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Human Colonization of Asia in the Late Pleistocene

The History of an Invasive Species

by Robin Dennell

Narratives of “Out of Africa 2”—the expansion of *Homo sapiens* across Asia—emphasize the pattern of human dispersal but not the underlying processes. In recent years, the main debates have been over the timing and frequency of dispersal. Here, I treat these issues as subordinate to biogeographic ones that affected the behavior of humans in Asia as an invasive species that colonized new environments and had negative impacts on indigenous hominins. I suggest that attention should focus on three issues: (i) geographic factors that molded human dispersal across Asia, (ii) behavioral changes that enabled humans to overcome previously insurmountable barriers, and (iii) demographic considerations of human dispersal and colonization of Asia, including interactions with indigenous competitors. Although a strong case can be made that humans dispersed across southern Asia before 60 ka, this should not detract from attention on the underlying processes of dispersal and colonization.

In recent years, discussion of the appearance of *Homo sapiens* in Asia (usually viewed as “Out of Africa 2” rather than as a process of indigenous evolution) has been dominated by three issues: (i) whether *H. sapiens* first appeared in various regions of Asia before 60 ka (e.g., Boivin et al. 2013; Dennell and Petraglia 2012) or after (e.g., Mellars 2006; Mellars et al. 2013); (ii) whether there were several dispersal events or only one (usually hypothesized as occurring ca. 50–60 ka); and (iii) when and how we can first identify “modern” human behavior in Asia. Most narratives rely upon three lines of evidence: archaeological, in which dated lithic assemblages (particularly those with blades) are treated as proxies of *H. sapiens*; a small, often ambiguous and poorly dated amount of human skeletal evidence; and genetic inferences from ancient DNA (aDNA) and modern populations (e.g., Klein 2009). Emphasis in most narratives has been on the pattern but not the process of dispersal. That is to say, most accounts are exercises in “joining up the dots,” of indicating when *H. sapiens* likely first appeared in various parts of Asia and by which routes. Here, I attempt to place the evidence for the dispersal of *H. sapiens* across Asia in a biogeographical perspective that draws upon literature on the invasion biology of plants and animals and also on ideas from colleagues researching the colonization of the Americas and Australia. Although there is much ignorance, doubt, and

controversy over the Asian evidence, I suggest that we should attempt to write narratives that go beyond basic outlines of when “modern” tool kits and skeletal remains are first evidenced across a continent as large and diverse as Asia. Such “first appearance data” are provisional and relatively uninteresting as explanatory devices. In any case, the first appearance of humans in a landscape might indicate a short-term and unsuccessful presence in an area and not the type of sustained, repeated settlement associated with colonization that is the main concern of this paper.

Most researchers (myself included) assume that our species originated in Africa and that its subsequent appearance in Asia (and Europe) resulted from one or more dispersal events. Nevertheless, the East Asian Upper Pleistocene skeletal record is complex, and a simple replacement model is probably inappropriate (Martín-Torres et al. 2016), especially in light of recent genetic evidence for interbreeding between *H. sapiens* and indigenous species of hominins (Fu et al. 2014, 2015; Reich et al. 2010, 2011).

Geographic Considerations

Regarding human dispersal across Asia, simple maps showing known sites and dates mask the most important topographic and climatic factors that most likely affected the rate and direction of dispersal.

Topographic Factors

In idealized circumstances, there are no impediments to a colonizing species dispersing into a new environment and

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occupying the entire space at a uniform rate. In reality, all environments offer “friction” that impedes, directs, and modifies the process of colonization. With the colonization of Asia by our species, the humans that dispersed across Asia and ultimately to North America and Australia had to traverse and inhabit an immense variety of landscapes. Some were occupied more or less continuously after colonization, others less so, and some were occupied rarely if at all. Following Veth’s (2005) discussion of the colonization of Australia, we can begin by recognizing three types of terrain relevant to a dispersing species: refugia, barriers, and corridors.

Refugia, barriers, and corridors. The key point about these categories is that they are not immutable but are dependent upon two factors. The first is the prevailing climate, because under some climatic circumstances, barriers could become corridors (or vice versa). The second and more important is that, through changes in behavior, *H. sapiens* was able to find refugia in climatic downturns in areas that earlier hominins would have found uninhabitable and colonize or use as corridors parts of the Asian landscape that had previously been barriers.

