

Fragmented Landscapes and Economies of Abundance

The Broad-Spectrum Revolution in Arid East Asia

by Lisa Janz

Increasing diet breadth, a distinguishing characteristic of human foraging strategies at the end of the Pleistocene and in the early Holocene, is known to be a key development contributing to domestication and the spread of agriculture and pastoralism. Many scholars have focused on broad-spectrum foraging as a result of resource depression due to demographic stress or environmental degradation. However, these factors are absent in an increasing number of cases. New research in the Gobi Desert shows that a dramatic change in organizational strategies, including the intensified use of low-ranked foods from dune-field and wetland habitats, is closely correlated with the establishment of dispersed patches boasting high species diversity and a concentrated abundance of small prey. According to a global suite of paleoenvironmental and archaeological data, it appears that the fragmentation of more homogeneous grassland habitats coincided with the rise of broad-spectrum foraging and that these fragmented ecosystems were ideally suited to the unique set of foraging strategies employed by modern *Homo sapiens*. This study shows how broad-spectrum foraging, increased human population density, and the shift toward food production should be considered by-products of major environmental changes that created an ecological setting ideal for enhanced human reproduction.

The Broad-Spectrum Revolution (Flannery 1969) represents a pivotal shift in hunter-gatherer land use and subsistence, a change characterized by an expansion in diet breadth and increasingly intensive manipulation of food resources. Diets during the Middle Pleistocene (MIS [marine isotope stage] 19–MIS 5, 781–71 kya) can be very broadly characterized by intense exploitation of large game complemented by the low-level use of various small species that were easy to collect and consume, such as nuts, fruit, tortoises, and sometimes shellfish (Aura Tortosa et al. 2002; Bocherens 2009; Lev, Kislev, and Bar-Yosef 2005; Marean et al. 2007; McBrearty and Brooks 2000; Naito et al. 2016; Speth and Tchernov 2002; Stiner 2013; Stiner et al. 1999; but see Cochard et al. 2012; Henry, Brooks, and Piperno 2014). The occasional use of these easily collected small species contrasts with the routine exploitation of species whose capture and/or consumption required significantly greater energetic cost, including fast-moving small prey, such as fish, birds, and rabbits, or foods that were often heavily processed, such as small grass seeds or acorns. Increased diet breadth, or broad-spectrum foraging (BSF), is recognized by a

shift toward the regular exploitation of these high-cost species and represents a notable change in subsistence strategies (Stiner 2001; Stiner, Munro, and Surovell 2000). Technologies permitting the more efficient exploitation of such resources are themselves time-consuming to manufacture (e.g., nets, formal milling stones, and pottery), and their use emphasizes a greater energetic investment in extraction (Bailey and Aunger 1989; Elston, Dong, and Zhang 2011; Lupo and Schmitt 2002). Changes in land use, including some decrease in residential mobility and a more specialized focus on habitats rich in small prey—characteristics that signal a set of increasingly complex interactions with plant and small-animal species—frequently accompany the adoption of BSF strategies. Increases in diet breadth may have occurred as early as MIS 4 (71–61 kya; Clark and Kandel 2013) but were increasingly widespread toward the end of MIS 3 (60–30 kya; Villa et al. 2012). During MIS 1 (14 kya to the present), BSF became the dominant subsistence strategy worldwide. Although diet breadth varied across different environmental contexts, some combination of species such as fish, birds, rabbits, and grass seeds became markedly important to human diets in virtually all regions.

According to the prey-choice model, an expansion in diet breadth is most often interpreted as a response to the reduced availability of large game and is categorized as resource intensification (see Morgan 2015). Historically, economists and other social scientists have focused on population pressure or

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other types of resource depression, such as environmental degradation, as the primary driver of resource intensification. This idea is so deeply ingrained in Western thought that very few other explanations for the origins of agriculture have been clearly articulated, and those that have been are given little attention (e.g., Hayden 1990, 2009). The theoretical relationship between population pressure and resource depression emerged during the Enlightenment, when increased population density and food shortages were of grave concern to political economists such as Thomas Malthus (1766–1834), who argued that population increased more quickly than food production (Malthus 1798). Sven Nilsson first applied this idea to archaeology in 1868, when he proposed that increasing population density had compelled Scandinavian hunter-gatherers to become herders and then agriculturalists (see Trigger 2006:129). The idea that major changes in human diet resulted from declines in available resources was carried on into the twentieth century by Raphael Pumpelly (1908:65–66), who proposed that environmental degradation following the late Ice Age forced hunter-gatherers to cluster around permanent sources of water and begin domesticating herd animals and grass seeds as a new avenue of subsistence for increasingly dense populations. This idea became highly influential and was most famously developed by V. G. Childe (1928), who argued that the enforced juxtaposition of man and beast within these oases promoted domestication. Braidwood and Howe (1960) later refuted Childe's popular "oasis theory," arguing that there was no significant evidence in the Middle East to support environmental degradation as a driver of domestication. Food production was instead viewed as "the culmination of ever increasing cultural differentiation and specialization of human communities . . . [who] had come to know their habitat so well that they were beginning to domesticate the plants and animals they had been collecting and hunting" (Braidwood 1960:134).

Although Lewis Binford (1968*b*) rejected both of these earlier theories in his seminal paper on post-Pleistocene subsistence, he returned to the idea of population density as a driving force. Binford posited that the intensified use of highly seasonal resources such as andromous fish and migratory fowl at the end of the Pleistocene resulted in uneven demographic expansion (1968*b*:334), which in some instances would have triggered the development of "more efficient subsistence techniques" (1968*b*:331). Drawing from research on population equilibrium by demographers Deevey (1960) and Wynne-Edwards (1962), as well as White's (1959) assertion that diminished food supplies could arise only from either a decline in local flora or increased population density due to immigration, Binford argued that only two conditions could have stimulated the need for increased food production: (1) a reduction in the biotic mass of the region, which would decrease the amount of available food, or (2) impingement of one group on the territory of another, resulting in a disequilibrium between population density and carrying capacity. Territories most susceptible to disequilibrium through demic expansion are marginal habitats, where inhabitants would need to develop

more productive approaches to subsistence (Binford 1968*b*:331–333). The term "broad-spectrum foraging revolution" was later coined by Flannery (1969) to describe this onset of increasing diet breadth that presaged domestication and the adoption of agriculture.

Since the publication of these landmark studies, many researchers have continued to pursue the theme of decreasing foraging efficiency in the face of increased population pressure with respect to BSF (Christensen 1980; Keeley 1988; Redding 1988; Stiner 2001; Stiner, Munro, and Surovell 2000). Stiner and colleagues have sought to test Binford's idea that population pulses following the Last Glacial Maximum (LGM) were integral to increasing diet breadth, identifying specific trends in the use of small-animal species. Increased harvesting pressure on tortoise and limpets is evident as early as 44 kya (but see Speth and Tchernov 2002) and was followed by an increase in the exploitation of small-bodied prey such as birds and lagomorphs (Stiner 2001; Stiner et al. 1999). Stiner et al. (1999:41) note that population pressure is unlikely to be an all-encompassing explanation for cultural evolution in the later Pleistocene but that density-dependent effects can play decisive roles in shaping evolutionary trajectories. These data support the idea that increased predation led to a decline in preferred prey types and resulted in expanded diet breadth. More recent studies of long-term trends in faunal assemblages from the eastern Mediterranean continue to be used to support this hypothesis (Munro 2009; Stiner and Munro 2011; Stutz, Munro, and Bar-Oz 2009). Stiner and colleagues posit modern human abilities to exploit stable protein reserves through food preservation and the use of small game as a key factor contributing to demographic expansion and regional pressures on carrying capacity.

Climate change has also played a key role in the development of explanatory models, which may be partially due to the fact that data on climatic and environmental change are more readily available than demographic data. There are various types of climate-driven models. One of the best known is that a brief reversion to the very cold and dry conditions characteristic of the LGM, known as the Younger Dryas, triggered domestication by motivating broad-spectrum foragers already heavily reliant on low-ranked foods such as grass seeds to develop more intensive methods such as cultivation in order to control returns (Bar-Yosef 2011; Bar-Yosef and Belfer-Cohen 2002; Bellwood 2005:58, 118, 144; Harris 2003; Hillman 2000; but see Eren 2012; Wright and Janz 2012). Other researchers have focused on the effects of post-Pleistocene climatic amelioration on demography, suggesting that increased climate stability and atmospheric CO₂ following the LGM contributed to enhanced biomass and demographic expansion (Richerson, Boyd and Bettinger 2001).

Indeed, some of the earliest evidence for diet-breadth expansion suggests a positive correlation between wider diet breadth and climatic amelioration. The use of small-bodied prey across southern Africa increased slightly during MIS 6 (191–130 kya), peaked during a localized phase of higher

effective moisture and forest expansion in MIS 4 (71–58 kya), and then subsided with an increase in aridity at the beginning of MIS 3 (Clark and Kandel 2013; see also Clark and Plug 2008; Marean et al. 2007; Villa et al. 2012). Even more importantly, the global boom in specialized BSF occurred within the context of warmer/wetter post-LGM environments. Climatic amelioration is also frequently associated with population increases (Barton, Brantingham, and Ji 2007; Gamble et al. 2005), but earlier periods of amelioration did not drive the type of significant increases in population that occurred, for example, in Europe after the LGM (Gamble et al. 2005). A different set of conditions must have existed in order to drive population increases beyond those of previous episodes. A broad-spectrum diet is one mechanism that could account for a more substantial demographic response after the LGM, as greater diet breadth can increase environmental carrying capacity by moving humans to a lower trophic level (O’Connell 2006) and mediates the risks of seasonal shortfalls (Morin 2012:255–256).

However, dominant interpretations of foraging, derived from optimization principles associated with foraging theory (see Stephens and Krebs 1986), are seemingly at odds with a positive relationship between climatic amelioration and BSF. Simple applications of the prey-choice, or diet-breadth, model posit that high-cost or low-ranked prey will be taken only when high-ranked prey, such as large-bodied ungulates, are encountered infrequently, thereby implying that BSF was indeed driven by resource depression due to population packing, environmental degradation, or a combination of both. At the same time, the archaeological record has revealed increasing evidence of diet-breadth expansion under circumstances where warmer/wetter conditions prevailed and there is no evidence of higher population densities (see below). This has encouraged some researchers to question the usefulness of diet-breadth models in understanding these changes in subsistence (Smith 2015; Zeder 2012; Zeder and Smith 2009; but see Piperno 2011). Surprisingly, there has been no clear attempt to respond to these criticisms by offering a coherent model that can explain the discrepancy between traditional applications of the diet-breadth model and these increasingly noticeable patterns in the archaeological data. The model that I am proposing uses the patch-choice model of diet breadth to challenge region-wide resource depression as the primary force driving early expansions in diet breadth, arguing that expanded diet breadth occurs very frequently under conditions of high environmental productivity and stable population density. I do not argue that environmental degradation and population pressure are antithetical to increased diet breadth. This model is based on my research in arid East Asia, where decreased residential mobility and the complementary use of both large ungulates and small-bodied species that require more extensive processing are correlated with the Holocene climatic optimum—a period when biomass productivity reached a point unprecedented since the arrival of anatomically modern humans.

This new model posits a synergistic convergence of three variables to explain the origins of widespread BSF: (1) the development of cooperative foraging among anatomically modern humans, (2) the geographic expansion of modern humans, and (3) a major ecological shift in floral and faunal distribution. I argue that human diet breadth became most widespread as grassland fragmentation and climatic amelioration reached their height, contributing to substantial population growth and ensuing changes in group organization in ways that eventually facilitated additional expansions in diet breadth and/or domestication.

The Evolution of BSF

There has been a long-standing interest among human ecologists in the way that hunter-gatherers divide labor among group members, particularly differences in the way that men, women, and children forage (Bailey and Aungur 1989; Bliege Bird 1999; Elston and Zeanah 2002; Elston, Zeanah, and Codding 2014; Hawkes 1990; Hawkes and Bliege Bird 2002; Hawkes, O’Connell, and Blurton Jones 1995; Kuhn and Stiner 2006; Lee and DeVore 1968; Lupo and Schmitt 2002; Noss and Hewlett 2001; Zeanah 2004). These studies show that, cross-culturally, adult males tend to focus on the pursuit of large game while adult females and children often hunt small game and forage for plant foods. Although there is no evidence of formal differences in foraging strategies among other primates, the sexual division of labor may be a part of our evolutionary heritage, as exemplified by possible sex-based differences in tool use among Neanderthals (Estalrich and Rosas 2015) and among chimpanzees (Boesch and Boesch 1981; Pruett and Bertolani 2007). Kuhn and Stiner (2006) have hypothesized that cooperative foraging, the more structured division of labor among human groups, improved foraging efficiency and flexibility beyond that of earlier hominins. The degree to which modern humans divide foraging tasks is known to vary according to group size and ecological conditions (Codding, Bliege Bird, and Bird 2011; Halpern 1980; Lee 1979; Marlowe 2007).

