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Explaining variability in Early Paleoindian foraging

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Abstract

We have argued elsewhere [Cannon, M.D., Meltzer, D.J., 2004. Early Paleoindian foraging: examining the faunal evidence for large mammal specialization and regional variability in prey choice. Quaternary Science Reviews 23, 1955–1987] that the North American archaeofaunal record provides little support for the notion that Early Paleoindians across the continent practiced a uniform subsistence strategy focused on the specialized hunting of large mammals; rather, there is some evidence for regional variability in human subsistence during the Early Paleoindian period (ca. 11,500–10,800 ^{14}C yr BP). Here, we further explore the archaeofaunal evidence for regional variability in subsistence behavior, focusing in particular on diet breadth and on the degree to which diets were dominated by large-bodied mammals. We also show how geographic variability in Early Paleoindian foraging can be understood in relation to environmental variability by employing a foraging theory model of patch choice in fractal environments [Ritchie, M.E., 1998. Scale-dependent foraging and patch choice in fractal environments. Evolutionary Ecology 12, 309–330]. Broad-scale patterns of regional variability in Early Paleoindian prey choice are consistent with the explanation—derived from the fractal patch choice model in conjunction with paleoenvironmental data on the "grain-size" of terminal Pleistocene environments—that the subsistence strategies of early Americans were sensitive to the tradeoff between searching for and foraging in resource patches in a patchy environment, and that those strategies varied in response to the heterogeneity of the environments that different early American groups inhabited. We conclude by briefly critiquing the use of foraging theory in Early Paleoindian research and by presenting suggestions for future improvements in our understanding of Early Paleoindian subsistence.

1. Introduction

For the last few decades, research into the subsistence adaptations of the earliest archaeologically known North Americans has centered on debate over whether they were specialized hunters of megafauna (see Cannon and Meltzer, 2004 and references therein). The "megafaunal specialist" view of Early Paleoindian subsistence has its roots in the early discovery of Clovis artifacts in association with the bones of megafauna— particularly mammoths—and the received wisdom within archaeology in the decades following the acceptance of Clovis was that, across the continent, the first North Americans were highly specialized "big game hunters" (see overview in Meltzer, 1993). Many have continued to hold this view of continent-wide megafaunal specialization despite the compelling arguments that others have made concerning, for example, biases in the way in which the Early Paleoindian archaeofaunal record has been sampled, evidence for more generalized diets during the Early Paleoindian period, and evidence for regional variability in subsistence during this period (e.g., Grayson, 1988; Meltzer, 1988, 1993). Spirited debate over such issues continues to the present day (e.g., Haynes, 2007).

We believe, however, that future progress in our understanding of the adaptations of early Americans will come not from continued pursuit of the "specialist–generalist" debate, but rather from a shift in the kinds of questions that we ask about subsistence during the Early Paleoindian period. The usual question—"were Early Paleoindians specialized megafauna hunters?"—no longer has much salience given the numerous empirical problems that have been shown to plague the received wisdom of megafaunal specialization. In addition, it is time to seriously question the assumption of continent-wide uniformity in subsistence that underlies this usual question (an assumption that is

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often implicit but that is occasionally made very explicit: e.g., Haynes, 1982). The assumption of continent-wide uniformity developed at a time when a paucity of data made the phenomena of interest appear to be fairly simple. However, as new data have accumulated—pertaining both to Early Paleoindian subsistence and to terminal Pleistocene environments—it has become increasingly clear that these phenomena are far more complex and variable than was once thought.

Given these points, it will likely be much more productive to pursue a different kind of question, one that allows for the possibility of variation in subsistence adaptations among Early Paleoindian groups. Specifically, we believe that it is more useful to ask how and why resource choice varied among those groups. As we will discuss, there is considerable evidence for regional variability in prey choice during the Early Paleoindian period. The goal of research into Early Paleoindian subsistence should be to understand the factors that resulted in that variability.

In this paper, we present the outline of an approach that may provide an answer to the question of how and why prey choice varied among Early Paleoindian groups. To answer the ‘‘how’’ part of the question, it is necessary to evaluate and analyze the relevant empirical evidence—which comes largely from faunal remains—in order to derive well-founded conclusions about the nature of Early Paleoindian subsistence adaptations and variability therein. We therefore begin by summarizing the results of such an empirical study that we have conducted, and we cannot stress enough how important it is for any consideration of Early Paleoindian subsistence to include a critical empirical analysis of this sort alongside theoretically informed arguments. Different theoretical arguments can lead to different conclusions (e.g., compare Waguespack and Surovell, 2003 to Byers and Ugan, 2005), and empirical evaluation, of course, is the way to determine which of those conclusions are correct.

To answer the ‘‘why’’ part of the question, we believe that it is necessary to develop a detailed understanding of the terminal Pleistocene environments that Early Paleoindian groups inhabited *and* to develop an understanding of the ways in which those environments influenced the subsistence-related decisions that early American foragers made. Models from foraging theory provide a very useful framework for doing this. Several researchers have already used foraging theory to provide insights into the subsistence and mobility practices of early Americans (see overview in Broughton and Cannon, 2008), and in this paper we discuss ways in which this line of research might be advanced.

1.1. Notes on terminology

Following our earlier usage (see Cannon and Meltzer, 2004, pp. 1956–1957), we use the term ‘‘Early Paleoindian’’ to refer to the archaeological complexes that represent the earliest secure evidence of a human presence within their respective geographic regions (ca. 11,500–10,800 ^{14}C yr BP). Our analysis thus includes ‘‘classic’’ Clovis archaeofaunal assemblages from the Plains and the Southwest as well as assemblages associated with other technological complexes in other parts of North America. This is justified given that issues of subsistence are generally recognized to be very relevant to colonization processes (e.g., Kelly and Todd, 1988; Surovell, 2000; Haynes, 2002a). We also note that other researchers have started with similar sets of assemblages in their own analyses of early American subsistence (e.g., Haynes, 2002a, b; Waguespack and Surovell, 2003).

In discussing vertebrate taxa, we use the term ‘‘megafauna’’ to refer to the largest-bodied of the North American Pleistocene mammals for which there is some evidence of human predation: specifically, mammoth (*Mammuthus*), mastodon (*Mammut*), bison (*Bison*), camel (*Camelops*), and horse (*Equus*). We use the term ‘‘large herbivores’’ for a broader group of taxa that includes megafauna and smaller mammals such as deer (*Odocoileus*) and caribou (*Rangifer*).

Finally, it is important to be clear what is meant by terms such as ‘‘specialist’’ and ‘‘generalist’’ (Waguespack and Surovell, 2003). Here, we treat subsistence specialization and generalization not as discrete categories but as opposite ends of a continuum of dietary diversity. As discussed further below, the analyses presented in this paper are based on measures of the two components of diversity (e.g., Magurran, 1988): richness, specifically the number of resource types included in the diet (i.e., diet breadth), and evenness, or the degree to which the diet is dominated by one or a few resource types. Consistent with the theme of moving beyond the ‘‘specialist–generalist’’ debate, we do not attempt to categorize Early Paleoindian foragers as either ‘‘specialists’’ or ‘‘generalists’’ in some absolute sense, but rather are concerned with documenting variability in dietary diversity, or in the relative *degree* of subsistence specialization or generalization.