Refugia. Refugia are areas that could still be occupied at times of increased aridity and/or decreased winter temperatures. Without refugia, a species would become regionally extinct because it had nowhere to live during the severest parts of a glacial/interglacial cycle. Refugia are also important as genetic bottlenecks; as stated by Bennett and Provan (2008:2453), “populations go through bottlenecks but come from refugia.” (Strictly speaking, we should distinguish between glacial and interglacial refugia, but here the term “refugia” denotes only glacial ones.) Glacial refugia are areas where the climate was sufficiently mild and where there were sufficient resources for humans to survive climatic downturns, such as Heinrich events and marine isotope stage (MIS) 2. The main glacial refugia in Asia (as in Europe) for hominins (including *H. sapiens*) would have been along the southern edge of the maximum human range. Although current data do not permit the identification of Asian glacial refugia, some of the most likely are the Levant, the Caspian foreshore, the Ganges floodplain, and Deccan peninsula in India; the Yangtze Valley and parts of South China; and the Sunda Shelf of island Southeast Asia (Dennell 2009; Louys and Turner 2012; Rabett 2012 for Southeast Asia). All these areas probably served as refugia for earlier hominins, and their settlement records should indicate (when better known) occupation during MIS 2, when conditions were the most severe. Two others that may have been used as refugia after 40 ka are a conjoined Hokkaido-Sakhalin Peninsula in northeast Asia (Izuho 2014) and perhaps also “Greater Beringia” between 30 and 16 ka (Mulligen and Kitchen 2014).

Our species widened its range of glacial refugia in two ways. One was by adapting to tropical rainforest, which *H. sapiens* was the first hominin species to colonize (Roberts and Petraglia 2015). At present, the earliest examples are from Sri Lanka

(see below), where rainforests were continuously occupied after 36 ka and were thus a glacial refugium. The second was at the northern limits of the hominin range, where *H. sapiens* (and perhaps Neanderthals) were able to survive climatic downturns by, for example, devising effective insulation in clothing and shelters or overcoming winter scarcity through food storage. As a consequence, *H. sapiens* may have been able to create refugia in northern areas that would have been previously uninhabitable. Beeton and colleagues (2013), for example, suggest that parts of Central Asia may have been a refugium throughout the last glaciation despite its harsh winter conditions. This possibility raises serious issues when considering the dispersal of *H. sapiens* across the northern part of the human range in Asia because of uncertainties over whether the presence of a site or group of sites in a cold period (such as a Heinrich event) indicates a successful adaptation in a refugium or a short-term failure by a population that foundered. At present, our information “is not sufficiently detailed to determine what sites can serve as evidence for survival through major natural calamities and what sites are those of people who perished” (Bar-Yosef 2017:66).

One measure of the effectiveness of a refugium is the ease with which species can disperse from it when conditions improve. Dispersal from the Levant either northward or eastward is easy, for example, relative to the Indian subcontinent, where dispersal outward is largely blocked by the Himalayas and Karakorum Mountains and the mountains of northern Myanmar, in much the same way as dispersal from an Italian refugium was blocked by the Alps (Hewitt 1999).

Barriers and corridors. The most obvious permanent barriers to human settlement in Asia before the terminal Pleistocene were areas above 3,000 m asl and deserts. The principal areas of high ground in Asia are shown in figure 1. The Anatolian Plateau, with its harsh winters, would also have been a barrier for much of MIS4 through to MIS 2 (Kuhn 2010). The height and extent of the Tibetan Plateau and adjoining Hindu Kush-Karakorum-Himalayan ranges made it inevitable that human expansion across continental Asia would split around them into a northern and southern route. This split might have occurred farther west because of the deserts of the Iranian Plateau and Central Asia. To the north, it may have been easier for humans to disperse north of the Pamirs into southern Siberia, as suggested by Goebel (2014), than southward across the corridor of the Taklamakan desert between the Tien Shan Mountains and the northern edge of the Tibetan Plateau. The principal Asian deserts (fig. 2) cover over 6 million square kilometers. Landforms vary from extensive dune fields (e.g., the Thar and Badan Jarain) to salt flats and playas (e.g., the Dashti-Lut) or stony pavements (e.g., the Gobi in China). Asian deserts are also either hot or cold, the latter being those in Central Asia, North China, and Mongolia, where winter temperatures are subfreezing for more than 2 months each year (Dennell 2013). As seen below, the deserts of Central Asia and North China and semiarid to arid Mongolia presented additional hazards to colonizers. The combination of mountain, desert,