Elston, Zeanah, and Codding (2014:202) suggest that division of labor is primarily tied to the “reliability of high-energy resource acquisition.” Foragers are not indifferent to risk (Stephens and Krebs 1986:134). Elston and colleagues observe that, because men are often more risk prone, they tend to pursue high-return resources with relatively little attention to risk, while women are more risk averse and minimize risk by favoring predictability at the expense of lower energetic returns. Women support men in obtaining high-energy resources when they are the most reliable source of food, but this focus will shift when the use of more reliable prey types becomes profitable (Elston, Zeanah, and Codding 2014). Kuhn and Stiner (2006:974) further hypothesize that cooperative foraging developed first in tropical and subtropical environments, where lower-ranked foods are more diverse and abundant, but the adaptation continued to confer specific

advantages once embedded in forager organizational strategies. When environmental conditions supported such an adaptation (see below), this ability to exploit a wider range of resources than our predecessors enhanced survivorship during periods of resource stress and enabled adaptation to a variety of ecological conditions.

The best evidence for committed diet-breadth expansion predating the later Stone Age/Upper Paleolithic comes from southern Africa at the onset of MIS 4. Zooarchaeological assemblages reveal the intensive use of both large and very small ungulates as well as other types of small animals and shellfish (Clark and Kandel 2013; Steele and Klein 2013). Beads, engraved ochre, engraved ostrich eggshells, and formal bone tools, along with what appear to be arrow points, illustrate a concomitant elaboration of material symbolism and technology (see Wurz 2013). Paleoenvironmental records and faunal remains suggest habitat characterized by a mosaic of riverine habitats and moist evergreen forest bordered by woodland-savannahs (Allott 2006; Chase 2010; Wadley 2010). Archaeological prey profiles closely reflect the local fauna, and Wadley (2010) argues that the diversity of small species suggests snaring or trapping in closed environments. Diet breadth contracts in MIS 3, with the onset of more arid conditions and the redevelopment of open grasslands (Clark and Kandel 2013). Subsistence diversity, as well as a more diverse material culture, reemerges somewhat later at Border Cave around 44–42 kya and becomes widespread in Africa in the later Stone Age (Villa et al. 2012). The data presented by Clark and Kandel (2013) could suggest that humans were able to forage cooperatively as early as MIS 4, in which case this adaptive strategy may have facilitated the spread of modern *Homo sapiens* out of Africa. Erlandson and Braje (2015) hypothesize that the use of marine habitats, such as biologically diverse and rich mangrove forests, would have made a coastal route appealing to early modern humans as they expanded into the Arabian Peninsula and eventually South Asia (see also Groucutt et al. 2015; Matter et al. 2015).

Evidence for the more regular procurement of small, fast prey after 40 kya is widespread and demonstrates that the ability to exploit a wider range of species had spread well beyond southern Africa. Many of the earliest examples continue to indicate a relationship with tropical climates. Some of the earliest evidence of modern humans in South Asia comes from Batadomba-lena rockshelter in Sri Lanka at 38 kya, where inhabitants of the equatorial rainforests foraged a range of small species that included monkey, squirrel, civet, and mongoose as well as limited numbers of many other species, such as jungle fowl, skinks, fish, and snails (Perera et al. 2011). O'Connor (2006) reports that by 40 kya hunter-gatherers at Jerimalai in East Timor exploited fish, murids, and various reptiles. In southeastern Australia, human foragers were already making extensive use of freshwater shellfish and occasionally fish by 36 kya (Habgood and Franklin 2008), and in the arid zone there are instances where seed- and plant-grinding tools date to earlier than 30 kya (Smith 2004).

Furthermore, it is clear that humans continued to exploit a wide range of prey even in environments where large game was abundant. Tortoise, shellfish, and, very occasionally, lagomorphs were utilized in the Mediterranean regions alongside large ungulates as early as the Middle Paleolithic, and avian fauna were introduced to the diet around 35 kya in Italy and after 28 kya in Israel (Stiner et al. 1999; Stiner, Munro, and Surovell 2000). Exploitation of tortoise, shellfish, and lagomorphs steadily increased throughout the Upper Paleolithic and Epipaleolithic (Stiner 2001; Stiner, Munro, and Surovell 2000). Rabbit hunting, which was rare in the Middle Paleolithic (Aura Tortosa et al. 2002), became intensive as early as 28 kya in Portugal (Manne et al. 2012). Rabbit hunting was more widespread during the terminal Pleistocene (Aura Tortosa et al. 2002; Jones 2012), a period when European populations were relatively stable and regional settlement patterns more nucleated (see Gamble et al. 2005:204). Within the mixed woodland and meadow-steppe mosaic of Moravia in northern Europe, inhabitants of large multicomponent sites were using nets to procure a wide range of avian and small-bodied mammalian fauna by 29 kya. These species were used for their feathers or pelage and consumed along with reindeer, mammoth, and horse (Bochenski et al. 2009; Musil 2005; Svoboda et al. 2009). Starch grain analysis of grinding tools shows that starchy grass seeds, roots, and rhizomes were also used here and across Europe by 30 kya (Revedin et al. 2010). Finally, during the extremely arid LGM there is evidence of fishing and the collection and intensive processing of wild seeds and tubers alongside large-game hunting, but these sites are found around ecologically productive wetlands in the Nile River Valley and the Levant (Bellwood 2005; Hillman 1989; Kislev, Nadel, and Carmi 1992; Ramsey and Rosen 2016; Stewart 1989; Wendorf, Schild, and Close 1983). The majority of these dates suggest that diet breadth had already increased before the first period of major demic expansion beginning at 19.5 ka cal BP (Gamble et al. 2005:204).

After the LGM and most notably during the Pleistocene-Holocene transition, BSF is demonstrated on an even wider global scale and in many instances is accompanied by a sharp decline in the relative importance of large ungulate species in comparison with a heavy reliance on plant foods and small animals, a proliferation of technologies associated with mass collecting and intensive processing, and a reduction in residential mobility. This trend is best documented in the Levant, beginning in the Upper Paleolithic and continuing through the Epipaleolithic/Natufian (Bar-Yosef 2011; Rosen and Rivera-Collazo 2012). Faunas from the Franchthi Cave site in Greece likewise demonstrate the gradual shift from a reliance on large terrestrial game to use of a diversified range of terrestrial game and finally to the incorporation of marine resources (Stiner and Munro 2011). Paleoenvironmental records show that the shift away from large terrestrial game at Franchthi Cave corresponds to post-LGM climatic amelioration and the rise of forest, woodland, and scrubland species. Settlements at Hallan Çemi, located in the Taurus Mountains

of southeastern Turkey, likewise date to a period of warmer, wetter conditions. After the end of the Younger Dryas (10,700–9700 cal BC), inhabitants took advantage of nearby resources across the open plains, floodplains, pistachio-oak inhabited foothills, gallery riparian forests, and wetlands (Rosenberg et al. 1998; Starkovich and Stiner 2009). The use of various distinct ecozones allowed them to exploit a wide range of animal species, including large ungulates, small mammals, birds, lizards, fish, and shellfish. Various plant foods, including grass seeds, nuts, pulses, legumes, sea club-rush, and dock/knotgrass, were also being intensively processed and consumed (Peasnell 2000; Rosenberg et al. 1998; Starkovich and Stiner 2009).

The archaeological record of East Asia is less well documented but nevertheless demonstrates a similar relationship between post-LGM amelioration and increased diet breadth. After the LGM, large herbivores such as *Palaeoloxodon naumanni* (Elephantidae) and *Sinomegaceros yabei* (Cervidae) disappeared in Japan, and the availability of edible plant foods increased as boreal conifer and temperate conifer/deciduous broadleaf forests were replaced with warm-temperate deciduous and evergreen broadleaf forests (Habu 2004:44–45). Jomon hunter-gatherers in Japan began exploiting coastal (e.g., shellfish) and forest (e.g., acorn, deer, and boar) resources, using a

schedule designed to take advantage of patterns in seasonal abundance (Habu 2004:62–77). Food storage was an important part of this strategy; the earliest evidence comes from an acorn storage pit dated to 11,590–10,990 cal BC (Habu 2004:64). After this shift in subsistence, the density of sites consistently increased until the Late Jomon, particularly in eastern Japan (Underhill and Habu 2006:138–140). At Nanzhuangtuo, a wetland site in North China (near Beijing; see fig. 1), inhabitants hunted terrestrial game and collected freshwater shellfish and tortoise (Cohen 2011; Lu 1999). Grinding stones and pottery suggest that foods were processed more intensively than in earlier periods (see Elston, Dong, and Zhang 2011). Chronometric dates for Nanzhuangtuo place its occupation between 10,550 and 8550 cal BC (Cohen 2011). This situates the occupation squarely within a phase of higher effective moisture that resulted in the development of an arboreal-rich woodland-steppe vegetation around local lakeshores (10,500–8500 cal BC; see Liu, Xu, and Cui 2002; Shi and Song 2003; Wang et al. 2001, 2010). Although population levels in the region appear to have been higher after the LGM (Barton, Brantingham, and Ji 2007), population seems to have remained limited, as low-density lithic scatters are most common and sites like Nanzhuangtuo very rare (Cohen 2011; Lu 1999).



Figure 1. Map of study area and locations.

Farther south along the Yangtze River, hunter-gatherers positioned themselves at the transition zone between the hills and river valleys, where they foraged in both wetlands and hill forests. Large-scale fishing complemented a diet that also included deer, buffalo, wild boar, and a range of forest and wetland plants (Fuller and Qin 2010). These habitation sites mostly date to a period of climatic amelioration when grassland, wetland, and acorn pollens were simultaneously stable and high (see fig. 7 in Fuller and Qin 2010).

A close relationship between the availability of small prey and BSF is likewise evident in Australia. For example, Late Pleistocene hunter-gatherers who inhabited rockshelters on Barrow Island and the Montebello Islands of northwestern Australia exploited a range of shellfish, reptiles, and small mammals from nearby sandplains and grasslands as well as from mangrove communities along the muddy coastlines. The shoreline was once part of an arid coastal plain, and there is a clear correlation between the increased use of shellfish and fish, relative to terrestrial resources, and rising sea levels throughout the terminal Pleistocene and early Holocene (Manne and Veth 2015; Veth et al. 2007).

The same pattern is reflected in the Americas, where colonization occurred later and population densities were much lower than those in western Eurasia. Intensive exploitation of plant foods, longer-term occupations, and the reuse of key habitats in the tropical lowlands of Central and northern South America began around the same time as in East Asia—at the very end of the Pleistocene, when patchy and heterogeneous environments were most dominant and patches of seasonal tropical forest had just begun to expand into the open plains (Piperno 2006, 2011; Piperno and Jones 2003). The establishment of patchy environments during the Pleistocene-Holocene transition likewise stimulated a pattern of more tethered land use in the arid Great Basin, where campsites were established in lowland settings from which inhabitants could easily exploit both wetland resources and mid- to low-elevation steppe (Elston and Zeanah 2002). Diets included a range of species such as mountain sheep, elk, antelope, birds, fish, shellfish, and plants. Likewise, BSF in eastern North America coincided with the initial stabilization of river valley and floodplain systems, which boasted concentrated and diverse plant and animal species by 4000 cal BC (Styles 2011). Hunter-gatherers established seasonal base camps around these diverse and resource-rich river valleys, hunting white-tailed deer and small mammals, fishing, and harvesting shellfish and seasonal plant foods such as pecan and hickory nuts (Smith 1986, 2011; Struever and Holton 1979).

Climatic amelioration and/or the exploitation of highly productive heterogeneous landscapes are the variables most common to instances of BSF, while evidence for population pressure or environmental degradation is less often attested. This relationship supports the likelihood of a more robust relationship between BSF and the formation of specific types of ecological systems. Such a relationship is most strongly supported by the earliest examples of BSF in the tropics and

northern Europe and by a florescence in MIS 1 of BSF economies across disconnected regions with very different records of human colonization and expansion (e.g., Turkey and Central America). Moreover, the discontinuous occurrence of BSF, including that within very early contexts, suggests that the ability to forage cooperatively already existed among modern humans at the time of their expansion beyond Africa but that it was used differently, depending on the environmental context.