2. Evaluating the Early Paleoindian archaeofaunal record

Before we discuss zooarchaeological evidence for variability in Early Paleoindian prey choice and an approach to making sense out of that variability, we first summarize the conclusions of recent evaluations of the existing Early Paleoindian archaeofaunal record. This provides important background for the new analyses that we present here.

Grayson and Meltzer (2002) began a critical evaluation of the Early Paleoindian archaeofaunal database by considering the state of the evidence for human predation on mammalian taxa that went extinct near the end of the Pleistocene. They concluded that a strong case could be made for human predation on only two of the approximately 35 genera of mammals that went extinct—mammoth and mastodon—and they noted that there are only 14 sites from North America north of Mexico that provide evidence for this predation. They also noted that there is suggestive evidence for human predation on two other genera—camel and horse—from one or two sites each.

We continued this evaluation by expanding the analysis to include all vertebrate taxa, extinct or extant, mammal or not (Cannon and Meltzer, 2004). We concluded that there is good evidence for human subsistence use of bison from six sites, and, when combined with the associations with extinct taxa discussed by Grayson and Meltzer (2002), this makes for a total of 23 reasonably convincing subsistence associations with megafauna. On the other hand, using the same standards for documenting subsistence use, we found that there are actually more—–at least 30—convincing subsistence associations with smaller prey, including a variety of mammals, birds, reptiles, amphibians and fishes. We noted that archaeologists, with their myopic focus on megafauna when it comes to the late Pleistocene, have typically ignored this evidence for fairly broad diets (also see Byers and Ugan, 2005 for a theoretical argument on this point).

We also showed that the way in which archaeologists have sampled the archaeological record has unquestionably resulted in a sample of Early Paleoindian faunal assemblages that is biased in favor of assemblages dominated by the bones of megafauna (e.g., Grayson, 1988). Moreover, we showed that when site function is taken into account, those sites that appear to provide evidence for a high degree of subsistence specialization by Early Paleoindians are better viewed simply as components of a broader subsistence and settlement system. Most Early Paleoindian archaeofaunal assemblages come from sites that appear to have been limited-function kill and/or butchery locales. It is to be expected that the remains of only one or at most a few prey taxa will be found at kill/butchery locales. It is also to be expected that the remains found at such sites should be from large-bodied taxa, rather than small-bodied taxa, since it is generally not economical to field process small resource packages prior to transport (e.g., Metcalfe and Barlow, 1992; Cannon, 2003). At residential sites, on the other hand, one should expect to find evidence of a much greater proportion of the full range of subsistence activities that a foraging group undertook, and Early Paleoindian archaeofaunal assemblages from sites that arguably did serve a residential function (e.g., the Aubrey site in north Texas, see Ferring, 2001) indeed suggest that diets were relatively broad and not dominated by megafauna (such is also the case for later Paleoindian residential sites, which include a wide variety of faunal remains and are not dominated by bison: e.g., Bamforth, 2007).

Finally, we pointed out that, while the archaeofaunal record provides no compelling evidence for a continent-wide focus on megafauna hunting, it does provide some evidence for regional variability in prey choice during the Early Paleoindian period (Fig. 1). Sites with strong evidence for human predation of proboscideans occur in the Southwest, the Plains and the Midwest, and sites with secure subsistence associations with bison occur at lower latitudes. On the other hand, it appears that caribou were the largest mammal targeted by hunters in the Northeast, and, though no site from the Great Basin has a compelling subsistence association with any vertebrate taxon due to questions about such things as dating or taphonomic history, the best candidate from this region, Smith Creek Cave in eastern Nevada, involves an association with mountain sheep (*Ovis canadensis*). Further consideration of these regional differences in the specific prey taxa hunted is beyond the scope of this paper, which focuses on more general variables related to dietary diversity, but we note that this area is ripe for future research.

3. Further evidence for variability in prey choice

Here, we present additional analysis of geographical variability in Early Paleoindian subsistence. Building on the evidence that we just summarized for regional variability in the kinds of vertebrate prey that early Americans hunted, we now consider evidence for variability in diet breadth and in the degree to which diets were dominated by large mammals, independent of the specific taxa involved.

3.1. Methods

Our analysis incorporates 22 Early Paleoindian faunal assemblages that provide convincing evidence for human predation on one or more mammalian taxa; as discussed elsewhere (Grayson and Meltzer, 2002; Cannon and Meltzer, 2004), these assemblages comprise the entire current sample of Early Paleoindian sites at which subsistence associations with faunal remains are thoroughly documented. Criteria used in evaluating subsistence associations are described in Grayson and Meltzer (2002) and Cannon and Meltzer (2004). The sites included in our analysis are shown in Fig. 2. Table 1 lists the mammal genera reported for the assemblages from these sites, with such taxonomic abundance information as is available, and the summary data used in the analyses presented below are provided in Table 2.

We explore regional variability in diet breadth as measured by the number of mammalian genera per assemblage for which there is compelling evidence of subsistence use. This variable of archaeofaunal richness should be related to prehistoric diet breadth (e.g., Broughton and Grayson, 1993; Grayson and Delpech, 1998), but we note that it likely systematically under-represents actual diet breadth for the Early Paleoinidan case due to the sampling and taphonomic issues summarized above. We explore variability in the degree of dominance by large mammals as measured by the proportion of those genera that are either megafauna or large herbivores more broadly. Because complete taxonomic abundance and