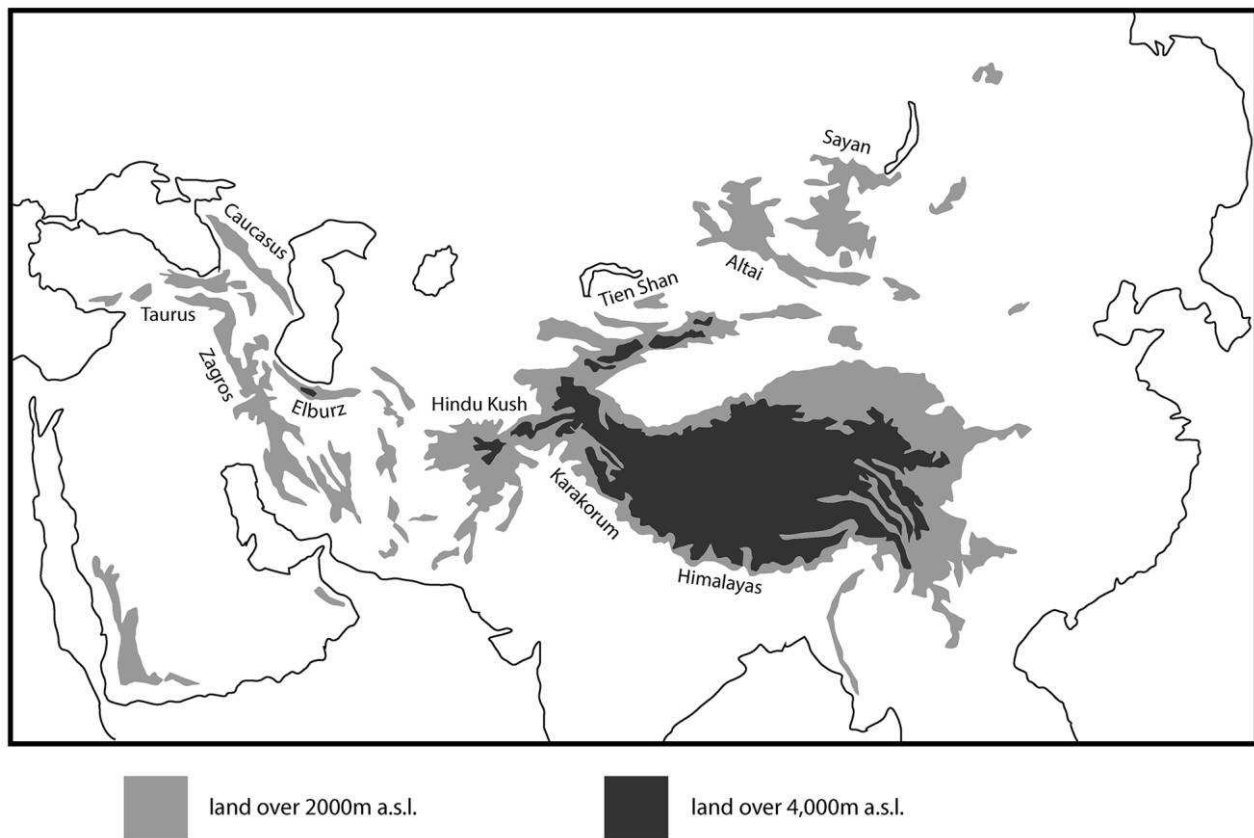


Figure 1. The principal mountain areas of Asia redrawn from *Philips New Reference Atlas* (1980).

and harsh climate across southwest and central Asia would inevitably have made a northern dispersal a much harder proposition than one along its southern flanks.

In continental Asia, barriers and corridors were sometimes interchangeable as part of the landscape dynamics of MIS 3. For example, mountain ranges, such as the northern Zagros and the Elburz in Iran, would have been barriers when snowlines were sufficiently depressed to prevent passage but corridors when the climate ameliorated. Similarly, deserts such as the Arabian and the Thar were likely barriers during arid periods but potentially corridors in moister episodes, such as MIS 5 and parts of MIS 4 and MIS 3, when there were active lakes and rivers (see Groucutt et al. [2015] and Rosenberg et al. [2011] for Arabia and Blinkhorn et al. [2013] for the Thar); the same is likely true of other Asian deserts, such as those of Central Asia and north and northwest China. Dispersal across continental Asia would have been harder when the climate became colder and drier because of the depression of snow lines and the expansion of deserts. As seen below, these conditions created additional hazards for colonizers that were not encountered across southern Asia.

Permanent corridors were probably low mountain passes and the lower parts of major river systems and their tributaries. The most useful for a species dispersing longitudinally were

those trending west-east, such as the extinct ones in Arabia (see Breeze et al. 2015) and also the Ganges and Narmada in India and the Yellow and Yangtze rivers in China.