Fragmented Landscapes and Economies of Abundance

The Cenozoic grassland/large-herbivore complex played an important role in hominin evolution; primates evolved largely within arboreal communities that were becoming increasingly bounded by grassland expansion, forest retreat, and the ascendancy of large grazing herbivores. Ungulate diversity reached its height during the late Miocene and Pliocene, but by the time that australopithecines emerged, this diversity had begun to decline as a result of shorter growing seasons (Guthrie 1984; Janis 2008; Janis, Damuth, and Theodor 2000). Despite the decline in diversity, surviving ungulates thrived and experienced an increase in body size (Guthrie 1984; Janis 2008; Janis, Damuth, and Theodor 2000). Hominins appear to have begun scavenging meat from these large herbivores by at least 2 million years ago, and thereafter meat became increasingly important to hominin evolution (Aiello and Wheeler 1995; Brantingham 1998; Stiner 2002, 2013). By at least 250,000 years ago hominins were highly effective predators of prime adult large- and medium-sized game (Richards et al. 2000; Stiner 2002). Body size peaked for many ungulate species, such as mammoth, bison, and horse, around the same time (see Guthrie 1984). Once hominins had begun to more effectively exploit large herbivores, they were able to expand across the multiple environmental zones that these species inhabited. Throughout MIS 5–1, the dominant grassland mosaics would have been broadly characterized by less dense arboreal growth and more homogeneous resource distribution, although this would certainly have varied at the local scale (see Potts 2012). Ungulate diversity had declined considerably since the Pliocene, but Pleistocene grasslands were still inhabited by a wide range of herbivores and other species. The multifaceted composition of floral and faunal species supported by these grassland mosaics is not analogous to that in any modern biomes, and many once-contemporary species are now considered incompatible under modern climatic regimes (Graham and Lundelius 1984; Guthrie 1984; Hibbard 1960, 1970; Lundelius 1989; Martin and Neuner 1978; Polly and Eronon 2010).

Major ecological shifts during MIS 2 and 1 represent a significant departure from the dominance of grassland ecosystems that provided a backdrop for hominin evolution. They began at different times in different regions of the world

and were expressed to varying degrees by elements such as heightened forestation and the expansion of riparian and lacustrine ecosystems. Fluctuations in temperature and precipitation, including warm/wet periods rivaling those of more recent millennia, occurred intermittently throughout the Pleistocene, but the restricted zonation of floral and faunal communities that occurred during the Pleistocene-Holocene transition was much more substantial and widespread. Although Pleistocene grasslands boasted high biological diversity, species distribution was relatively homogeneous across large swaths of territory. Guthrie (1984) makes a strong argument that more extreme seasonality at the end of MIS 2 and the beginning of MIS 1 fragmented the savannah-like grasslands of earlier periods, causing those multifaceted biomes to produce increasingly distinct biogeographic ranges as species distribution fractured and shifted along latitudinal and altitudinal gradients (see also Graham and Lundelius 1984:243; Sher 1997). Widespread forestation (Lowe and Walker 1997:343–351), the corresponding contraction of open grasslands, and the stabilization of marshlands around lakes and streams would all have contributed to the creation of distinct and highly divergent patches, or what archaeologists refer to as a “patchy landscape.”

An attendant decline in the diversity and abundance of large herbivores adapted to open grasslands is well known but not well understood (Guthrie 1984; Pushkina and Raia 2008; Sher 1997). Guthrie (1984, 2006) argues that shorter growing seasons and the more simplified floral assemblages could no longer support a diverse array of grazing herbivores that required large quantities of varied forage, whereas they favored a smaller range of specialists that could take more efficient advantage of seasonally restricted high-quality foods. Mammoth, horses, and rhinoceros declined, while other species that had long been a major component of human subsistence were more prominent (e.g., deer, gazelle, and bison; Guthrie 1984:272–274, 277–287). A decline in large grazers may or may not have been a key element in forest expansion across many regions, but it would have provided additional feedback through which reduced grazing pressure allowed forest development to exceed that of the previous epoch (Bakker et al. 2016; Barnosky et al. 2016). Increased levels of atmospheric CO₂ (Richerson, Boyd, and Bettinger 2001) might have further contributed to amplified forestation and greater biomass in high-diversity patches.

More heterogeneous floral and faunal distributions offered specific advantages to human foragers. During most of the Pleistocene, the small game and plant foods that sustained hunter-gatherers between high-return kills of large ungulates would have been fairly evenly dispersed in the savannah-type settings, limiting the length of time that foraging groups could remain sedentary. Hunter-gatherers would need to reorganize land use in order to take full advantage of changes in species distribution. Many of the large-bodied game animals favored by Pleistocene hunter-gatherers (e.g., bovids, cervids, and equids) were also abundant during the Holocene

and continued to be favored prey; however, the territorial range of such species was differently restricted by habitat fragmentation. This does not necessarily imply a depression in large herbivores but rather implies a shift in the distribution and type of those species. At the same time, expanded wetlands and woodlands created extensive new habitats supporting large game and high concentrations of edible plants and small animals (e.g., Elston, Zeanah, and Coddling 2014). An ideal range of foraging opportunities would have occurred at the juncture of significant altitudinal or hydrological gradients, where overall species diversity would be exceptionally high. Such environmental conditions became increasingly common during MIS 1 and created an opportunity for foragers to organize land use around patches where species diversity and abundance were most highly concentrated. According to our current knowledge about human foraging strategies, we should expect that the more stable base of highly reliable small game and plant foods would appeal to women’s foraging goals, while men would ideally continue to pursue mobile large game in nearby wetlands, woodlands, and steppes.

Neither BSF nor highly patchy environments were unique to MIS 2 and MIS 1, but they both appear to have been much more widespread than at any other time since the evolution of modern humans. The fragmentation of grasslands through the expansion of forests and open woodlands is especially significant, as it amplified patchiness and created additional habitats for important game such as deer and boar. After the LGM, forestation at higher latitudes meant the expansion of evergreen forests, but much warmer and moister conditions during MIS 1 led to their replacement by nut-bearing deciduous trees. The global importance of these particular forest species in BSF economies, along with grass seeds, fish, and shellfish, underscores the relationship between human foraging strategies and greater spatial patchiness—a pattern that is also reflected in Neanderthal diet breadth (see El Zaatari et al. 2011). Thus, it can be expected that, rather than continuing to concentrate all of their efforts on hunting large grazing herbivores, foragers were more likely to exploit habitats that contained a range of both high-ranked large game and more reliably available lower-ranked prey.

Case Study: Arid Northeast Asia

During MIS 1, changes in subsistence and land use among hunter-gatherers in the Gobi Desert of Mongolia and China (fig. 1) exemplify this model of ecological change and adaptive response. The Gobi Desert covers a broad swath of southern Mongolia and northern China and is today covered by sparsely vegetated erosion basins, former lake beds, gravel plains, dune fields, and areas of less arid desert-steppe. It has been suggested that desert hunter-gatherers played an important role in the development of agriculture in North China (Bettinger, Barton, and Morgan 2010; Bettinger et al. 2010), but there is currently no direct evidence that these particular groups were involved in intensive millet storage and consumption (for the earliest ex-

ample farther south, see Lu et al. 2009). Current data characterize Holocene subsistence economies as reliant on BSF until the adoption of domestic herd animals between 2000 and 1000 BC (Janz 2012; Janz, Feathers, and Burr 2015). Recent analysis of post-LGM assemblages suggest three distinct phases in post-glacial technology and land use: Oasis 1 (Epipaleolithic/Mesolithic), 11,500–6000 BC; Oasis 2 (Neolithic), 6000–3000 BC; and Oasis 3 (Late Neolithic/Eneolithic), 3000–1000 BC (Janz 2012; Janz, Feathers, and Burr 2015). The onset of a distinct post-LGM adaptation correlates well with major ecological changes that began during the terminal Pleistocene and continued into the middle Holocene.

Hominin species may have been present in Northeast Asia as early as the Middle Paleolithic, but modern humans probably did not colonize the region much earlier than 40 kya (Brantingham et al. 2001; Fu et al. 2013). Only minor attention has been devoted to interpreting land use during this time, but a summary of Paleolithic sites from the Valley of the Gobi Lakes shows that long-term occupation sites were absent or rare (Derevianko 2000:241–243; Janz 2006). Faunal remains from Paleolithic sites across northern East Asia indicate a long-standing preference for equids and gazelle, complemented by easily foraged plant foods such as berries and fruit, ostrich eggs, and the infrequent exploitation of extinct megafauna such as *Megaloceros*, rhinoceros, and mammoth (Aigner 1981; Deng 2006; Jaubert et al. 2004; Jia and Huang 1985). The earliest millennia of modern human occupation are linked to relatively warm/wet conditions typified by paleosol formation, the infilling of massive paleolake basins, the expansion of steppe and forest-steppe on the Loess Plateau (Feng et al. 2007a; Grunert and Lehmkuhl 2004; Herzsuh et al. 2007a), and desert vegetation dominating the Gobi Desert lowlands (Herzsuh et al. 2004). Coniferous forests were dominant and deciduous species poorly represented (Feng et al. 2007a). These conditions lasted until about 23,000 cal BC, when mean moisture values decreased. Hyperaridity dominated between 19,300 and 17,000 cal BC (Feng et al. 2007b; Herzsuh 2006; Lehmkuhl and Haselein 2000). Many lakes dried out completely, and aeolian deflation contributed to the formation and expansion of local dune fields (see Grunert and Lehmkuhl 2004).

Oasis 1 corresponds to a period of gradual post-LGM climatic amelioration, episodic aridity, and persistently low population densities (see Barton, Brantingham, and Ji 2007:111). A cold

Younger Dryas occurred across monsoonal Central Asia between 11,000 and 9600 cal BC (Herzsuh 2006), but sedimentological and limnological data vary greatly at the local level (Wright and Janz 2012). There is some evidence of early BSF during Oasis 1, which represents a period of incipient dune-field/wetland use. A pattern of high residential mobility resulted in the formation of low-density site assemblages distributed primarily around the newly infilled lakes, rivers, and streams in both mountainous and upland plateau environments and the lowlands of this basin-range landscape (table 1; fig. 2). Assemblages are dominated by microblade technology, with the occasional use of small grinding stones and pottery (Elston et al. 1997; Elston, Dong, and Zhang 2011; Janz 2012). Excavations at the Chikhen Agui cave site in the Gobi-Altai Mountains (11,728–6445 cal BC) have revealed the use of both large- and small-bodied prey, including *Lepus capensis* (poss. *Lepus tolai*), *Marmota* sp. indet., *Equus hemionus*, *Procapra gutturosa*, and *Capra sibirica sibirica* (Derevianko et al. 2003, 2008). The intensive hunting and processing of hares and various large and small ungulates at Shuidonggou Locality 12, near the Ordos Desert (fig. 1), offers additional evidence for the use of low-ranked game at 10,200–9000 BC (Yi et al. 2013). Pottery was introduced to the Gobi Desert by at least 7736–7547 cal BC (table 2; Janz 2012; Janz, Feathers, and Burr 2015).

A long-term shift toward increased vegetative biomass began by about 9500 BC (Gunin et al. 1999; Tarasov et al. 2000). Effective moisture peaked at different times between 9000 and 6500 BC across the region (Gunin et al. 1999; Hartmann and Wünnemann 2009; Herzsuh et al. 2004; Liu, Xu, and Cui 2002; Shi and Song 2003; Tarasov et al. 2000; Wang et al. 2010; Yang 2006; Yang and Williams 2003). While earlier post-LGM climatic amelioration had promoted the stabilization of hydrological systems and grassland or mosaic grassland ecosystems, Holocene climatic amelioration led to more substantial changes in vegetation. Desert vegetation initially gave way to desert-steppe or steppe, followed by the gradual development of mixed *Pinus* (pine), *Picea* (spruce), *Quercus* (oak), *Betula* (birch), and *Ulmus* (elm) woodlands at higher elevations and around lakes and rivers between 6000 and 4000 cal BC (Liu, Xu, and Cui 2002; Shi and Song 2003; Wang et al. 2001, 2010; Zhao, Yu, and Chen 2009; with *Salix* [willow], *Hippophaë* [sea buckthorn], *Nitraria* [duneberry or *sonduul*], and *Betula* in the west—see Felauer et al. 2012; Mischke et al. 2005; Yang and Williams 2003). Abundant *Quercus* pollen was recovered from

Table 1. Actual and expected distribution of Gobi Desert sites according to each ecozone

Ecozone	Paleolithic/Epipaleolithic		Oasis 1		Oasis 2		Oasis 3	
	Actual	Expected	Actual	Expected	Actual	Expected	Actual	Expected
Lowland dune field/wetland	1	7.7	4	4.7	20	17.8	33	27.8
Lowland river	2	1.2	1	0.6	2	2.8	4	4.4
Lowland dry	3	0.8	0	0.4	1	1.8	2	2.9
Upland	3	2.4	3	1.3	7	5.6	5	8.7
Upland dry	4	0.9	0	0.5	0	2.2	3	3.4

Note. $\chi^2 = 32.544$, $P = .0011$.