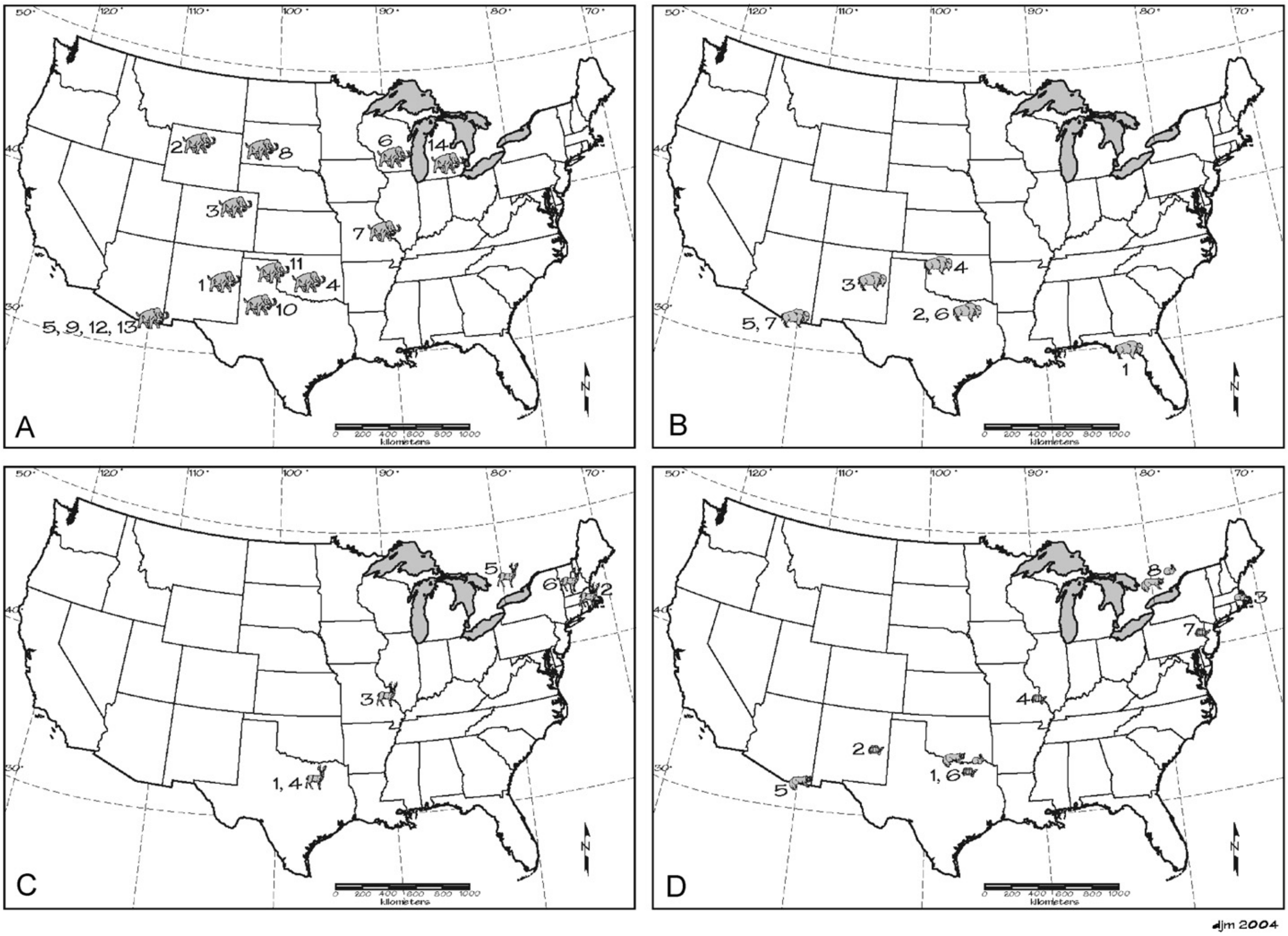

Fig. 1. Sites for which there is strong evidence of Early Paleoindian subsistence use of vertebrates. (A) Sites with strong evidence for Early Paleoindian use of mammoth (1–6, 8–13) and mastodon (7, 14): (1) Blackwater Locality 1, (2) Colby, (3) Dent, (4) Domebo, (5) Escapule, (6) Hebior, (7) Kimmswick, (8) Lange-Ferguson, (9) Lehner, (10) Lubbock Lake, (11) Miami, (12) Murray Springs, (13) Naco, (14) Pleasant Lake. (B) Sites with strong evidence for Early Paleoindian use of bison (1, 2, 3, 4, 5, 7), camel (5), and horse (3, 6): (1) Alexon, (2) Aubrey, (3) Blackwater Locality 1, (4) Jake Bluff, (5) Lehner, (6) Lewisville, (7) Murray Springs. (C) Sites with strong evidence for Early Paleoindian use of deer (1, 3, 4) and caribou (2, 5, 6): (1) Aubrey, (2) Bull Brook, (3) Kimmswick, (4) Lewisville, (5) Udora, (6) Whipple. (D) Sites with strong evidence for Early Paleoindian use of carnivores (5, 6, 8), leporids and rodents (1, 3, 6, 8), and birds, reptiles, amphibians and fish (1, 2, 4, 6, 7): (1) Aubrey, (2) Blackwater Locality 1, (3) Bull Brook, (4) Kimmswick, (5) Lehner, (6) Lewisville, (7) Shawnee-Minisink, (8) Udora.

sample size information is not reported for all Early Paleoindian assemblages (see Table 1), these "megafauna proportion" and "large herbivore proportion" variables are the only measures of large mammal dominance that can presently be used with this dataset (see Cannon and Meltzer, 2004 for further discussion).

Each of the variables that we use, of course, reflects not just prehistoric human prey choice but also various taphonomic and sampling-related factors (Cannon and Meltzer, 2004), and the statistical analyses presented here take the effects of such factors into account. Specifically, we take into account the fact that assemblage richness and the degree of dominance by large-bodied taxa both vary depending on whether or not sediments were screened during excavation and depending on whether a site appears to have been a limited function kill/butchery location or whether it likely served a residential purpose; the presence or absence of hearths at a site is used as a proxy measure for this latter "site function" factor (Table 2).[1]

We compare assemblage richness and the degree of dominance by large-bodied taxa among assemblages

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[1] Two other taphonomic or sampling related factors were also considered in Cannon and Meltzer (2004), but it is not necessary to do so here. Those factors were discovery method (i.e., whether a site was excavated due to the discovery of large mammal bones or for some other reason) and deposit type (i.e., cave site, open site, or underwater site). Among the 22 assemblages that we use in this analysis, all but three (those from Bull Brook, Udora and Whipple) were excavated due to the discovery of megafaunal remains, and all but one (from Alexon) are from open sites. Consequently, the discovery method and deposit type factors have no statistically significant effect on assemblage richness or the degree of dominance by large-bodied taxa in the set of assemblages that we use here.