An important point about corridors is that they are not simply parts of the landscape through which people pass but may also be major areas of settlement. For example, the western Zagros Mountains are corridors between present-day Iraq and the Iranian Plateau and north-south between northwest Iran and the Arabian/Persian Gulf, but they have also been (and are) important areas of settlement in their own right. The same is likely true of Beringia (Goebel, Waters, and O'Rourke 2008) and the major river valleys of Siberia (Goebel 1999) and East and Southeast Asia.

Navigability (wayfinding) and ease of movement. The humans that dispersed across Asia had to traverse an immense variety of landscapes. From a colonizer's viewpoint, two important factors are navigability and ease of movement (Meltzer 2009:221–224). Areas offering easy movement and abundant landmarks (such as along major rivers or broad intermontane valleys) are easier to colonize than those with few landmarks and those that are difficult to traverse, such as mountain ranges, dense rain forest, or sand deserts. In addition, there was the need for potable water; Por (2004), for example, high-

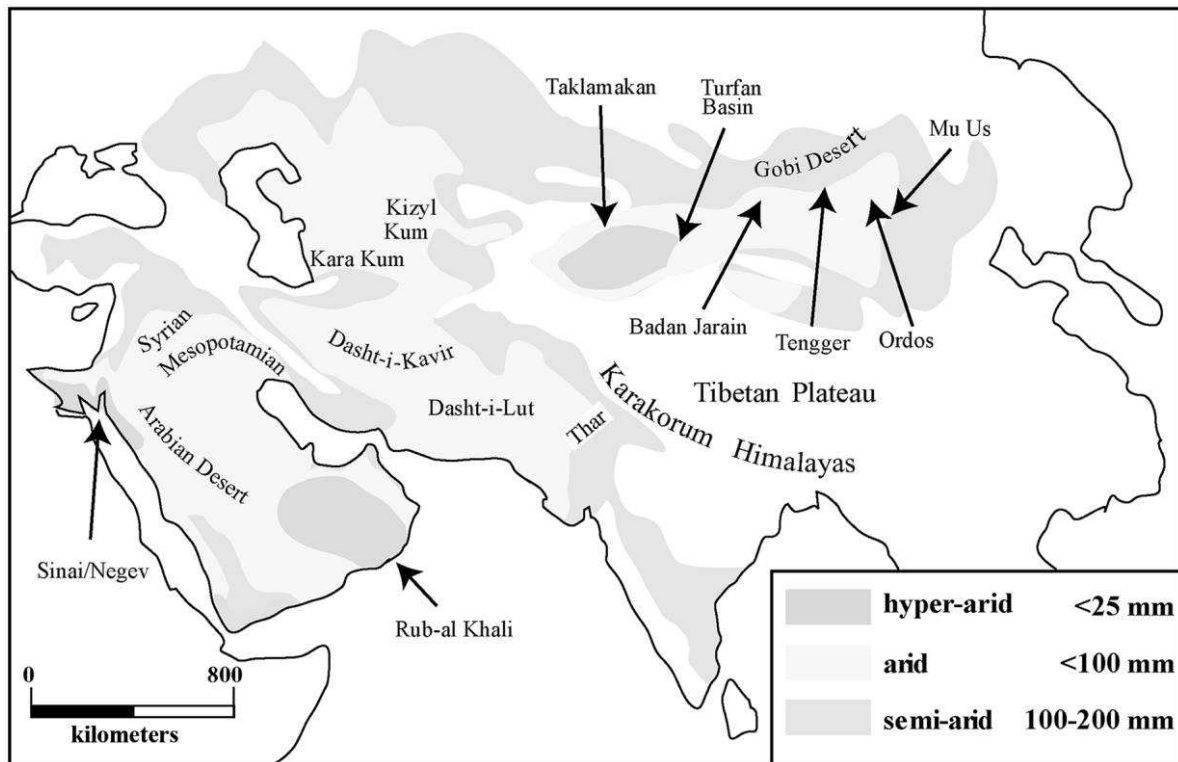


Figure 2. The principal desert areas of Asia. A color version of this figure is available online.

lighted the importance of springs along the southern edge of the Taurus Mountains to groups dispersing eastward from the Levant. Similarly, in deserts such as the Arabian (Breeze et al. 2015) and the Tengger (North China; Pachur, Wünnemann, and Zhang 1995; Zhang et al. 2002), the non- or moderately saline paleolakes that developed in the Upper Pleistocene would have been essential for human dispersal and survival.