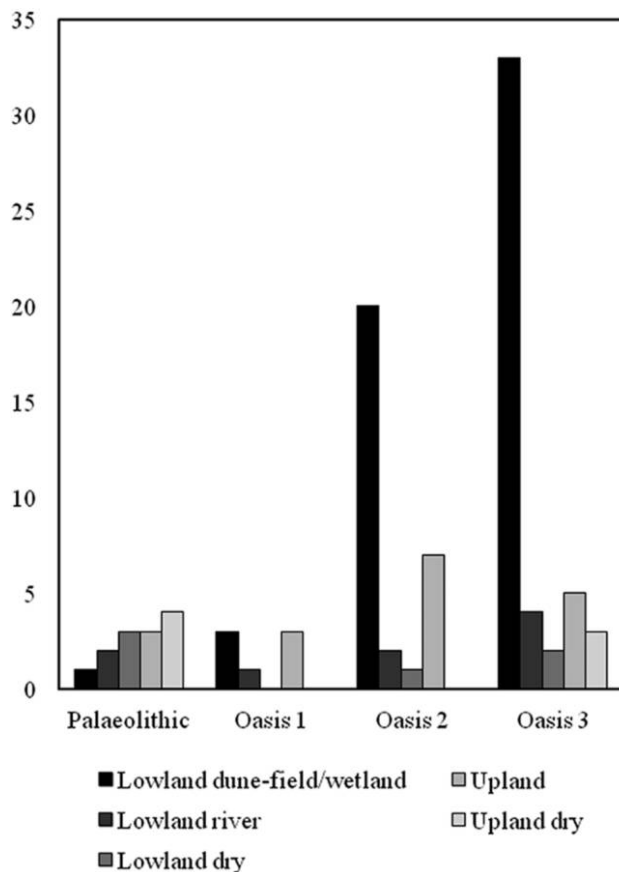


Figure 2. Number of sites found in each ecozone ($\chi^2 = 32.544$, $P = .0011$). Periodicity of each site was based on chronometric dates and/or presence of diagnostic artifacts (see Janz 2012).

Holocene paleosols amid the sand dunes in the Hulun Buir sandy land (48°N, 120°E; fig. 1; Winkler and Wang 1993:236). Mountains, rivers, and dune fields were probably important centers of forestation.

A marked shift in the pattern of land use from high residential mobility to an emphasis on logistical foraging began around 6000 cal BC and lasted until 1000 BC (Oasis 2 and Oasis 3). Across the Gobi Desert, Oasis 2 and 3 habitation sites were consistently established near wetlands, with smaller task sites spread out across a range of environmental settings (Janz 2012). Lowland dune-field/wetland complexes were heavily favored (fig. 2). Here, archaeological remains are most dense and include expansive multicomponent sites (Cybiktarov 2002; Nelson 1926a, 1926b; Janz 2012; Maringer 1950, 1963). The most famous of such localities is Shabarakh-usu, or Bayandzag, in the South Gobi province of Mongolia (Ömnögov *aimag*; Chard 1974; Fairservis 1993; Gábori 1962; Kozłowski 1972; Nelson 1926a, 1926b). Numerous surface and subsurface sites were found around dune-field margins in the vicinity of a small, seasonally wet lake, or playa. The environmental setting of this locality is characteristic: along the margins of extensive lowland dune fields associated with one or more small lake

basins and surrounded by open plains. Many sites are within a few hundred meters of an upland plateau. Specialized tools, such as chipped and/or partially ground adzes and axes and small points (or arrowheads) worked bifacially on expedient flakes, distinguish this phase. The use of extractive technologies such as pottery and/or grinding stones is ubiquitous in such settings, and textile impressions on pottery suggest the use of nets (Maringer 1963). Pottery and grinding stones are usually restricted to dune-field/wetland sites, although their range of distribution expanded slightly during Oasis 3 (table 3). The uneven distribution of specialized processing technology, such as grinding stones and pottery, suggests that those tools were an integral element of foraging strategies within dune-field/wetland environments but were not used in other habitats. Faunal remains are rare in these largely surface-collected assemblages, but remains from bovids, equids, fox, bird, hare, and frog have all been recovered (Janz 2012:394–395). Habitation sites dating to between 3000 and 1000 cal BC (Oasis 3) are more common than those from any other time period, but there is currently no information about potential changes in diet.

Oasis 2 and Oasis 3 sites are not entirely restricted to dune-field/wetland habitats, but variability in artifact assemblages and lithic reduction strategies suggest that this was where settlement was focused. High-density sites with evidence of cooking and multiple activities (“residential A” sites; see Janz 2012:248–254) are almost always situated around dune fields/wetlands. Lithic analysis consistently reveals high relative frequencies of informal to formal (e.g., microblade) core types (table 4; fig. 3), greater cortical surface area, and larger core size at high-density dune-field/wetland sites (Janz 2012:281–283). The regular use of cores that were less formally designed and less extensively reduced often demonstrates ample availability of raw material (Andrefsky 1994; Parry and Kelly 1987; Torrence 1989), which suggests that dune-field/wetland sites were regularly revisited and provisioned. Provisioning of key foraging localities with raw material, particularly in conjunction with the probable caching of processing equipment, can be related to the use of these sites as logistic extraction locales (see Kuhn 1995b, 2004; Wallace and Shea 2006). The lack of midden sites or dwelling structures and a continued focus on formalized tool kits at these locations suggest that residential mobility remained relatively high despite an environmentally tethered mode of land use. Sites outside the dune-field/wetland habitats are represented by low-density lithic scatters (>100 artifacts) with no evidence of hearth sites or processing, indicating a pattern of short-term, task-specific activities. Land use can thereby be characterized by logistical foraging from temporary base camps positioned within the dune fields/wetlands.

Pollen records show that marshes, open lakes, grassy dunes, and mixed or deciduous woodlands then characterized settings that are now typified by mobile dune fields and either completely dry or seasonally wet lake basins. The recovery of Oasis 2 sites from loam and paleosols supports this (Chard

Table 2. New chronometric dates for Gobi Desert sites

Site, museum catalog no.	Laboratory no.	Method	$\delta^{13}\text{C}$	Reported date	Calibrated range ^a ($P \approx .95$)	Environment
Jabochin-khure: K13203:5	UW2361	L		3500 ± 300 ka	1800–1200 BC	Basin/plains
Gashun Well: K13207:1	AA91693	R	-32.4	3385 ± 40 BP	1862–1535 BC	Dunes/well
Yingen-khuduk: K13212:6	UW2358	L		3910 ± 300 ka	2220–1620 BC	Dunes/lake
K13212:123	UW2357	L		5690 ± 350 ka	4060–3360 BC	
K13212:128	UW2360	L		3910 ± 230 ka	2150–1690 BC	
Mantissar 12: K13298:15	UW2362	L		6460 ± 720 ka	5190–3750 BC	Dunes/lake
K13298:25	UW2359	L		3840 ± 340 ka	2180–1500 BC	
Shabarakh-usu 1: 73/654 C	AA89871	R	-24.9	2586 ± 38 BP	825–555 BC	Dunes/lake
73/655 A	AA89872	R	-20.9	4308 ± 40 BP	3023–2879 BC	
Shabarakh-usu 4: 73/887 A	AA89873	R	-21.9	3680 ± 76 BP	2296–1831 BC	Dunes/lake
73/890 A	UW2453	L		5690 ± 300 ka	3970–3370 BC	
Shabarakh-usu 10: 73/1189 A	AA89877	R	-24.6	3595 ± 41 BP	2122–1781 BC	Dunes/lake
73/1190 A	UW2451	L		5030 ± 360 ka	3380–2660 BC	
73/1194 A	AA89878	R	-23.4	3246 ± 39 BP	1614–1436 BC	
Ulan Nor Plain: 73/1608 D	UW2454	L		2170 ± 330 ka	490 BC–AD 170	Dunes/stream
73/1609 A	AA89879	R	-23.1	5116 ± 41 BP	3988–3797 BC	
73/1609 C	AA89880	R	-23.3	5061 ± 49 BP	3965–3714 BC	
Barun Daban: 73/1702 A	AA89881	R	-27.5	1661 ± 42 BP	AD 256–533	Dunes/lake
Orok Nor: 73/1791 K	UW2452	L		2480 ± 130 ka	600–340 BC	Dunes/lake
Shara Kata Well: 73/466 A	AA89868	R	-24.4	8604 ± 51 BP	7736–7547 BC	Mountains
Spring Camp/Site 16: 73/2526 A	AA89892	R	-20.1	866 ± 51 BP	AD 1040–1260	Mesa/river
Baran Shabaka Well/Site 19: 73/2229 A	AA89885	R	-25.7	5609 ± 47 BP	4532–4353 BC	Dunes/lake
73/2231 A	AA89886	R	-24.3	5954 ± 52 BP	4979–4717 BC	
73/2237 B	UW2450	L		940 ± 80 ka	AD 990–1150	
Chilian Hotoga/Site 35: 73/2797 A	AA89897	R	-25.5	6728 ± 45 BP	5721–5561 BC	Dunes/lake
Shavartain bulag: NA	AA32511	R	-24.5	4435 ± 41 BP	3332–2925 BC	Dunes/river
Zaraa Uul 2: T2-3g:1	UG22333	R	-25.5	6580 ± 30 BP	5611–5480 BC	Hills/lake
T2-3m:1a	UG22334	R	-18.3	5910 ± 30 BP	4844–4715 BC	

Note. Both luminescence (L) and radiocarbon (R) are direct dates on pottery sherds (Janz, Feathers, and Burr 2015; Odsuren, Bukhchuluun, and Janz 2015). NA = not applicable.

^a Calibrated with OxCal 4.2 [74].

1974:82; Derevianko and Dorj 1992). The development of woodlands across dune fields and along riparian corridors in the early to middle Holocene would have created a balanced variety of ecozones capable of providing an exceptional range of food resources and raw materials. Along with an abundance of plant foods, the more developed hydrology and vegetation could have created stable and varied habitats for many animal species that are now rare or absent among Gobi Desert fauna, including deer, boar, waterfowl, amphibians,

and fish. Even though large herbivores such as mammoth and ostrich were locally extinct by this time (Janz, Elston, and Burr 2009; Liu and Li 1984), adjacent grasslands continued to support a profusion of large ungulate species (e.g., camel, wild cattle, horse, and ass). Consequently, the dune-field/wetland complex that hunter-gatherers were intensively exploiting would have provided a uniquely rich and diverse array of local resources. By positioning themselves within reach of riparian woodland, dune field, wetland, and grass-

Table 3. Combined environmental distribution of pottery and grinding stones from studied Oasis 2 and Oasis 3 sites

	Dune field/wetlands	Other habitats
Pottery/grinding stones	27	11 ^a
None	7	17
Total	34	28

Note. Data from Janz (2012). $\chi^2 = 9.87$; $P < .01$.

^a At least 8 (72%) of these sites are from Oasis 3.

land, hunter-gatherers would have benefited from unparalleled foraging opportunities. Elston and colleagues (Elston and Zeanah 2002; Elston, Zeanah, and Codding 2014) describe a similar system for the US Great Basin during the early Holocene. Hunter-gatherers maintained high residential mobility across low-elevation wetlands in order to hunt the abundant large- and medium-sized game in low- to mid-elevation steppes or riparian valleys while simultaneously allowing women and children reliable opportunities to forage plant foods and small game around low-elevation wetlands.

The form of specialized BSF represented by Oasis 2 and Oasis 3 is distinct from earlier systems because land use represents a reorganization of settlement, subsistence, and technology around the use of environments rich in plant and small-animal foods. The distribution of radiocarbon dates and the high visibility of Oasis 2 and 3 sites infer a peak in population density—presumably as a response to this change in foraging strategies—after the beginning of Oasis 2 and at least 2 millennia after the height of climatic amelioration. Inferred increases in population density should be viewed with caution, considering potential differences in the visibility of later sites. Oasis 3 sites were deposited during a time of increased aeolian deposition (see Chard 1974:82), and they may be overly visible now because of substantial deflation. Oasis 1 sites might also be underrepresented when present in undated surface assemblages, because they contain only a few traits to distinguish them from later microlithic sites (Janz 2012). At the same time, such problems are greatly reduced at the end of Oasis 1 into Oasis 2, and the number of sites dating to this time period is similarly low across other parts of Northeast Asia, where such problems do not exist (Barton, Brantingham, and Ji 2007; Habu 2004; Jia 2007; Kuzmin and Orlova 2000; Kuzmin and Shewkomud 2003). As in other world regions, specialized BSF lasted for many millennia (at

least 5,000 years) in the Gobi Desert and preceded the emergence of a production economy.