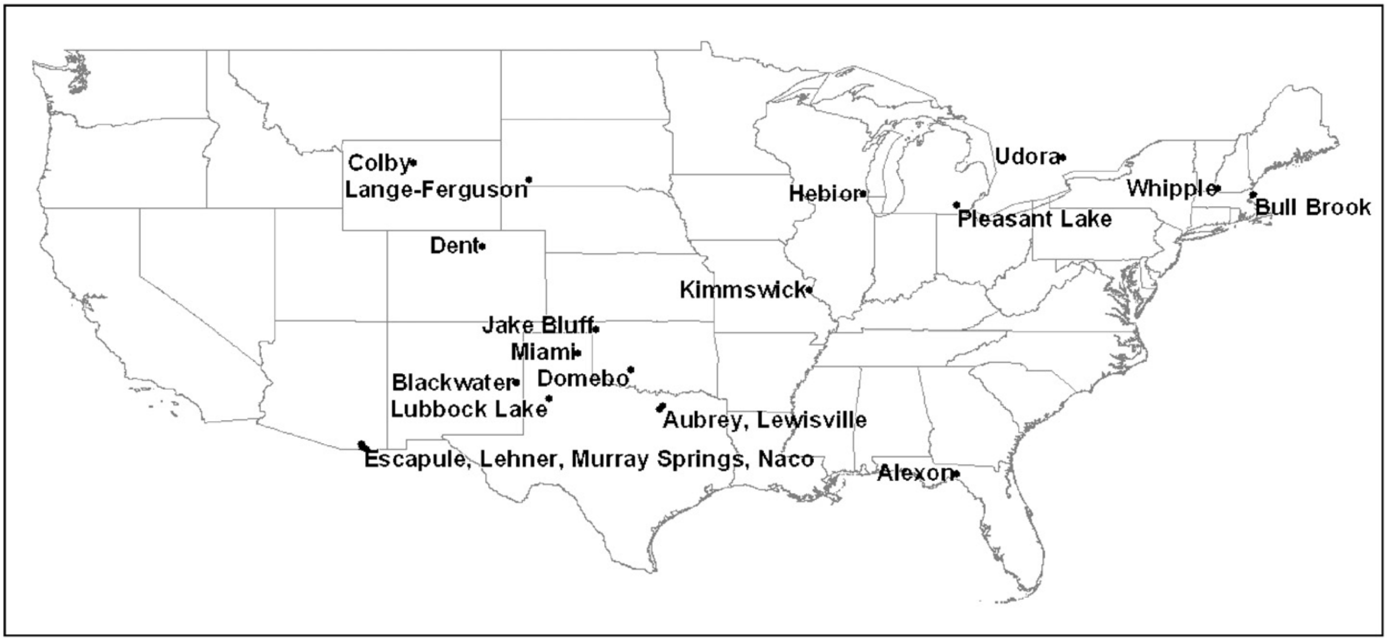

Fig. 2. Locations of sites that provide compelling evidence of Early Paleoindian subsistence use of one or more mammalian taxa.

aggregated into three large regions based on physiographic provinces (Fig. 3; the physiographic province boundaries used here follow US Geological Survey, 2004). These three regions include the Great Plains, everything to the west of the Plains, and everything to the east of the Plains. Obviously, it is quite likely that Early Paleoindian subsistence varied on a geographic scale much finer than that which is captured by these large regions. However, the size of these regions is mandated by the small sample of sites that are presently useful for an analysis of this sort: grouping sites into regions smaller than the ones that we use would render results statistically meaningless. We look forward to the publication of detailed taphonomic analyses of the faunal assemblages from additional Early Paleoindian sites so that regional variability in the subsistence adaptations of early Americans can be explored at an even finer scale, as it is very likely that the accumulation of additional high-quality data will provide further evidence for variability in early American subsistence.

3.2. Results

There is some variability in diet breadth among the three regions that we consider (Fig. 4). In particular, assemblages from the East tend to be richer than those from the Plains or the West (East mean number of genera = 2.40, Plains mean = 1.29, West mean = 1.80). A multifactor analysis of variance, which also incorporates the factors of site function (i.e., hearths present or absent) and recovery method (i.e., whether or not it is known that screens were used in excavation), indicates that the differences in mean number of genera among the regions are significant (region factor $p = 0.001$, hearth factor $p < 0.0005$, screening factor $p < 0.0005$, model $r^2 = 0.912$, model $p < 0.0005$).[2]

More striking than these regional differences in richness are differences in the degree to which assemblages are dominated by megafauna (Fig. 5) or by large herbivores more broadly (Fig. 6). Compared to assemblages from the Plains and the West, which consist almost entirely of large-bodied taxa, much lower proportions of the mammal genera in assemblages from the East, on average, are either megafauna or large herbivores (megafauna proportion: East mean = 0.49, Plains mean = 1.00, West mean = 0.95; large herbivore proportion: East mean = 0.77, Plains mean = 1.00, West mean = 0.95). Multifactor analyses of variance indicate that the differences among the regions in both mean megafauna proportion and mean large herbivore proportion are significant (megafauna proportion: region factor $p = 0.005$, hearth factor $p = 0.062$, screening

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[2] There are significant interactions in this model between region and the presence or absence of hearths ($p = 0.001$) and between the hearth factor and the screen factor ($p < 0.0005$). The more relevant of these interactions, that between region and the hearth factor, can be dealt with by considering sites with and without hearths separately. When this is done, mean richness remains highest for the East region among both sites with hearths (East mean number of genera = 4.00, Plains mean = 2.00, West mean = 3.00) and sites without hearths (East mean number of genera = 1.33, Plains mean = 1.00, West mean = 1.00). The effect of the region factor remains significant for sites with hearths ($p = 0.026$; model $r^2 = 0.893$, model $p = 0.021$), though it becomes insignificant for sites without hearths ($p = 0.376$; model $r^2 = 0.222$, model $p = 0.798$), which is perhaps not surprising given that most of the sites without hearths are likely kill/butchery locales at which richness should be expected to be low regardless of geographic region. Thus, these results suggest that, despite the presence of the interaction, it is still reasonable to conclude that Early Paleoindian diets were broader in the East, on average, than in the Plains and the West.

Table 1
Mammal genera reported for assemblages with compelling evidence for human subsistence use of one or more mammalian taxa

Assemblage	Abundance units	*Didelphis*	*Holmesina*	*Glyptotherium*	*Glossotherium*	*Dasypus*	*Blarina*	*Sorex*	*Scalopus*	*Alopex*	*Canis*	*Vulpes*	*Smilodon*	*Mephitis*	*Mustela*	*Procyon*	*Arctodus*	*Ursus*	*Mammut*	*Mammuthus*	*Equus*	*Tapirus*	*Mylohyus*	*Platygonus*	*Camelops*	*Hemiauchenia*	*Palaeolama*
Alexon[a]	M/N																				1/1					1/2	2/2
Aubrey	N				135				55											3	1						
Blackwater, BSW	N	1				4		2			3	1				1		1		10*	2*						
Blackwater, GS	N										6	1	2							306*	72			2	4	3	
Bull Brook	N																										
Colby	M/N																			7/424*	1/1				1/2		
Dent	M																			12*							
Domebo	M/N																			1/~75*							
Escapule	M/N																			1/18*							
Hebior	M																			1*							
Jake Bluff	M/N																										
Kimmswick					+		+				+				+				+*				+				
Lange-Ferguson	M/N						2/7	5/?												2/153*							
Lehner	M/N										2/8							2/9*		13/104*	2/6	1/3			3/41*		
Lewisville, 1950s	M/N			1/?					1/1		2/?*			2/2		5/?*		1/1		2/2	8/˜10*			1/?	2/?		
Lubbock Lake	N		2				1				+	+					6			>50*	27			1	12	2	
Miami	M/N																			5/>54*							
Murray Springs	N										18									149*	45			1	8		
Naco	M/N																			1/35*							
Pleasant Lake	M																		1*								
Udora	N									1*																	
Whipple	N																										