Climatic Factors

The dispersal of *H. sapiens* across most of Asia occurred during MIS 3 and MIS 4, both of which were periods of climatic instability. At times, climatic change was short but severe, most notably in Heinrich events 4, 5, and 6 (ca. 38 ka, 45 ka, and ~60 ka; Blunier and Brook 2001) and are detectable in the East Mediterranean (Bartov et al. 2003), the Arabian Sea (Schulz, Rad, and Erlenkeuser 1998), and southern (Wang et al. 2001) and central (Porter and An 1995) China as well as in Greenland (Hemming 2004). Their effects would have been most strongly felt at the northern limits of the human range, north of 40°N (roughly from Beijing to Dmanisi, Georgia), and in desert/semiarid environments. In North China, for example, the decrease in rainfall of up to 50%–75% (Liu et al. 1995) resulted in the southward advance of desert at the expense of semiarid grassland; in Arabia and

the Thar Desert, decreased rainfall led to fewer lakes and permanent streams and increased dune mobility. In Central Asia, strengthened northern wind systems and weakened, rain-bearing westerlies reduced biological productivity and increased dust storms (see below) and loess deposition. Rainfall decreases would also have affected ecosystems in the southern parts of the human range in Asia (such as Central and South India and Southeast Asia) by causing some loss and fragmentation of habitats, and these too would have necessitated responses by humans. In Asia, climatic change had major consequences on coast lines, accessibility to upland areas, and the extent of deserts and steppe.

Coastal changes. Climatic changes affected coastal topographies by exposing or inundating areas of land and changing the length of rivers. In western Asia, the two main affected areas were the Arabian/Persian Gulf and the Red Sea. Regarding the Arabian/Persian Gulf, a sea level fall of 100 m would have exposed almost all of it as a sandy plain covering approximately 96,000 square miles (250,000 km², or approximately the same size as mainland Britain; Lambeck 1996) and allowing dispersal across its southern end from Oman into southern Iran. With the Red Sea, the Bab el Mandab crossing would have narrowed to <4 km during the last glacial maximum (LGM; Lambeck et al. 2011) and would thus have been less of an obstacle in cool periods.

Sea level changes were most pronounced in East and Southeast Asia. In East Asia, a fall in sea level of 120 m added 2 million square kilometers of coastal plain (Liu and Ding 1998:140) and briefly conjoined Hokkaido with Sakhalin Island but left Paleo-Honshu (Honshu, Kyushu, Shikoku) isolated across the Tsuguru Strait (Kudo and Kumon 2012; Yokoyama et al. 2007). In Southeast Asia, a comparable fall created Sunda, which conjoined mainland Southeast Asia with Sumatra, Java, and Borneo (Voris 2000). Conversely, rises in sea level fragmented this landmass into an archipelago and drowned the Molengraaf River, which flowed between Sumatra and Borneo. The repeated fissioning and fusing of islands in Southeast Asia may help explain the precocious development of seafaring (see, e.g., O'Connor, Ono, Clarkson et al. 2011), because there were ample opportunities and incentives for experimenting with different types of water craft as well as navigational skills and sailing techniques.

Altitudinal changes. In climatic downturns, lowered snow lines would have made some mountain passes unusable as corridors or usable for a shorter period each year. This was probably important in Southwest Asia, where summer snow lines were depressed by 1,200–1,800 m in the northern Zagros (Wright 1962), by 1,600 m in the Southeast Zagros (Kuhle 2007), and by 1,000–1,500 m in the Taurus and eastern Turkey (Sarıkaya, Çiner, and Zreda 2011), with the consequence of some habitat loss and fragmentation and greater restrictions on movement.

Deserts and semiarid landscapes in Central Asia and North China. Three major hazards would have impeded dispersal across the semiarid and arid regions of Central Asia and North China. These were drought, dust storms, and dzuds.

Drought. A dominant feature of arid and semiarid landscapes is their short-term variability in rainfall. “Average” totals mean little when the equivalent of 10 years’ “average” rainfall might fall in a day, followed by 10 years of almost no rainfall. Long-term climatic trends toward greater aridity simply mean that extreme events, such as droughts, become more frequent and severe. Reductions in rainfall across Asia between MIS 4 and MIS 2 would have led to an expansion of deserts and, during periods of maximum aridity (as in the LGM), would have created a largely continuous desert belt (“aridistan”) from Arabia through Iran and Central Asia into North China (Dennell 2009:256, 2013). Xiao et al. (1995) observed that, in North China, the winter monsoon (denoting increased aridity) peaked at 50 ka, 42 ka, and 30 ka. In southern Arabia, the movement offshore of the Indian summer monsoon would have made Arabia even drier than it is today (see Fleitmann and Matter 2009; Fleitmann et al. 2011; Glennie and Singhvi 2002). In the desert belt from Central Asia to North China, reduced rainfall would also have had two other undesirable consequences.