Diet Breadth and Patch Choice in Holocene Ecosystems

For more than 40 years, archaeologists concerned with human ecology and the origins of BSF have drawn heavily on diet-breadth models to explain the relationship between diet breadth and resource depression. The idea that an expansion in diet breadth occurred under favorable ecological conditions and contributed to, rather than being forced by, population increases is controversial because it undermines the traditionally accepted unidirectional relationship between resource depression and diet breadth. The archaeological data outlined above counter a uncausal relationship between the availability of large game and greater diet breadth. As I will now demonstrate, increases in diet breadth can also occur when diversity-rich patches become highly ranked through habitat fragmentation and climatic amelioration, even when large game is abundant.

Foraging theory was developed by ecologists to explain animal feeding behaviors in terms of cost-and-benefit analysis (Emlen 1966; MacArthur and Pianka 1966; Perry and Pianka 1997; Pianka 1978; Pulliam 1974; Stephen and Krebs 1986). The theory posited that observed foraging strategies had developed because individuals who seek to maximize energetic returns are, in the long term, evolutionarily more successful. In this approach, observed foraging strategies were assumed to be “commensurate with fitness” (Schoener 1971:369). The prey-choice, or diet-breadth, model ranks prey according to energetic return per calorie expended in postencounter handling time. High-ranked prey are those whose energetic returns are very high in relation to handling time, and the relative abundance of the most profitable prey type moderates prey choice in predictable ways. When a forager encounters potential prey, it makes a decision to pursue the prey or not based on an intrinsic understanding of that species’ relative ranking; the forager can decide to keep searching for more highly ranked prey or can use its time to capture and consume the encountered prey. According to Sih and Christensen (2001), three fundamental predictions, which have been robustly supported by experimental and observational data, thereby arise: (1) foragers will preferentially select prey that

Table 4. Frequency of informal cores in relation to formal cores at residential A and other site types both within and beyond dune-field/wetland habitats

	Residential A		Other site types	
	Informal cores (mean %)	No. of sites	Informal cores (mean %)	No. of sites
All zones	33.6	21	24.3	34
Outside dune field/wetlands	27.7	7	37.4	14
Within dune field/wetlands	39.6	14	11.2	20

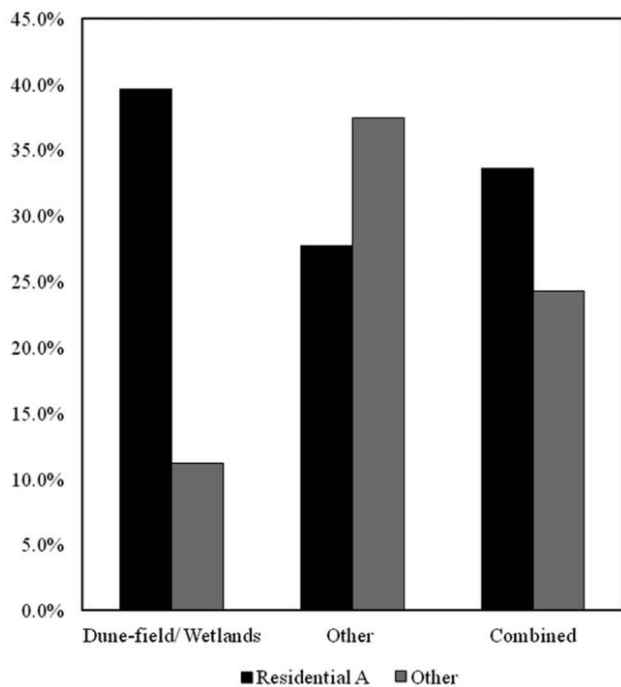


Figure 3. Frequency of informal core types between high-density residential and other site types.

yield more energy per unit of handling time, (2) lower-value prey will be dropped from the diet as the abundance of higher-value prey increases, and (3) foragers should obey a quantitative threshold rule for when specific prey types should be included or excluded from the diet.

Archaeologists built on this model in various ways. Recognizing that accurate methods of calculating actual cost and return rates were problematic in archaeological contexts, researchers suggested body size as a suitable proxy. The largest species were considered to be the most highly ranked because of their potential for abundant caloric returns regardless of the time and effort expended in pursuit and capture (Bayham 1979; Broughton 1999; Griffiths 1975; but see Morin 2012:27–37 for an alternative body-size rule). Since a decline in the exploitation of high-ranked prey should scale to its availability, greater diet breadth was considered to represent a decline in the abundance of such species. It has been repeatedly demonstrated that many of the new foods being incorporated into hunter-gatherer diets during the Broad-Spectrum Revolution had much higher handling costs and lower energetic-return rates than those intensively exploited earlier in the Pleistocene (Bayham 1979; Botkin 1980; Broughton 1999; O'Connell and Hawkes 1981; Simms 1987; Stiner, Munro, and Surovell 2000). The explanation that seemed most consistent with this framework was that BSF was driven by a decline in the abundance of high-ranked prey, through either overhunting or climatic deterioration.

While this approach worked well within a variety of contexts, the increasingly common cases of expanded diet breadth

under conditions of neutral population growth and climatic amelioration complicate the picture. Before dismissing a methodological framework that has already proven its substantial interpretative value (see Zeder 2012) or, on the other hand, ignoring the relationship between climatic amelioration and BSF outlined above, it is more prudent to assess whether we can reconcile the data. To address this issue, we must examine two major weaknesses of the diet-breadth model. The first is its application to mobile prey. Meta-analysis of foraging studies on nonhuman species show that the model is a poor predictor of prey choice when applied to mobile prey, because the interplay of a more complex set of variables is rarely well understood or considered (Sih and Christensen 2001). Bird, Bliege Bird, and Coddling (2009) have effectively shown that when pursuit costs are considered, highly mobile large-bodied prey regularly have lower postencounter return rates than less mobile small prey among Martu hunters in Australia's Western Desert. Kelly (2001:59–62) also shows that small-mammal and fish in Great Basin wetlands can provide higher returns than bighorn sheep, depending on the season, base-camp location, and technology. These observations do not completely discredit the use of body size as a proxy for resource ranking, but they suggest that more accurate prey ranking requires a case-by-case consideration of prey mobility (Bird, Bliege Bird, and Coddling 2009; Elston and Zeanah 2002; Kelly 2001; Morin 2012). This idea weakens the interpretation of small-bodied prey use as an indicator of intensification, since changing technology and environmental context may reduce the energetic investment required to capture and consume such species (Elston and Zeanah 2002:122 and references therein; Simms 1987).

The second major problem with the diet-breadth model in archaeological applications is that it assumes a homogeneous environment in which encounter rates are evenly distributed (Kelly 1995:90). Most researchers recognize this problem, and some use modified prey-choice models when quantifying their data (e.g., Morin 2012), but such strategies have not been clearly articulated within the interpretation of broader cross-regional trends. The issue of environmental grain size becomes extremely important when we consider the types of ecological change that were occurring at the end of the Pleistocene. During MIS 2, the Gobi Desert and other grassland ecosystems would have been characterized by a pattern of dispersed and highly mobile large game and more even distribution of edible plants and small game. Foragers would utilize such a coarse-grained landscape in a specialized manner when species were distributed in low, even densities over an extensive geographic range. In contrast, the fragmented landscapes of MIS 1 were characterized by the uneven distribution of high-density patches. Hunter-gatherers appear to have positioned themselves at the juncture of several ecotones, creating fine-grained landscapes particularly well suited to a more generalized mode of land use (Brown 1990; Ritchie 1998; Rosenzweig 1987). Although MacArthur and Pianka (1966) predicted narrower diet breadth in more productive envi-

ronments, they also explicitly stated that this does not apply to predators in patchy environments, who spend most of their time searching (MacArthur and Pianka 1966:608). Charnov's (1976:133) marginal-value theorem deals specifically with the exploitation of patchy environments, predicting that a forager will continue to exploit one patch until its capture rate drops below the habitat's average capture rate. The fractal patch-choice model further places foraging theory in a spatial context and accounts for scale-dependent trade-offs between high densities of small-resource patches and low densities of large-resource patches (Ritchie 1998). The model predicts that a more generalized pattern of resource use should emerge within fragmented landscapes (Ritchie 1998). Cannon and Meltzer (2008) apply this model to differences in foraging among Early Paleoindian groups across North America, where the specialized exploitation of large game was typical of the Southwest, Plains, and Midwest regions, while the more heterogeneous landscapes of eastern North America were associated with wider diet breadth and reduced reliance on large mammals. Considering differences in the way that each type of environment is most efficiently exploited, when we compare subsistence among foragers living in a homogeneous environment to that among those living in a heterogeneous environment, all else being equal, we will always find that the latter have a wider diet breadth.

Within the Gobi Desert, hunter-gatherers became dune-field/wetland specialists, but they also adopted a more generalist subsistence strategy. Under conditions described for much of the Pleistocene, a reliance on large game reflects specialized use of the highest-ranked patches: ungulate herds. According to the marginal-value theorem, which states that a forager will remain in a patch until "the marginal capture rate in the patch . . . drops to the average capture rate for the habitat" (Charnov 1976:132), foragers should leave when the return rate on a patch of highly mobile large game collapses once they are taken and/or the herd dispersed. High mobility is expected unless the patch is continuously occupied by ungulate herds. During MIS 1, heightened forestation and more expansive wetlands in the Gobi Desert contributed to the formation of large dune-field/wetland patches containing many smaller resource patches. The marginal-value theorem would predict that more stable high return rates within such habitats in comparison to travel times between them would have prolonged patch use until exploiting one patch became more costly than moving to the next. Elston, Zeanah, and Coddig (2014) argue that the distance between patches would play an essential role in determining exactly how wide a range of lower-ranked species were taken. The greatest diet breadth should occur in environments with the most widely spaced high-return patches. A formal division of labor would allow foragers to simultaneously exploit risky large game and more reliable smaller-bodied prey, which would be more highly concentrated and thereby more highly ranked once search times were reduced. The ability to efficiently utilize both types of resources would have served to further extend

the patch's overall return rate. These circumstances are not necessarily commensurate with higher energetic costs overall, since the frequent residential moves often needed to focus exclusively on large game have not been demonstrated to be less costly than the energy required for one subset of the population to pursue fast-moving small game.

Discussion and Conclusion

The global expansion of BSF during MIS 1 can be linked to the establishment of spatially diverse ecosystems and the ability of modern humans to efficiently exploit them through cooperative foraging. Patches of higher species abundance and diversity did exist in earlier Pleistocene landscapes, but never on such a scale in conjunction with the extreme geographic expansion of modern humans. As extensive grassland ecosystems were fragmented through forestation and wetland expansion, cooperative foraging imparted specific adaptive advantages. Higher effective moisture and atmospheric CO₂ during the early to middle Holocene led to the further expansion and productivity of woodlands, wetlands, river valleys, and dune fields where high concentrations of small animals, eggs, seeds, nuts, tubers, fish, and/or shellfish could be collected and processed in large quantities by some group members while their companions concentrated on the high caloric returns available from large game. The marginal-value theorem predicts that the most highly ranked prey would have been exploited first, while progressively more low-ranked species would be taken until this process became more costly than moving to the next patch.

Archaeological proxies for demic expansion and increased population density (Bocquet-Appel et al. 2005; Gamble et al. 2005), in combination with the longevity of broad-spectrum economies in the Gobi Desert and many other regions, suggest that adaptive fitness improved (*sensu* Levins 1968; also Bruggeman and Ó Nualláin 2000) because of this restructuring of ecological niche. Expanded diet breadth moved humans into a lower trophic level, thereby supporting higher population densities per unit of land (*sensu* O'Connell 2006). The shift in land use would have affected demography in a number of tangible ways. First, it would have increased territoriality, because the locations of high-return patches, typically at junctures of several ecozones, were highly predictable and seasonally diverse. These characteristics promote regular reuse. Evidence for redundant occupation of Gobi Desert dune-field/wetland sites over at least 5 millennia, including caching of raw materials and heavy tools, supports the more tethered pattern of land use that we would expect in light of contemporary ecological changes. People became tied to highly productive patches that they repeatedly exploited. Repeated use would have encouraged a sense of ownership over local resources and increased territoriality as populations increased. Higher population densities would have fed back into a pattern of tethered land use and greater territoriality by increasing competition at local and regional scales.