Assemblage	*Odocoileus*	*Rangifer*	*Antilocapra*	*Capromeryx*	*Bison*	*Ovibos*	*Cynomys*	*Marmota*	*Sciurus*	*Spermophilus*	*Castor*	*Geomys*	*Thomomys*	*Dipodomys*	*Perognathus/ -Chaetodipus*	*Zapus*	*Clethrionomys*	*Microtus*	*Ondatra*	*Synaptomys*	*Neotoma*	*Onychomys*	*Oryzomys*	*Peromyscus*	*Reithrodontomys*	*Sigmodon*	*Sylvilagus*	*Lepus*
Alexon	+				1/~22*																							
Aubrey	17*				26*					2		127*		1	5			119	6	15	5		1	12	2	6	8	2
Blackwater, BSW	1			1	161		4		1			7						>14	6		9			3	2	5		1
Blackwater, GS					44*														2									
Bull Brook		1*									1*																	
Colby			1/6		2(?)/4	1/2																						1/3
Dent																												
Domebo															1/1											?/2		
Escapule																												
Hebior																												
Jake Bluff					15/167*																							
Kimmswick	+*							+	+	+		+						+	+	+				+			+	
Lange-Ferguson	1/5				1/?					1/2			5/?			1/2	1/?	17/?	1/2			1/?		4/?	1/1			1/1
Lehner					4/38*								?/9		1/1			1/1	1/1								1/1	
Lewisville, 1950s	9/?*				2/5		8/8*		1/?	1/?								1/?*			4/?*			8/?*			13/~15*	13/?
Lubbock Lake				2	+		+			+		+	2		+			+	+		+	+		+	+			+
Miami																												
Murray Springs					338*													5			1							
Naco					+																							
Pleasant Lake																												
Udora		3*																										3*
Whipple		3*																										

Note: Sources for the information in this table are listed in Cannon and Meltzer (2004, Table 1). For taxonomic abundance units, "M" = MNI and "N" = NISP. Plus signs ("+") indicate the presence of mammal genera for which abundance values are not reported. Asterisks ("*") indicate taxa in individual assemblages for which there is compelling evidence for human subsistence use for at least some specimens, as discussed in Cannon and Meltzer (2004) and Grayson and Meltzer (2002).

[a] As discussed in Cannon and Meltzer (2004), the Alexon site may post-date the Early Paleoindian period.

Table 2
Summary data for assemblages with compelling evidence for human subsistence use of one or more mammalian taxa

Assemblage	Region	Screened	Hearths	Number of mammal genera	Number of large herbivore genera	Large herbivore proportion	Number of megafauna genera	Megafauna proportion
Alexon	East	Unknown	No	1	1	1.00	1	1.00
Aubrey	East	Yes	Yes	3	2	0.67	1	0.33
Blackwater, BSW	Plains	Yes	Yes	2	2	1.00	2	1.00
Blackwater, GS	Plains	Yes	Yes	2	2	1.00	2	1.00
Bull Brook	East	Unknown	No	2	1	0.50	0	0.00
Colby	West	Yes	No	1	1	1.00	1	1.00
Dent	Plains	Unknown	No	1	1	1.00	1	1.00
Domebo	East	Yes	No	1	1	1.00	1	1.00
Escapule	West	Unknown	No	1	1	1.00	1	1.00
Hebior	East	Unknown	No	1	1	1.00	1	1.00
Jake Bluff	Plains	Unknown	No	1	1	1.00	1	1.00
Kimmswick	East	Yes	No	2	2	1.00	1	0.50
Lange-Ferguson	Plains	Yes	No	1	1	1.00	1	1.00
Lehner	West	Unknown	Yes	4	3	0.75	3	0.75
Lewisville, 1950s	East	Unknown	Yes	9	2	0.22	1	0.11
Lubbock Lake	Plains	Yes	No	1	1	1.00	1	1.00
Miami	Plains	Unknown	No	1	1	1.00	1	1.00
Murray Springs	West	Unknown	Yes	2	2	1.00	2	1.00
Naco	West	Unknown	No	1	1	1.00	1	1.00
Pleasant Lake	East	Yes	No	1	1	1.00	1	1.00
Udora	East	Yes	Yes	3	1	0.33	0	0.00
Whipple	East	Yes	Yes	1	1	1.00	0	0.00

Note: All "numbers of genera" include only taxa for which there is compelling evidence of subsistence use by humans at the site in question (see Table 1).

factor $p = 0.929$, model $r^2 = 0.714$, model $p = 0.028$; large herbivore proportion: region factor $p = 0.031$, hearth factor $p = 0.035$, screening factor $p = 0.138$, model $r^2 = 0.644$, model $p = 0.078$; there are no significant interactions in either of these models).

To summarize these results, assemblages from the East contain, on average, slightly higher numbers of genera with evidence of subsistence use, and much lower proportions of those genera, on average, are either megafauna or large herbivores more broadly. In other words, based on the database of well-documented Early Paleoindian faunal assemblages that is currently available, we can conclude that the diets of early Americans in eastern North America were broader and less dominated by large mammals than were the diets of their contemporaries to the west. Our previous analysis (Cannon and Meltzer, 2004) suggested that, once sampling and taphonomic biases are taken into account, Early Paleoindian diets across the continent were more generalized than the received wisdom would have us believe. The present analysis suggests that there was substantial regional variability in the breadth of those diets and in the degree to which they were dominated by large-bodied prey.

4. Explaining variability in Early Paleoindian subsistence

The question now becomes, how can we explain this regional variability in subsistence? A productive approach, which we outline here, may be to draw on a model of landscape use developed for patchy environments with fractal qualities (Ritchie, 1998). This "fractal patch choice model" builds upon basic foraging theory models of patch choice (e.g., Stephens and Krebs, 1986) by being more explicit about the spatial distribution of resources. This model can be used to develop predictions about the proportion of resource patches within an environment that a forager should use—that is, whether a forager should be a "patch specialist" or a "patch generalist"—based on the "grain-size" of the environment, or the degree of spatial heterogeneity that it exhibits. These predictions can be tested by comparing data on environmental grain-size to subsistence data, and if the predictions are met, then variability in subsistence can be explained in terms of environmental variability, as we discuss next (for a general discussion of the relationship between foraging theory models and explanatory mechanisms, see, e.g., Cannon and Broughton, 2008).