Dust storms. Mahowald et al. (1999:15895) note that, in the LGM, dust deposition in higher latitudes was up to 20 times

higher than at present due to stronger winds, an enlarged dust area attributable to reduced vegetation and soil moisture, and drier conditions that allowed dust to stay longer in the atmosphere. For example, the Tajik loess records show an increase in depositional rates from 12.1 cm/millennium at 250 ka but 20 cm/millennium thereafter (Yang and Ding 2006:336). Much of that loess would have been transported and deposited through dust storms. Typically, these mostly occur in spring, but they can happen year round. Central Asia is especially prone to dust storms. Orlovsky, Orlovsky, and Durdyev (2005) observe that these occur approximately 67 days/year in the Central Karakum desert of Turkmenistan and up to 146 days/year in western Turkmenistan. For comparison, the maximum frequency is 110 days/year in Mongolia, 102 days/year in southwest Kazakhstan, but only 20–30 days/year in Inner Mongolia (Wang 2004). The frequency, duration, and severity of dust storms would have increased under the drier-than-today conditions of MIS 4 and 3. Xiao et al. (1995:22) note that the Chinese Loess Plateau record of the last 130 ka shows “high-frequency, high amplitude variations . . . that imply rapid and significant changes in atmospheric conditions that affect dust transport and deposition.”

Dust storms can be extremely hazardous, especially if they are long lasting. In 1910, one lasted 3 days in Turkmenistan and destroyed or buried much of the vegetation: an estimated 29,000 out of 30,000 cattle died during the storm, and many of those that initially survived the dust storm starved afterward (Orlovsky, Orlovsky, and Durdyev 2005:95). It can be assumed that the frequency and severity of dust storms would have increased during MIS 3 and especially MIS 2 and would have made human dispersal and survival in Central Asia and Mongolia especially hazardous, particularly if and when there was no suitable shelter.

Dzuds. Dzuds occur when a summer drought is followed by a harsh winter, usually with deep snow and abnormally low temperatures, causing animals to die from starvation and cold. They are a hazard particular to Mongolia but also occur in parts of Central Asia and North China. Five types are recognized (Begzsuren et al. 2004; Tachiiri et al. 2008). The severest occur when a summer drought is followed by deep snow (a white dzud); even worse is an iron dzud, when snow melts but then refreezes, thus forming an iron-hard ice crust over the surface that prevents animals from grazing. Livestock losses from dzuds in recent times have often been catastrophic for pastoral communities; for communities reliant on hunting, a severe dzud would provide a short-term bonus of frozen carcasses, but the hunting grounds would be depleted of prey the following summer and thus would have to be temporarily abandoned.

Colonizing Areas That Were Previously Barriers

As noted above, definitions of a barrier are dependent upon the colonizing abilities of an invasive species. Regarding *H. sapiens* in Asia, the Upper Pleistocene provides three examples of how

improved human abilities as a colonizer enabled them to convert a barrier into a corridor and resource zone.

Rainforests. The first were the rainforests of Sri Lanka and mainland and island Southeast Asia, which do not appear to have been occupied prior to the arrival of *H. sapiens* (see, e.g., Dennell 2014a, 2014b). Life in rainforests requires thorough knowledge of an extensive array of plant resources; the ability to hunt mammals, birds, and reptiles that live in dense vegetation or high in the tree canopy; and great skill at way-finding. Sri Lanka currently has the earliest indisputable evidence of human settlement in rainforests at ca. 36 ka (Perara et al. 2011; Roberts et al. 2015). If Storm and colleagues (2005) are correct, humans were part of the Punung Fauna in Java ca. 100–125 ka during MIS 5 along with sun bear, orangutan, tapir, and other rainforest animals. Even if the identification of the Punung molar as *H. sapiens* is ambiguous (Polanski, Marsh, and Maddux 2016), the point still remains that “the presence of *H. sapiens* in a rain forest environment is more likely than occupation of this habitat by *H. erectus*” (Sémah and Sémah 2012:124). Evidence from Niah Cave (Barker et al. 2007) also indicates the use of rainforest resources, although perhaps not as exclusively as in Sri Lanka. The occupants of Niah inhabited a mosaic landscape that included rainforest, and thus they hunted monkey as well as pig and other animals. A Hoabinhian assemblage at Xiaodong, Yunnan Province, in Southwest China dated at 43.5 ka may provide another example of an early adaptation to rain forest. Pollen data indicate that the site was in rainforest, and the faunal remains are consistent with that interpretation (Ji et al. 2016). Isotopic analysis is needed to see whether these early Hoabinhians were living in rainforest.