Second, frequent and predictable reuse of locales facilitated strategies such as food storage. Drying and storing lower-ranked foods for use during lean seasons might improve their energetic returns (*sensu* Woodburn 1980; also Bettinger 1999), and it has been shown that food caching is closely tied to seasonal shortages and lends some mammals an adaptive advantage (Gerber, Reichman, and Roughgarden 2004). Site reuse and the newly concentrated abundance of storable foods such as nuts and seeds would have promoted an investment in processing and/or storage and contributed to the development of an economy more reliant on seasonal abundance. This ability to store food in case of seasonal shortage would have worked with other changes in human organizational strategies to boost reproductive fitness. Reduced residential mobility and expanded diet breadth can themselves contribute to additional declines in reproductive stress (Bocquet-Appel 2011; Handwerker 1983; Hassan 1973, 1981; Lee 1979), but a subsistence strategy based on the consumption of reliable small species would have further improved the ability of foragers to mediate the risks of hunting shortfalls and withstand periodic stress (Morin 2012:254–256) while providing a more nutritionally diverse diet, particularly when food storage was employed in climates with seasonal shortages (see Hockett and Haws 2003; Speth and Spielman 1983). At the same time, the trend toward higher population densities since the end of the Upper Paleolithic does not mean that population growth remained constant either after the adoption of BSF or after the adoption of agriculture (Gamble et al. 2005; Shennan et al. 2013).

Reduced perinatal, early-childhood, and geriatric stress would have had significant impacts on demography in terms of capacity and/or need for geographic expansion, but it also directly affected group organization. Better survival rates for vulnerable individuals would increase group size but not necessarily the labor force, which places greater pressure on provisioning members. According to traditional applications of the diet-breadth model, we would expect these greater caloric demands to stimulate the even more intensive use (*sensu* Boserup 1965; also Morgan 2015) of lower-ranked species and further broaden diets as higher-ranked resources were depleted. In this way, population pressure is certainly capable of stimulating more intensive types of BSF, specialization, and food production; however, social organization, ideology, local environment, and historical events would have placed different limits on various human groups, and this regional variability played an important role in individual trajectories, including the adoption of agriculture or the persistence of hunter-gatherer economies. Both the persistence and the eventual decline of BSF are significant research questions that can help us to better understand important socioecological changes that occurred across the globe during MIS 1.

Evidence for the emergence of BSF in the Gobi Desert and many other world regions suggests an explanation that is fundamentally different from resource-depression models favored by human behavioral ecologists. First, the model posits that early forms of BSF emerged as a response to large-scale

redistribution of resources rather than resource depression. Second, it asserts that an organizational strategy focused on habitats rich in small-bodied prey was the optimal solution for modern humans under this new pattern of resource distribution. Third, this model implies that BSF and related changes in land use caused increases in population density. The upsurge in BSF strategies during MIS 1 can no longer be thought of simply as a response to population pressure, part of an unremitting cycle of increasing energetic cost and diminishing return. Rather, BSF was an optimal foraging solution that set the stage for explosions in regional demography. In many world regions, BSF appears to have provided a relatively stable economic strategy over many millennia, but under certain conditions, shifts in demography and group organization could have facilitated domestication, stimulated bursts in population growth, and contributed to the spread of food production economies—all of which laid a foundation for even more structurally complex economic and social systems worldwide.

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Comments

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Here I summarize and offer comments on some selected aspects of the paper, identify some other views and suggestions regarding the theoretical models used, and suggest areas where additional research findings would assist the understanding of the current level of study in regard to the issues raised.

Lisa Janz gives an overview of major changes in the environment and organizational strategies of food foraging during the transitional period between the Pleistocene and the Holocene among ancient populations of the Gobi Desert (northeastern Asia), using the “patch-choice” model of diet breadth within optimal-foraging theory to explain the phenomenon of broad-spectrum foraging (BSF), which significantly contributed to human population growth and subsistence in the re-

gion. It is clear from the abstract that it is no simple issue to follow such changes, because of the scarcity of the data.

Janz begins by stating that her purpose is not to argue that environmental degradation and population pressure are antithetical to increased diet breadth but to provide arguments to support the “patch-choice” model of diet breadth that do not explain it only within the context of resource depression caused by either demographic pressure or environmental deterioration, unlike many other scholars. She states, “The model that I am proposing uses the patch-choice model of diet breadth to challenge region-wide resource depression as the primary force driving early expansions in diet breadth, arguing that expanded diet breadth occurs very frequently under conditions of high environmental productivity and stable population density.” This statement is supported by some archaeologists, who conclude that BSF in Mesolithic Age did not occur in food-crisis conditions (Vishnyazki 2005:229). Moreover, others say that the broadening of the resource base among broad-spectrum revolution economies is not only a response to resource depression but rather the result of people taking advantage of environmental opportunity (Zeder 2012:258). In another example, Emily Jones wrote in her book that a “the bigger the better” assumption about BSF can be considered more through the lens of opportunity than as restriction (Jones 2016:18).

Janz then goes on to describe the development of BSF in the theoretical framework of archaeology, displaying her model in records of paleoclimatology, human paleoecology, and human evolution from all over the globe. On the basis of this exercise, she concludes that the discontinuous occurrence of BSF depended on specifics of environmental settings and was known much earlier, for Upper Paleolithic populations. It is obvious that she has analyzed everything related to the topic of her research to get a more relevant and objective picture of the past.

Janz then discusses fragmented landscapes and economies of abundance during MIS 2 and MIS 1 in Gobi Desert, to give an understanding of how these landscapes changed and under what kind of factors they were generated. Considering the Gobi Desert, she presents three distinct phases in postglacial technology and land use: Oasis 1, Oasis 2, and Oasis 3, dating from 11,500 to 1000 BC. Each of these stages is characterized very well to give a common picture of paleoecology, climatic changes, and lithic assemblages in the region, despite the lack of data in the latter case, especially for earliest period. We still need to conduct more multidisciplinary research in the region, which might help to get a more concise and detailed picture in the future.

The next part of the paper is devoted to dynamics of “patch choice” and diet breadth in Holocene ecosystems. Janz considers the weakness of the diet-breadth model, such as its application to mobile prey, and the assumption of a homogeneous environment. At the same time, she explains the role of these factors and how they contribute to economies of ancient populations.

For such a complicated issue Janz sums the research up well by saying “People became tied to highly productive patches

that they repeatedly exploited. Repeated use would have encouraged a sense of ownership over local resources and increased territoriality as populations increased.” This is a good concept for how the issue of transition to production of food economy and human adaptation in Gobi Desert might be handled. At the same time, I am sure that using other theoretical models, such as niche-construction theory, to explain the phenomenon of BSF might give some additional clues to understanding this part of prehistory in the Gobi Desert.

As I know, on the basis of recent evidence, the potential use of models developed in Western archaeology is in fact unlimited (Bettinger 1991; Borgerhoff-Mulder 1988). Probably, some of these models do not compete with each other but are complementary in studying systems of land occupation and use. To be sure and to know more, research should be conducted in years to come.

Overall, this is a good, well-written paper with an important message for those specialists interested in the prehistory of the arid zone of Asia. The piece of Gobi Desert prehistory, when taken as a whole, looks relevant and very convincing in theory. The theoretical model that Janz presents is very interesting, and she does a great job of illustrating how this model works with her own personal experiences. I would like to express my appreciation to her for conducting this research, which is a significant contribution to the archaeology of Central Asia.

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I welcome the opportunity to comment on Janz’s interesting contribution to the scholarly debate on the broad-spectrum revolution (BSR) concept and its expression in the arid East Asian Gobi Desert. My comments are mainly theoretical, dealing with forager prey choice and population sizes under changing circumstances and with the models governing them.

In particular, I deal with that part of the discussion concerning the relationship between diet breadth and population growth, where a sticking point seems to be the late Pleistocene expansion of diet breadth in the absence of a major increase in population. This is taken by many to be problematic, on the assumption, evidently, that either (1) diet breadth invariably expands as a response to population growth (population growth → expanded diet breadth) or (2) expanding diet breadth invariably results in population growth (expanded diet breadth → population growth). Neither expectation is correct. Diet breadth expands not in response to population growth but rather in response to population pressure in the form of declining foraging return rates as the result of natural or forager-induced reductions in resources. Population pressure and population growth are quite different, indeed inversely related, population growth typically

signaling the absence or lifting of population pressure (Bettinger 2015:40). By definition, growing populations are under less demographic pressure than static or stable populations, which are not growing precisely because of such constraints. As for the idea that population should increase after expansion of diet breadth, whether expanding diet breadth increases, decreases, or leaves population size unchanged hinges on the density and, to a lesser extent, the reproductive rate of the lower-ranked resources being added to the diet (Winterhalder and Golland 1993:710, 714–715).

Given the above, the varied and convincing lines of evidence cited by Janz documenting the late Pleistocene expansion of diet breadth in the absence of population growth are exactly what one would expect of a population pushing against an upper size limit imposed by hostile, wildly fluctuating, and CO₂-poor Pleistocene climatic conditions that limited environmental, and especially plant, productivity (Richerson, Boyd, and Bettinger 2001:389–391, 393–394). Post-Pleistocene climatic amelioration (dampened climatic fluctuation and CO₂ enrichment) provided vastly better conditions for groups operating at Pleistocene levels of diet breadth, resulting in population growth and expansion (Richerson, Boyd, and Bettinger 2001), just as Janz argues. The point to keep in mind here is that, since populations are always growing to their upper limits, creating population pressure more or less constantly, if expanding diet breadth were enough to counter population pressure and invariably resulted in population growth, human populations would have grown much larger much faster than they actually did.

Before closing, I would like to take the opportunity to clarify an issue in Janz's discussion of the marginal-value theorem that may confuse readers unfamiliar with foraging theory. In particular, Janz argues that the "marginal-value theorem predicts that the most highly ranked prey would have been exploited first, while progressively more low-ranked species would be taken until this process became more costly than moving to the next patch." This is not a prediction of the marginal-value theorem, which is silent regarding prey rank and choice. The marginal-value theorem can be configured to generate approximately the same result (Bettinger and Grote 2016), but only by invoking special assumptions much less general than the diet-breadth rule that resources should be ranked by, and added to the diet in order according to, rate of energy acquisition per unit of handling (postencounter) time. The problem is that phrasing diet-breadth predictions in terms of the marginal-value theorem risks giving individuals just learning the subject the unfortunate misimpression that high-ranked prey are taken first, then lower-ranking prey, during a single foraging bout, which is, of course, incorrect: at any given level of diet breadth, narrow or broad, prey that are in the diet at that level are always assumed to be taken whenever encountered, regardless of rank; high-ranking prey are not taken first. Thus, if diet breadth includes two prey types, both the higher- and the lower-ranking are taken whenever encountered.

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A Half-Century on the "Broad-Spectrum Revolution" and Associated Themes

In 2001, Stiner (2001) published a remarkable review on the various avenues in the study of the Broad-Spectrum Revolution (BSR) during the past 30 years and emphasized the role of data on small-game use in Europe and western Asia during late Pleistocene (also see Stiner, Munro, and Stovell 2000). In 2012, Zeder (2012) also reviewed explanatory frameworks for the BSR, wherever it occurred, in terms of resource diversity and intensification. This topic and the associated themes, which include prehistoric demography, human behavioral ecology, the Upper Paleolithic revolution, domestication, and the like, construct a vital part in Paleolithic archaeology and inspire scholars from both the New World and the Old World. Lisa Janz's paper "Fragmented Landscapes and Economies of Abundance: the Broad-Spectrum Revolution in Arid East Asia," which presents much more than its title, once again looks back on the research history of the BSR and goes through the whole evolution of it, which started from the division of labor during a very remote time in the Paleolithic.

In this paper, Janz presents a patchy-landscape perspective and proposes that the fragmentation of grasslands through the expansion of forests and open woodlands is especially significant, as it amplified patchiness and created additional habitats for large game and high concentrations of edible plants and small animals. In most BSR studies, animal resources have been deeply discussed. However, plant food has not, mostly because of data limitation. The exploitation of plants is an involved procedure that is both complex and systematic. With regard to the Upper Paleolithic, archaeological evidence suggests that ancient humans gained recognition of the nutritional value and seasonality of plants and gradual enhancement of processing and storage technologies. Thus, high-energy-consuming resources (e.g., grass seeds) began to be incorporated into their daily diets and eventually increased in proportion (Binford 1968*a*; Flannery 1969, 1973; Guan et al. 2012). In Janz's paper, plant resources are equally discussed, although mostly not on the basis of archaeological remains but from an ecological point of view. Such perspective enlarges our knowledge when we deal with a comprehensive case study and could make a good use of modern flora atlas as comparison. In the same way, animal resources are evaluated at the same time with more archaeological supporting evidence.

