hunting specialization often argued to characterize early Paleoindian subsistence. We note that as the faunal record receives more and more attention, the evidence points to a broader spectrum of prey choice than has often been suggested. However favored megafaunal prey might have been, a wide range of game was still necessary to keep these hunting and gathering groups fed.

It is also worth pointing out that there is a potential semantic argument lurking in our discussion of "specialization". Throughout this paper, we take specialization to mean exploiting megafauna to the exclusion of other, smaller prey and go to some lengths to suggest this was unlikely. At the same time, we also assume that megafauna were regularly and successfully hunted. Consequently, the actual proportion of the overall diet made up by megafauna in Table 7 is on the order of 60 percent. While we would expect early Paleoindians to take a wide range of taxa, which we consider "generalist" in this context, megafauna would still make up the bulk of men's contributions to the diet and we might expect them to exert a strong influence on material culture and behavior as a result.

That being said, the operative word is "might". Optimal diet models such as this one are static constructs applied to particular places and points in time. We do not consider how prehistoric hunters may have depleted particular patches. We also do not address the issue of how often they may have been able to exploit "megafauna rich" patches. If megafauna were quickly depleted, scarce across much of the landscape, or subject to high hunting failure rates, diets would have been correspondingly broad and the contribution of these rarer megafauna more subdued. The influence of mammoth and other large game on human subsistence decisions, material culture, mobility, and other aspects of behavior and social organization would be reduced as a result. How these factors played out prehistorically is a different question which deserves separate consideration.

Finally, it should be obvious from this study that evaluating early Paleoindian prey choice requires that we take the time to fully understand the environments these foragers lived in, the types and abundances of food items they hunted and gathered, and the costs and benefits involved in procuring and processing both plants (which we have admittedly shorted here) and animals. In this case, much of the strength of our conclusions rests on whether or not we have adequately modeled late Pleistocene prey population densities. Indeed, if this paper points to any one issue, it is that estimates of encounter rates with ancient faunas are critical to interpreting any record of prehistoric hunting, especially within an optimal foraging context. Whatever the true breadth of the early Paleoindian diet, a great deal of research still lies before us.

Acknowledgements

We would like to thank Jack Broughton, Mike Cannon, Judson Finley, David Meltzer, James O'Connell, Craig Smith, Todd Surovell, and two anonymous reviewers for their helpful comments on earlier versions of this paper and Gary Haynes and Bob Kelly for their discussion at the 2005 SAAs. We also give special thanks to Robert Bailey, who was kind enough to share his observations on elephant handling time.

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