The sea. The second barrier that was overcome was the sea. Previously, the only records of hominins crossing open sea before MIS5 are from Flores, which was reached at 1.0 Ma and 0.86 Ma, and Sulawesi, where hominins (type unknown) were present between 100 ka and 200 ka (van den Bergh et al. 2016). As most researchers rule out navigable boats at this time, the arrival of hominins on these islands may have been inadvertent via rafts of vegetation after tsunamis or cyclones (Dennell et al. 2013; Smith 2001). In the Upper Pleistocene, East and Southeast Asia show remarkably early evidence for the use of boats and/or rafts that could be steered. The earliest evidence is from Callao Cave, in the Philippines, where hominin remains (type unknown but possibly *H. sapiens*) date from 67 ka (Mijares et al. 2010); Japan, colonized ca. 38 ka (and a major colonization event that deserves greater attention by Western researchers; Izuho and Kaifu 2015); Okinawa, from ca. 36 ka (Kaifu et al. 2015); Timor, from 42 ka (O’Connor, Ono, and Clarkson 2011); and, of course, Sahel, with evidence from highland New Guinea by ca. 49 ka (Summerhayes et al. 2010) and mainland Australia by ca. 50–60 ka (Hiscock 2008; Roberts et al. 1994; Smith 2013). Timor

also shows evidence of pelagic fishing at 42 ka (O’Connor, Ono, and Clarkson 2011); what had previously been a barrier became not only a corridor but also a resource zone.

It has been proposed that humans dispersed across southern Asia to Australia via a coastal route (Mellars 2006; Mellars et al. 2013; Stringer 2000) and thus used a previously vacant (or rarely used) niche as a major corridor. Because this hypothetical dispersal occurred when sea levels were ~50 m lower than today (Mellars et al. 2013:10703), it is impossible to confirm or refute this hypothesis. As seen below, it is at least as likely that humans dispersed overland, particularly along river valleys or between lake systems.

Subarctic and Arctic northern Eurasia. The recent discovery that humans (possibly *H. sapiens*) were likely hunting mammoth by the Arctic Ocean at 72°N as early as 45 ka (Pitulko et al. 2016) shows that they had learned how to survive the extreme conditions of the Arctic, although it is too early to say whether this discovery denotes a failed dispersal or a short but successful foray. At the Yana site (71°N), repeated visits involving hunting, butchering, and occupation over a 3,000-year period starting at ca. 32 ka indicate unequivocally that humans (presumably *H. sapiens*) were able to operate in extremely cold environments (see fig. 3; Hoffecker et al. 2016; Nikolskiy and Pitulko 2013; Pitulko et al. 2004, 2014) and this leads us to consider the survival technologies that must have underpinned the colonization of arctic northern Asia.

Survival technologies. These primarily involved ways of being mobile over snow and ice and keeping warm, especially in winter. The invention of skis, snowshoes, and/or sledges would have enabled groups to move in winter across ice or compacted snow as easily (and perhaps more so) as across land in summer. Sewn, insulated clothing and footwear made from degreased and softened skins and furs would also have provided greater protection against the cold. The small toes of the 40-kyr-old individual from Tianyuandong, North China, provide a hint of what is currently the earliest indirect evidence of the habitual use of footwear (Trinkaus and Shang 2008). Additional requirements for survival in northern Eurasia would have been goggles against the glare from snow and ice; effective fire-lighting and food-storage techniques; effective cordage for sewing, lashing, tying, and so on; reliable lamps for coping with long winter nights; and well-constructed winter residences. Shipman (2015) has also highlighted the importance of dog domestication, perhaps as early as 32 ka in Siberia (Ovodov et al. 2011), in providing a hunting aid and potential pack animal. If humans were able to be mobile in winter by using improved methods of transport, they must also have developed their cognitive skills in navigation by starlight, given the short length of winter daylight at high latitudes. These and other innovations may have made it possible for humans to establish refugia in northern areas previously considered uninhabitable. (Nevertheless, Siberia was probably depopulated during the LGM; Graf 2014.)