The background introduction of the BSR is elaborated in the paper, which introduces readers to the significant past half-century's study on this subject and, as mentioned above, means more than only its title. However, the case study discussion

would have been more dominant and would have covered a larger time range for representing the whole procedure of the BSR in arid East Asia. This area is special and relatively isolated in the west margin of Eurasia continent and underwent considerable climatic fluctuation during late Pleistocene. It was much more sensitive in terms of faunal and floral responses before the Industrial Revolution than tropic and subtropic regions. On the other hand, the lithic technology evolution, to take China as an example, is distinguished from the Western counterpart by the absence or rarity of mode 2, a tradition of large bifacial cutting tools; mode 3, prepared-core technique; and mode 4, blade technique. During the later stage of MIS 3, mode 5, microblade technique, appeared in North China (Nian et al. 2014) and chronologically dovetailed with the sprouting of the BSR in Europe, western Asia, and some area in China (Zhang et al. 2010). Plant seed exploitation before the Last Glacial Maximum has also been discovered (Guan et al. 2012, 2014). Evidence thus indicates that the associated discussion should not focus only on MIS 1, during which the natural environment was much more appropriate to human beings than that of MIS 3 and 2.

Most of the human behavioral ecology models carry theoretical weakness or shortage when they are applied in the prehistoric study, as mentioned in Janz's paper, concerning the ignorance of animal mobility and the assumption of an even encounter rate. These situations could be worse if sites are not well identified, the chronology is not precisely evaluated, and so on. Nevertheless, these two major weaknesses should not be considered obstacles.

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Operationalizing the Patch-Choice Model in a Broad-Spectrum Foraging Context

Within archaeological applications of optimal-foraging theory, the patch-choice model has long taken a back seat to other models. In the past decade this has begun to change, with more and more archaeologists taking a patch-oriented approach. This paper is thus part of a larger trend considering landscape heterogeneity and its impact on prehistoric foraging. What Flannery (1969) so famously termed the Broad-Spectrum Revolution has long been the domain of prey-choice-oriented archaeologists. Janz here argues that patch choice is a better fit for understanding this transition.

One of the problems archaeologists have struggled with in applying patch choice is paleoenvironmental reconstruction; patches are even harder to identify in the archaeological record than are prey types. Resource patches are by their nature environmentally particularistic. Broadly applying patch choice to

a global problem is thus a bold and interesting approach to take, and the resulting paper is an important contribution. Janz provides, among other things, a potential explanation for some noted latitudinal differences in the onset of broad-spectrum foraging (see, for instance, Conrad 2015 and Jones 2016).

I do worry about the impact of site type and recovery on the global record as well as on the case study discussed here (Jones 2013; Jones and Gabe 2015). Janz discusses the shift from residential to logistical approaches in the record through time, but not how this shift in landscape use and site type would affect data recovery, particularly the recovery of organic remains. Like the issues of gendered foraging (which the paper does explore), issues concerning the very nature of the archaeological record are difficult to address empirically—but their potential role in structuring the data we have on hand must be acknowledged. This point does not, however, take away from the paper's primary point: that the fragmentation of grasslands that occurred at the end of the Pleistocene cannot be ignored as a potential contributor to the Broad-Spectrum Revolution.

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On the basis of the patch-choice model of diet breadth, Janz proposes a model for explaining subsistence patterns relying on broad-spectrum foraging (BSF) in the Gobi Desert, in arid East Asia, during the Holocene. The Broad-Spectrum Revolution, as well as other hunter-gatherer organizational properties (e.g., complexity), can be firmly knowable from approaches that include mechanisms such as intensification. As a result of the latter, understood from approaches linked to optimal-foraging models, diet breadth subsistence is expected (see discussion in Morgan 2015). Janz offers an excellent state of the art about the classic and modern models proposed for different continents as regards the evolution of BSF. Among several factors, she stresses the idea that diet breadth increased in a context of habitat fragmentation accompanied by climatic amelioration. This scenario, in turn, promoted organizational changes and population growth. The proposal offers a broader view of BSF, adding flexibility and richness to optimal-foraging models. Especially interesting is the proposition that “BSF and related changes in land use caused increases in population density.” Janz proposes that changes in organizational strategies were mainly focused on the intensification of low-ranked resource exploitation, associated with the reoccupation of dispersed patches and characterized by a concentration of species diversity and an abundance of small prey. These patches are high-return ones located at the intersections of ecozones that

made them highly predictable and seasonally diverse. Janz's interpretation of Holocene fragmented landscapes and the uneven distribution of high-density resource patches in relation to BSF strategies is an original one. In this sense, her explanation does not entirely rely on extreme climatic changes and/or increases in population numbers as "prime movers" and thus breaks away from traditional interpretations (see many examples in Janz's paper). The case study Janz presents is appropriate for discussing the issue of BSF and diet-breadth subsistence strategies, although more data on faunal assemblages, species consumption, and indexes used for measuring diversity would have reinforced her arguments.

Janz derives interesting implications as part of the organizational changes proposed in her model. The change in land use promotes a "patchy" settlement produced by the reuse of dune-field/wetland settings from which logistical foraging movements were organized. These are mainly characterized by reoccupations of multicomponent sites. Caching and equipping the settings with raw material and site furniture artifacts (e.g., grinding stones) seem to indicate a strategy of "provisioning places" (Kuhn 1995a).

Given this background, Janz's model offers an excellent scenario for thinking about economic, as well as social, expectations. As part of the change in settlement strategies, which is focused on the reuse of dune-field/wetland settings unevenly distributed throughout the landscape, one expected implication is the emergence of new relationships between humans and environment, related to niche construction and/or to human disturbances. As stated elsewhere (see Bird, Bliege Bird, and Codding 2016), these processes can be the core of complex socioenvironmental phenomena such as subsistence, intensification, and diet-breadth changes. Also, a long-term "built environment" (Ingold 1993) can be proposed.

Beyond the implications of this paper for economy and BSF, I found many other aspects linked to these issues equally interesting. Janz stresses that changes in organization "would have affected demography in a number of tangible ways," such as territoriality and a tethered patterns of land use. The author argues that "rather, BSF was an optimal foraging solution that set the stage for explosions in regional demography." With the uneven distribution of high-quality resources throughout the landscape, the employment of a BSF strategy in a context characterized by a higher demography appears to be the starting point for the development of new historical trajectories experienced by these desert societies. These changes were part of a social scenario that includes "ownership over local resources" and "increasing competition at local and regional scales." In short, the important changes in organizational group strategies proposed in Janz's model surely must have affected the reorganization of social relations and the construction of new social networks that triggered novel social demands (e.g., land and resource claims). Among other things, this would have affected the formation of territorial systems and the degree of openness and/or closedness of social formations (Gamble 1982; Lourandos 1997). These "fragmented envi-

ronments," although sparsely rich in resources, most likely caused tensions and competition. This would lead to the display of strong regional territorial protocols as well as rules on when and how to exploit these patchy resources. Nevertheless, the production and reproduction of these desert communities would also have depended on some degree of social complementarity and alliances. In arid heterogeneous environments, where resource richness is concentrated at certain points of the landscape, producing some degree of risk and uncertainty, "neighbors" play a central role in periods of stress (Hitchcock and Bartram 1998). Furthermore, the presence of other groups sharing a landscape can stimulate or inhibit an intensification process (Holly 2005) that may be characterized by a strategy of diet breadth (see discussion in Morgan 2015).

At this point, it should be asked what kind of relationships developed between groups in this density-dependent social context linked to high territoriality and a demographic explosion (see Binford 2001). Were they relatively closed social formations in which each group would have controlled certain points of this patchy environment? Is there evidence for the construction of identities and group differentiation? Were they relatively open social formations dominated by a fluent circulation of people, material culture, and meanings? Was there a dual strategy that, according to environmental and social particularities, combined both types of social formations throughout time? Janz's paper offers a productive case study for discussing the nature of social relationships in these desert societies.

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Talking about a Resolution

Lisa Janz presents a bird's-eye view of the broad-spectrum foraging (BSF) stage in the Gobi Desert of East Asia, attributing it to environmental change (specifically, a more fragmented landscape favoring small-animal exploitation in specific patches). This huge and sparsely populated landlocked region witnessed the relatively late adoption of a food production economy and sedentarization. The most pertinent points of Janz's model may be compared with the very different record of Southwest Asia, the focus of our ongoing work. Our commentary deals with the measurement of BSF and its cultural and environmental context and interpretation in the eastern Mediterranean Levant region of Southwest Asia.

Resolution is the key to identifying BSF and assessing the multiple, and often conflating, mechanisms for its source and effects. How can BSF be measured and demonstrated? Ex-

actly how broad a spectrum is “broad”? Was BSF more of a revolution or, rather, a gradual evolution? Essentially, all long-term trends perceived by archaeological research involve some form of “connecting the dots” to establish a process; the more dots you have (or the smaller the region, temporal span, etc.), the more robust the proposed model is likely to be. Specifically, the field of BSF studies has benefitted from increasingly rigorous testing, as more data and theoretical approaches have become available (see Davis 1991; Munro 2004; Stiner 2001; Zeder 2012). In this light, the environmentally diverse yet small and circumscribed region of the southern Levant stands out in the study of post-LGM adaptations (Stutz, Munro, and Bar-Oz 2009).

The period between the LGM and the end of the Pleistocene, the Levantine Epipaleolithic, provides a detailed record of foraging adaptations culminating in the late Epipaleolithic Natufian culture (ca. 15,000–11,700 cal BP). Large, deeply stratified sites with good preservation of features and cultural remains characterize the Epipaleolithic. While the roots of a BSF economy can be seen before the LGM and onward (Bar-Oz 2004; Stiner et al. 1999), only in the Natufian stage did foragers begin to systematically exploit low-ranked small game. The archaeofaunas of several Natufian base camps, sampled by excavating the huge quantities of animal bone refuse from within and around repeatedly built dwellings, are dominated by small-game species such as tortoises, hares, birds, small carnivores, fishes, snakes, and lizards. This unprecedented phenomenon is side by side with the marked decrease of larger ungulates and the appearance of durable architecture, groundstone technology, and other signs of social and economic intensification related to sedentism. Thus, an authentic economic transformation is reflected in the Natufian, one associated with decreasing mobility (Munro 2004, 2009; Stutz, Munro, and Bar-Oz 2009; Yeshurun, Bar-Oz, and Weinstein-Evron 2014). But was it deterministically caused by environmental changes, as has been suggested for the Gobi Desert?

In our view, the evolution of BSF in the Levant cannot be shown to correspond to environmental changes (see the discussions in Bar-Oz, Yeshurun, and Weinstein-Evron 2013; Lev-Yadun and Weinstein-Evron 2005; Weinstein-Evron et al. 2007; for different views, see Bar-Yosef 2011; Bar-Yosef and Belfer-Cohen 2002; Rosen and Rivera-Collazo 2012). The entities of the middle Epipaleolithic (characterized by lower-degree BSF) and the late Epipaleolithic (typically with high-degree BSF) both flourished in the rich Mediterranean landscape of the Levant in a period of climatic amelioration (e.g., Caracuta et al. 2016). The latest part of the sequence (Late Natufian), partly coinciding with the Younger Dryas, was once thought to reflect a climatically forced retreat to mobility; this view is currently being abandoned in light of the chronological mismatch between the Younger Dryas event and the observed change in the archaeological record, as well as the multiplying lines of evidence for increasingly complex lifeways of the Late Natufian, including the building of permanent hamlets and the practice of

even more amplified BSF (Yeshurun, Bar-Oz, and Weinstein-Evron 2014).

Moreover, virtually all of the major Paleolithic and Epipaleolithic camps in the Mediterranean Levant are located in ecotones enabling easy access to resources of different ecological landscapes. The “fragmented landscape,” a feature of the Levant since the early Pleistocene (Schattner and Lazar 2009), did not lead to BSF until the very end of this epoch, so other factors must have been at play. It is possible that a gradual increase in population during the Epipaleolithic may have reached some threshold that forced groups to stick to their territories or extend the seasonal periods of aggregation (Kaufman 1992; Rosenberg 1998; Valla 1998). These communities had to come up with a series of socioeconomic adaptations for living together and for extracting more nutrients from a contracting exploitation territory, hence the Natufian BSF. The activities of the relatively permanent settlers created localized population pressure and undoubtedly had a lasting impact on the faunal and floral communities around the sites (Munro 2004; Yeshurun, Bar-Oz, and Weinstein-Evron 2009).

After these developments, the Holocene in the Levant saw the development of complex societies of farmers and herders, whose hunting decisions departed from the sustainable practices of earlier periods. Large-scale landscape modifications and global mass kill accelerated dramatically (Smith 2013). This includes the desert-kite phenomenon, massive ungulate-game traps that were repeatedly used in wide areas of western and central Asia (Bar-Oz and Nadel 2013). These kites essentially caused landscape fragmentation and had a strong negative impact (extirpation) on ungulate herds (Bar-Oz, Zeder, and Hole 2011; Zeder et al. 2013).