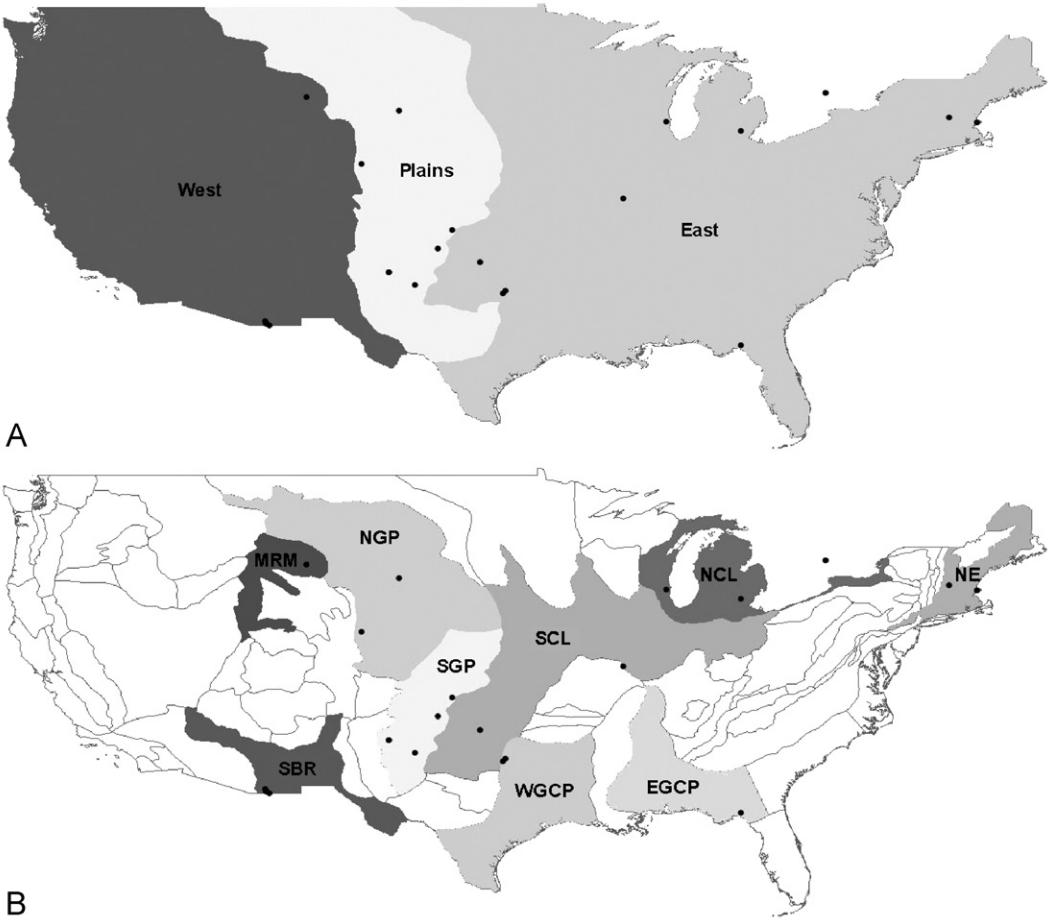

Fig. 3. Regions used in analysis of geographical variability in Early Paleoindian subsistence (A), and the physiographic provinces on which those regions are based (B; SBR = southern portion of Basin and Range province, MRM = Middle Rocky Mountains, NGP = northern portion of Great Plains province, SGP = southern portion of Great Plains province, SCL = southern portion of Central Lowland province, NCL = northern portion of Central Lowland province, WGCP = West Gulf Coastal Plain, EGCP = East Gulf Coastal Plain, NE = New England). Dots indicate locations of sites used in this analysis (see Fig. 2).

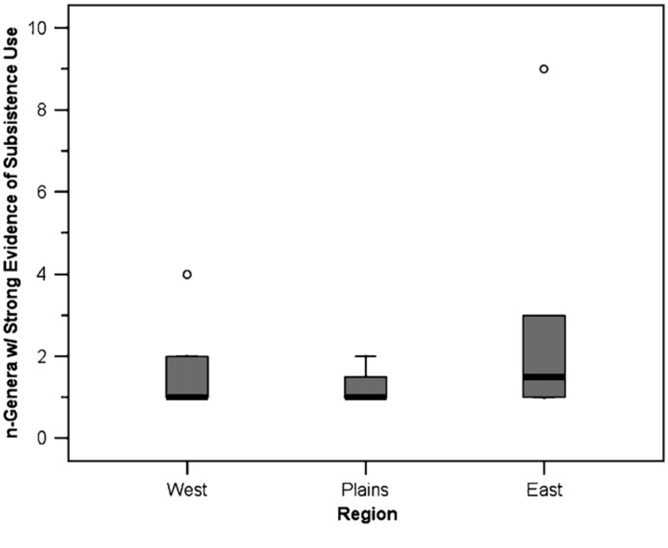

Fig. 4. Boxplot comparing numbers of mammalian genera per assemblage with compelling evidence of subsistence use among geographic regions.

4.1. The fractal patch choice model

Ritchie's "fractal patch choice model" is intended primarily to predict the spatial scale at which a forager should perceive differences among resource patches. In doing so, however, it also makes predictions about the relationship between environmental structure and the proportion of the patches within an environment that a forager should use. The model can thus be thought of as making predictions about "optimal patch breadth".

The model shows that in coarse-grained environments—or environments that are homogenous (relatively few resource patches, which, on average, are large in size)—the most efficient foraging strategy is to use only the few largest patches and to ignore the rest. On the other hand, in fine-grained environments—or environments that are heterogeneous (many small resource patches can be found within a given area)—the most efficient strategy is to forage in a larger proportion of the patches within the environment. This prediction is based on the tradeoff between

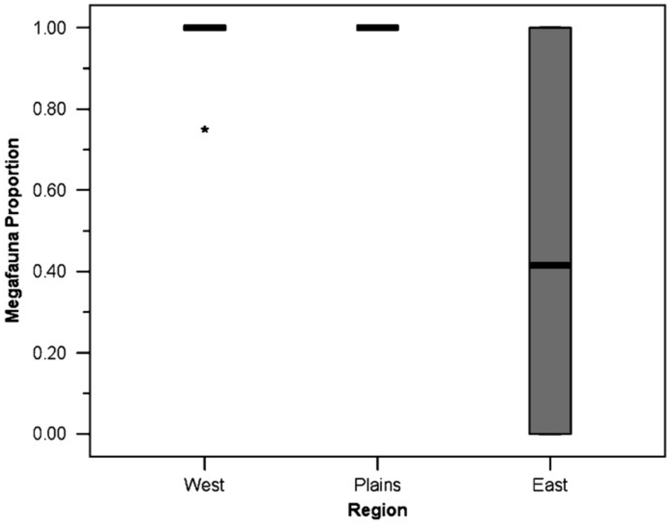

Fig. 5. Boxplot comparing proportions of mammalian genera with compelling evidence of subsistence use that are megafauna.

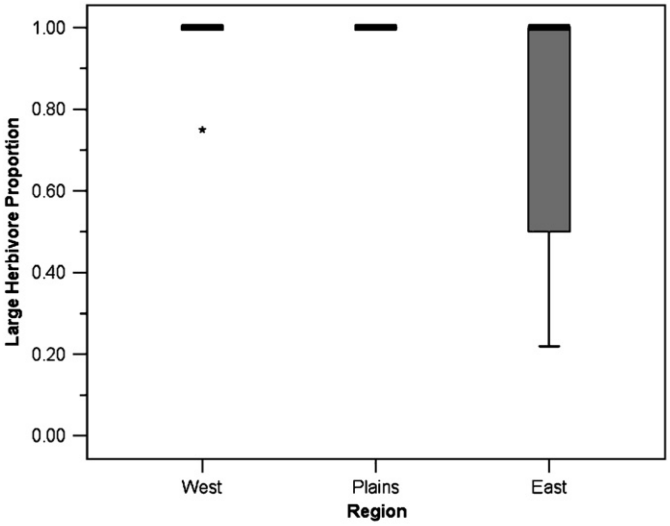

Fig. 6. Boxplot comparing proportions of mammalian genera with compelling evidence of subsistence use that are large herbivores.

searching for and foraging in resource patches that any forager in a patchy environment faces: when large resource patches are abundant, the opportunity costs of time spent traveling between patches are higher than is the case when large patches are rare. This prediction about patch choice is somewhat analogous to the prediction about prey choice that the basic prey model of foraging theory makes based on the tradeoff between searching for and handling resources (e.g., Stephens and Krebs, 1986), which is that low-return resources should be pursued only when higher-return resources are rare.