Given the significant differences in ecology and human population history in eastern and western Asia, the different trajectories of the BSF are not surprising. A rigorous testing of Janz’s model is needed to fine-tune the transition to BSF in the early-middle Holocene of the Gobi Desert and to correlate it with independent lines of evidence for landscape fragmentation and population expansion. The ongoing debates concerning the BSF in the Levant, a much smaller region with immensely more archaeological data and a long history of research compared to the Gobi Desert, emphasize the importance of increasing the resolution of the archaeological record as a means to disentangle the hypotheses surrounding the definition of BSF, its evolution, and its implications.

Reply

The commentators have offered a series of thought-provoking remarks, throughout which there runs a single connecting tissue: a concern with resolution. Resolution will always present significant methodological challenges for archaeologists, whether we are dealing with a record of relatively high reso-

lution, such as that described by Yeshurun and Bar-Oz, or a much coarser archaeological record resembling the one that currently exists in arid Northeast Asia. Site preservation is poorer there than in the Levant, and by comparison there has been relatively little research done. The Levant, and more broadly western Asia and the greater Mediterranean region, has long held ascendancy within the domain of higher-level archaeological interpretation, first because of its cultural importance in the florescence of Western civilization and later because of the more intensive level of research. Consequently, many important theoretical paradigms, particularly with regard to the origins of agriculture, have rightfully emerged from the study of that region's archaeological record. However, despite problems of resolution outside the Levant, the archaeology of other world regions is not unknowable and can be used to improve the general applicability of high-level theory. The commentators clearly recognize this, and it is for the benefit of the readers that I make the reminder that if we are to understand the nature and limits of human adaptability, it is crucial that we give adequate consideration to contributions from the widest range of geographical context, even while maintaining a level of skepticism appropriate to the burden of proof.

With this idea in mind, I first address Yeshurun and Bar-Oz's question about how broad is "broad spectrum." There is increasing evidence that small game, aquatic resources, various plant foods, and even grass seeds were exploited earlier in our evolutionary history than anyone had anticipated (Cochard et al. 2012; El Zaatari et al. 2011; Henry, Brooks, and Piperno 2014; Marean et al. 2007; McBrearty and Brooks 2000). Flannery drew attention to this point 16 years ago in his response to Stiner, Munro, and Surovell's (2000:64) critical paper on the exploitation of small, fast prey, in which he commented that the earliest evidence of a broad-spectrum diet is the Mousterian site of Devil's Tower in Gibraltar. At the same time, he emphasized the simple inclusion of *r*-selected species as a defining moment in the process leading up to agriculture. The intervening years have shown this assertion to be misplaced. The emerging picture of Pleistocene hominids is of an omnivorous species that excelled at exploiting large game but also pursued a range of other prey types, depending on ecological context. If humans were always capable of foraging broadly, can we still argue for BSF as a distinct phase in human evolution? Indeed we can: our ancestors were probably always omnivores, but they were much more specialized during most of the Pleistocene, when large ungulates and grasslands dominated global ecosystems (see Brantingham 1998; Stiner 2002). Despite this regular but opportunistic use of *r*-selected prey, ample research has shown that diet-breadth expansion, particularly during MIS 2 and MIS 1, was significant at the global scale. Since Stiner and colleagues published their aforementioned paper, researchers have mostly focused on temporal changes in relative frequency, specifically, changes in the importance of fast and small-bodied relative to large-bodied prey. Zooarchaeology is uniquely suited for this type of analysis, but other methods can be used to investigate associated organizational changes. In order to facilitate the

long-term maintenance and gradual amplification of BSF, a number of organizational changes must accompany the targeted use of small, fast prey and other "low-ranked" foods such as grass seeds. Exploiting *r*-selected prey to the extent that there emerges a reorganization of land use and technology is singularly important in driving later socioeconomic change (see Martínez's comment). This shift occurred in the Gobi Desert around 8.0 kya but many millennia earlier in the Levant. Such changes can be most effectively recognized in the archaeological record through spatial analysis and studies of assemblage variability. We know that the shift toward a broad-spectrum-based economy was gradual and cumulative. This paper suggests that the defining moment was when hunter-gatherers began restructuring organizational systems in order to support the planned use of *r*-selected prey. Such organizational changes are clearly reflected in the Gobi Desert during the Holocene. That being said, the explosion of "durable architecture, groundstone technology, and other signs of social and economic intensification related to sedentism" exhibited during the Natufian are well beyond early expansions in diet breadth that characterize the onset of BSF, as elucidated by Stiner, Munro, and Surovell (2000), or the reorganization of technology and land use described here. Rather than reflecting early organizational change facilitating the use of small game, Natufian strategies reflect a later stage that Martínez succinctly describes as the "reorganization of social relations and the construction of new social networks that triggered novel social demands."

Nevertheless, Jones voices what are crucial lingering concerns about the effect of changes in land use and site structure on data recovery. The difficulties surrounding preservation and recovery of ephemeral campsites is much more pronounced when those sites are compared to higher-density sites that have accumulated under superior depositional contexts. Problems related to the preservation of organic remains are clearly demonstrated at the global scale in the lack of evidence for plant use that dominates Pleistocene sites. With this in mind, it is important that we avoid comparing archaeological oranges with archaeological apples: recent sites that contain macrobotanical or faunal remains cannot be quantitatively compared to Pleistocene sites where such remains were not preserved. One of the few advantages to the poor resolution of subsistence data in the Gobi Desert is that the quality of preservation is not strikingly dissimilar between Holocene and Pleistocene sites, as a result of comparable processes of deposition and deflation—few faunal remains are preserved, and botanical remains are exceptionally rare. Organic remains from both periods preserve either well or not at all. The irregularity of faunal preservation means that it is not viable to rely on faunal-diversity indices. Using lithic assemblages to reconstruct land use and intensity of occupation is a much more reasonable approach, but even in this endeavor there are clear challenges. Locating late Pleistocene sites is the most significant issue in the Gobi Desert, because the ubiquity of post-LGM microlithic surface assemblages obscures temporal depth. It is not even known

whether the Gobi Desert proper was inhabited between the onset of the LGM and 13.5 kya (Janz, Odsuren, and Bukhchuluun 2016). Researchers are conscious of this issue and are keen to discover evidence for LGM and early post-LGM habitation sites. As research progresses in less well-known regions such as the Gobi Desert, issues of resolution will become less of a concern, but, as Jones points out, there will always be limitations on the data that will have to be acknowledged.

Limitations in our ability to clearly understand extinct patch types are another central concern with my advocated approach. Increasing interest in this topic and ongoing advancements in paleoecological reconstruction and modeling suggest that our understanding of archaeological patch types will improve considerably over the next decade. That being said, Guan raises the important point that theoretical models from behavioral ecology are frequently limited in their application to prehistoric studies and that these weaknesses are accentuated by poor-resolution data. This is particularly true when it comes to exercises such as calculating energetic return rates, which are nearly impossible to accurately apply mathematically, especially when utilizing models such as patch choice or the marginal-value theorem. I likewise reserve doubts that we will ever be able to calculate accurate return rates for extinct ecosystems. At the same time, the true value of these theoretical devices is their ability to guide research in a way that encourages the recovery of higher-resolution data, the integration of multiple types of data, and the motivation for pursuing a more nuanced understanding of the archaeological record.

Bettinger raises another issue that can be addressed within the context of concerns over resolution. There is a long-standing assumption, clearly voiced here by Bettinger, that human populations are “always growing to their upper limits, creating population pressure more or less constantly.” Bettinger posits that Pleistocene populations were “pushing against an upper size limit imposed by hostile, wildly fluctuating, and CO₂-poor . . . climatic conditions” and that “vastly better conditions” spurred population growth and expansion during the Holocene. Some Pleistocene groups with greater diet breadth may have existed at a lower trophic level, but the millennial-scale resolution for which we have data urges us to assume that even these populations were living at equilibrium with their environment. Great landscape heterogeneity stimulated changes in foraging behavior and facilitated higher fertility. Populations then expanded until they reached a new equilibrium. These distinctions may seem to be an issue of perception, but they are significant. The idea that populations subsisted for millennia under conditions of continual resource stress counters what we know about the punctuated nature of population dynamics (Carey and Lopreato 1995; Shennan 2013; Shennan and Edinborough 2007) and is problematic with regard to research in human demography. Binford’s (1968*b*) paper cited numerous contemporary demographers who argued that human population levels typically stay below carrying capacity through cultural regulation of

fertility. More recent research drawing on historical and regional examples of the relationship between fertility and mortality supports these early studies, arguing that human populations maintain fertility-mortality quasi-equilibriums, which are controlled intuitively through various cultural mechanisms (Carey and Lopreato 1995). Long-term population dynamics tend to be characterized by equilibrium rather than resource stress (Hanski 1998; Hui 2006), with population pulses occurring through in-migration or when groups experiencing high levels of fertility-mortality experience a decline in mortality through factors such as the cessation of disease epidemics or violent conflict, reduction in predation pressure, more reliable access to food, better nutrition, or improved medical care (Carey and Lopreato 1995; Hanski 1998; Scott and Duncan 2002). Opportunities for outward migration can also mimic mortality in a way that ensures continued high fertility. If diet breadth is an indicator of constant population pressure, driven by Malthusian-type levels of gross mortality, malnutrition, and starvation, we should certainly expect to see this in the bioarchaeological record. As of yet, there is no archaeological evidence for a contraction in diet breadth during the first stages of climatic amelioration and population expansion. Nor is there any independent evidence in this region (e.g., harvesting pressure, *sensu* Stiner et al. 1999; Nagaoka 2005, 2006) that can support a positive correlation between diet breadth and population pressure; therefore, Bettinger’s argument for population pressure is at present a circular one.

To remain for a moment in Northeast Asia, Guan makes an interesting connection between a relationship between the earliest microblade technology in China and the broadly contemporaneous rise of BSF in Europe, West Asia, and parts of China. This is a relationship that bears continued investigation, although evidence of BSF in Ma’anshan Cave in South China (Zhang et al. 2010) is not correlated with the use of microblade technology (Qu et al. 2013). Recent research on phytoliths and starch grains, including Guan’s own, suggests that grass seeds, geophytes, and legumes were exploited in arid North China during the LGM and later (Bestel et al. 2014; Guan et al. 2014; Liu et al. 2013, 2014; Wang et al. 2016), but it was not until the early to middle Holocene that equipment for plant processing was widespread and land use shifted in a way that supported the intensive use of *r*-selected prey. In notable contrast with organizational trajectories leading up to the Natufian, the lithic assemblages and faunal remains that we do have from the Gobi Desert suggest that high mobility and the exploitation of large game continued well into the Bronze Age (Janz, Odsuren, and Bukhchuluun 2016). This sharp contrast between the course of BSF in the Gobi Desert and that in West Asia and China highlights the wide range of socioeconomic responses to diet-breadth expansion that can be expected. Each group functioned within different demographic, social, ideological, and environmental parameters. Therefore, from a comparative perspective it is the global trend toward a shift in both group organization and subsistence that is most compelling.

It is precisely within the context of these later stages of BSF that the niche-construction framework emerges as a thought-provoking device, despite its lack of operational tools. Some authors have pitted niche construction and optimal foraging as mutually exclusive modes of interpretation (Smith 2015; Zeder 2012; Zeder and Smith 2009), but Abdykanova thoughtfully proposes that they are in fact complementary. At the same time, each framework seems suitable for exploring different questions. Proponents of niche-construction theory have yet to provide a clear explanation for how niche construction initially contributed to expansions of diet breadth or why landscape husbandry did not play a role, or at least such a more recognizable role, in human land use during the Pleistocene. Martínez points out that the rise of BSF inspired important changes in organizational strategies that must have been interconnected with anthropogenic disturbance, which he states are “the core of complex socioenvironmental phenomena such as subsistence, intensification, and diet-breadth changes.” It is not hard to see how intensive ecosystem management would be inspired by greater redundancy of site occupation, enhanced territoriality, and the desire to maintain highly successful and increasingly normative foraging strategies. This idea underlies Braidwood and Howe’s (1960) explanation for the origins of agriculture. Abdykanova suggests that niche-construction theory would be a useful theoretical tool for understanding BSF in the Gobi Desert, and I wholeheartedly agree and look forward to pursuing this avenue of research once the resolution of our data is sufficient.

In conclusion, the key point that emerges here is the same that emerges from any theoretical proposition: additional research is needed to test the relationship between human evolution, landscape fragmentation, and the emergence of BSF. Just as zooarchaeology is uniquely capable of discovering differences in the relative importance of different prey types, spatial and lithic analysis can contribute to our understanding of key organizational changes that helped sustain and intensify expansions in diet breadth. My main hope is that this discussion will contribute fresh ideas to the greater conversation surrounding landscape ecology and human foraging.

—Lisa Janz

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