The fractal patch choice model provides several advantages in comparison to more basic foraging theory models. First, unlike the more basic models, this model makes fewer assumptions that complicate archaeological applications (for example, the "fine-grained search assumption" of the basic prey model: for discussion see, e.g., Broughton, 1994; Cannon, 2003). Second, it is not simply a model of resource choice but a more general model of landscape use, and we would argue that many of the questions about the Early Paleoindian period that interest archaeologists are fundamentally questions about landscape use. Along these lines, the "fractal patch choice model" makes predictions about both subsistence and mobility, predicting that foragers in finer-grained environments should move over shorter distances as they use a greater proportion of the relatively small patches in their environment. Though outside the scope of this paper, we note that such predictions about mobility could easily be tested with Paleoindian lithic sourcing data that are readily available for various parts of North America (e.g., Meltzer, 1988; Jones et al., 2003).

Finally, this model can be used to make predictions about landscape use based on known characteristics of the terminal Pleistocene environment. Testing predictions derived from this model simply requires reconstructing the grain-size of ancient environments and then comparing variability in that grain-size to variability in measures of diet breadth or mobility. As we discuss next, reconstructing environmental grain-size can be done in a relatively straightforward manner using paleoenvironmental data. On the other hand, it is much more difficult—if not impossible—to validly estimate prehistoric encounter rates for a wide range of resource types, which is what would be required before the basic prey model of foraging theory could be used to make comparable testable predictions (see Byers and Ugan, 2005 for a consideration of this issue).

4.2. The grain-size of terminal Pleistocene environments in North America

Paleoenvironmental data that bear on the structure of terminal Pleistocene environments in North America are available, and these data suggest that those environments did vary in a manner that would favor a greater degree of subsistence generalization in the East than in the Plains or the West.

For eastern North America, a temporal heterogeneity analysis of pollen data conducted by Williams et al. (2001, 2004; see also Shuman et al., 2005; Webb et al., 2004) suggests that this part of the continent saw very rapid changes in vegetation communities during the late Pleistocene and early Holocene, and particularly during the period between about 13,000 and 10,000 ^{14}C yr BP. This likely would have led to environments that were much more heterogeneous—or "fine-grained"—than the modern environments of the East by creating a mosaic-like pattern of patches of vegetation at different successional stages (e.g., Sousa, 1984; this proposition could be tested more directly in the future through a spatial heterogeneity analysis of pollen data). On the other hand, western environments (or at least the environments of the Great Basin and Southwest, which includes the location of the San Pedro Valley Clovis sites included in our analysis) were likely more homogenous during the terminal Pleistocene than they are today. This is because elevational zonation of vegetation—the main source of modern environmental heterogeneity in the west—appears to have been much less pronounced than it is today, a pattern revealed by numerous packrat midden records (e.g., Betancourt et al., 1990).

In addition, an analysis of mammal community richness that one of us has conducted (Cannon, 2004) using paleontological and archaeological assemblages from the FAUNMAP database (FAUNMAP Working Group, 1994) also suggests that environments of the East were more heterogeneous than those of the West, as well as those of the Plains, during the terminal Pleistocene. Habitat heterogeneity is one of the primary factors that underlies patterns in mammal community richness because areas that have a greater number of vegetation types can support a wider variety of mammalian taxa (e.g., Kerr and Packer, 1997; Simpson, 1964). Thus, mammal community richness can provide a proxy measure of habitat heterogeneity. In contrast to the modern situation in North America, in which western regions tend to have mammalian faunas that are much more diverse than those of eastern regions, it appears that environments of the East were richer in mammalian taxa than those of the West or the Plains during the late Pleistocene (Fig. 7).[3] This suggests, in turn, that there was a greater degree of environmental heterogeneity in the East than in the West or the Plains during that period.

Taken together, these studies suggest that, relative to the terminal Pleistocene environments of the West and the Plains, those of the East were, as a generalization, vegetationally more heterogeneous, incorporating a greater number of habitat types within any area of a given size. Making the reasonable assumption that the variability in vegetation community structure suggested by these studies correlates with variability in the size and distribution of the resource patches that were relevant to human foraging decisions, the fractal patch choice model predicts the observed pattern of a greater degree of subsistence generalization in the East than in the Plains or the West (Fig. 8). It should be further noted that, since the fractal patch choice model is designed to help understand the spatial scale at which foragers perceive their environments (Ritchie, 1998), the model itself might be used to help evaluate the assumption about the relationship between vegetation community structure and resource patches that is required here. The model should provide insight into questions such as whether it was an expanse of grassland, for example, that constituted the "patch" that was economically relevant to prehistoric foragers, or whether it was smaller aggregations of plants and animals within that grassland. Though doing so is beyond the scope of this paper, application of the model, or extensions thereof, to question of this sort has the potential to improve our more general understanding of Early Paleoindian landscape use (and, for that matter, landscape use in later Paleoindian times, for which we seek to answer some of the same questions regarding subsistence and adaptive strategies: e.g., LaBelle, 2005; Bamforth, 2007).

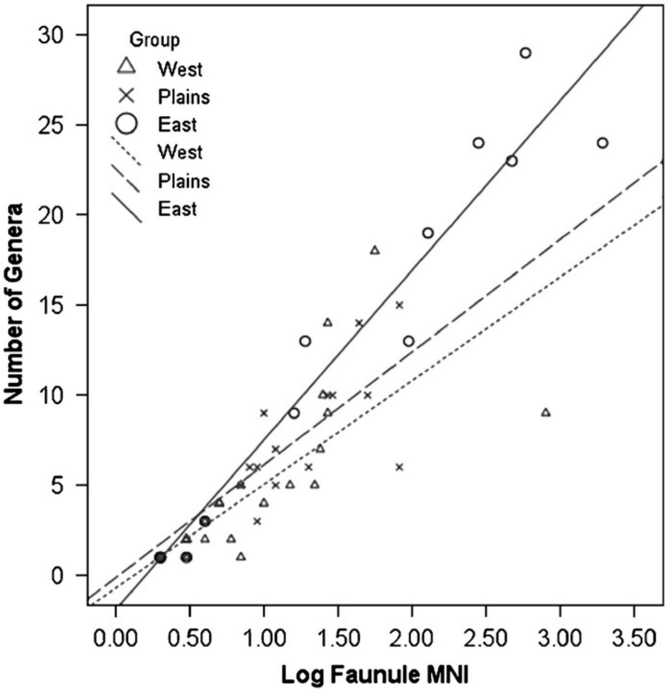

Fig. 7. Relationships between mammalian richness and sample size (measured as minimum number of individuals) for terminal Pleistocene FAUNMAP faunules from the East, Plains, and West regions. Richness increases more quickly with sample size for the East than for the Plains or the West, consistent with greater faunal community diversity in the East. Data are from faunules that date to FAUNMAP's "Late Glacial" period (15,000–10,000 ^{14}C yr BP), and come primarily from paleontological assemblages, though some archaeological assemblages are also included. (After Cannon, 2004: Fig. 4a; see that article for further discussion.)

5. Discussion and conclusions

Based on the available evidence that can be used to make inferences about the grain-size of North American environments during the terminal Pleistocene, it would appear that variation in the structure of those environments can account for the variability in prey choice that is evident in Early Paleoindian faunal assemblages, in accordance with predictions derived from the fractal patch choice model. The existing archaeofaunal and paleoenvironmental records are consistent with the explanation that the subsistence strategies of early Americans were sensitive to the tradeoff between searching for and foraging in resource

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[3] The high mammal richness of the East during the late Pleistocene is associated with the presence during this period of "non-analog" faunas. These are sets of taxa that are allopatric today but that were sympatric during the late Pleistocene, presumably due to greater habitat heterogeneity at that time (e.g., Graham, 1985a, b; Graham and Mead, 1987; Lundelius, 1989; Stafford et al., 1999). In North America, non-analog faunas are mainly a phenomenon of the part of the continent that corresponds to the East region used in this analysis (e.g., Lundelius et al., 1983, p. 346). See Cannon (2004) for further discussion.

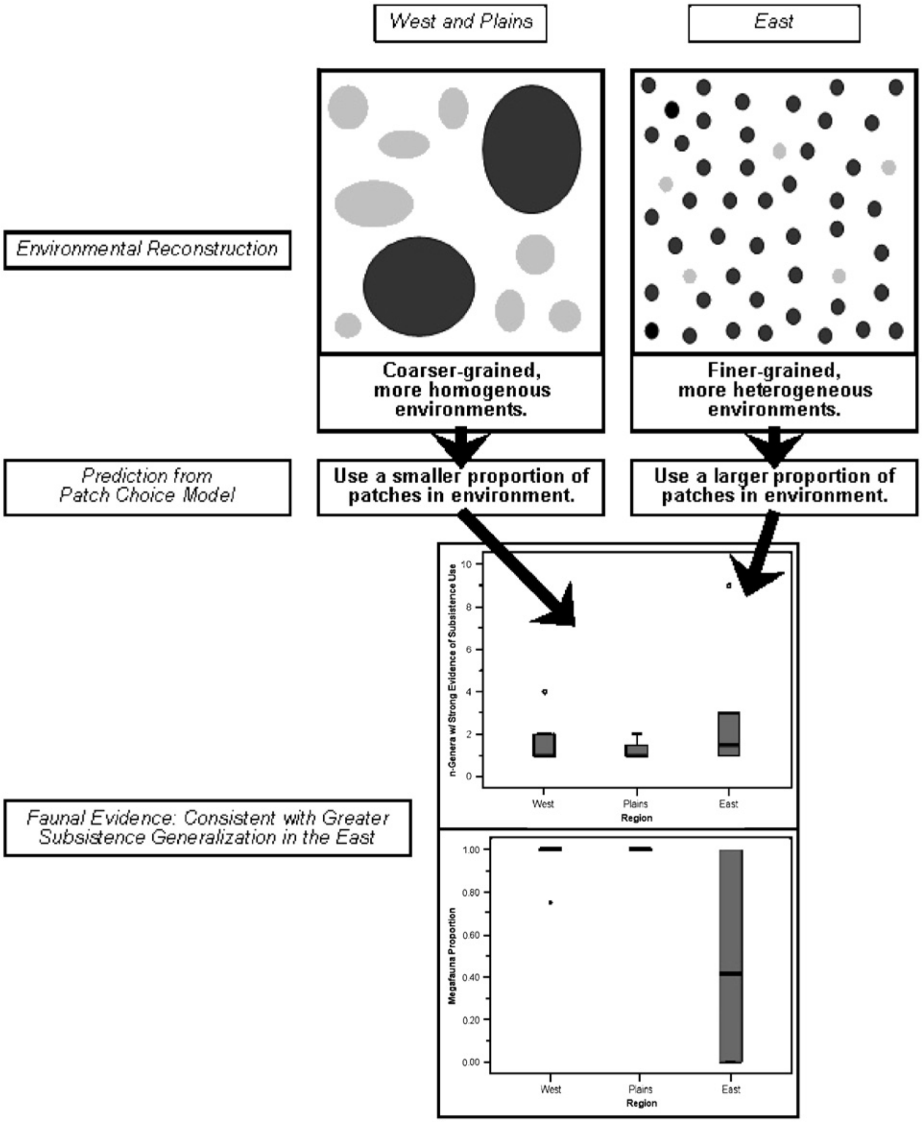

Fig. 8. Schematic representation of the relationship between environmental structure and subsistence strategy, as discussed in the text. (Black patches are those that are used and gray patches are those that are not used.)

patches in a patchy environment, and that those strategies varied in response to the heterogeneity of the environments that different Early Paleoindian groups inhabited.

There is certainly more to be done to test this ‘‘grain-size explanation’’ for variability in Early Paleoindian subsistence. Additional paleoenvironmental data directed at better understanding the structure of terminal Pleistocene environments are necessary, and one benefit of using an explicit theoretical construct like the fractal patch choice model is that it points to the specific kind of information about past environments that is required to adequately test explanations for prehistoric human subsistence and settlement patterns. Likewise, as we have pointed out before (Cannon and Meltzer, 2004), more thorough analysis and publication of Early Paleoindian archaeofaunal data are absolutely critical if our understanding of subsistence during this period is to advance. On the theoretical front, it would be very worthwhile to extend the fractal patch choice model to incorporate variability in the content of patches (rather than just the size of patches), which it does not presently do. And finally, a consideration of variability over time would be a useful complement to the purely synchronic analysis presented here. Pursuing avenues of research such as these should substantially improve our knowledge of Early Paleoindian subsistence, and perhaps the greatest advantage of the theoretical framework discussed here is that it provides guidance about how best to do so.

Along these lines, we conclude by offering some general observations on the current state of research into Early Paleoindian subsistence. First, as we have argued both above and elsewhere (Cannon and Meltzer, 2004), we cannot stress enough how important it is that fundamental issues of sampling and taphonomy be carefully investigated. Such issues cannot merely be argued or assumed away, but must instead be addressed head-on if we are to learn anything meaningful about Early Paleoindian subsistence. Second, for reasons that we discussed at the outset of this paper, we believe that it is time that archaeologists also begin to take seriously the issue of variability in the subsistence and mobility adaptations of Early Paleoindians. The use of foraging theory models can help us to understand the causes of such variability, as we have illustrated here, and it is far more productive to use foraging theory models in this capacity than it is to use them simply to pigeon-hole all early American groups into some category—either specialist or generalist—which is largely how foraging theory has been used to date in discussions of Early Paleoindian subsistence. The pigeonholing approach amounts to little more than foraging theory in the service of culture history (cf. Broughton and Bayham, 2003, p. 788), and foraging theory has much more to offer to archaeology than this. We have attempted to show here what it can offer by illustrating how, when coupled with appropriate paleoenvironmental data, it can help us explain variability in Early Paleoindian subsistence.

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