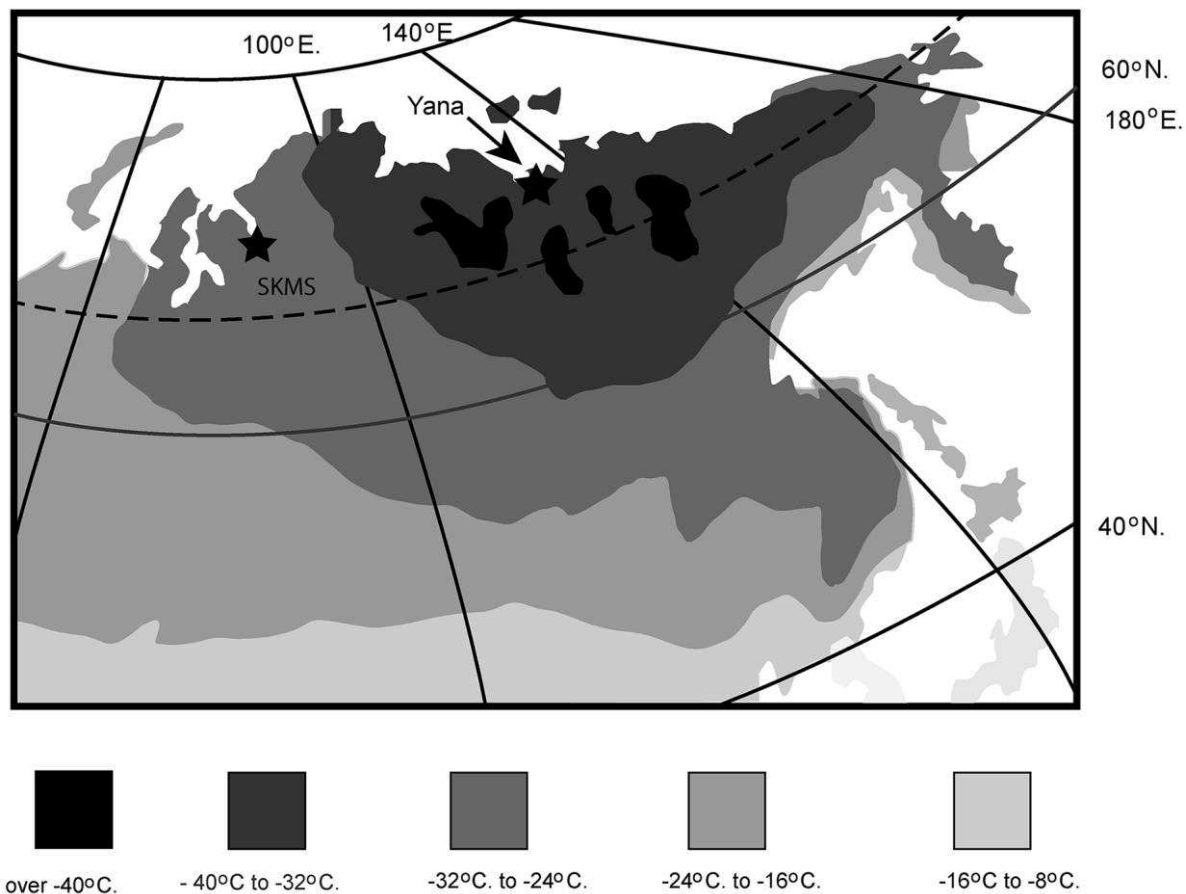


Figure 3. January average temperatures in northern Siberia and location of Yana and the Sopochnaya Karga mammoth site (SKMS). Redrawn from the *Encyclopedia of World Geography* (1974).

Hunting technologies. Shea and Sisk (2010) have drawn attention to the invention of stone-tipped projectiles in north-east Africa during the African Middle Stone Age and their subsequent use in the Levant. These, they argue, were a game-changer, as a heavier projectile point would have greater penetrating power and a more even flight, thus improving the hunter's aim and success rate. These, however, are little evidenced outside the Levant, so they may have had only a regional impact. Other innovations may have occurred in hunting technologies. For example, if the inhabitants at Niah Cave were able to remove toxins from plants before eating them (Barker et al. 2007), they may also have realized the value of adding toxins to projectiles to impair their prey. For hunting animals like monkeys in the tree canopy of Sri Lanka ca. 36 ka (Roberts et al. 2015), hunters may have relied upon bows and arrows or blow pipes and darts. Pit traps were another innovation that currently appears unique to Japan and dates from 38–35 cal ka (Sato 2015). In northern latitudes, traps, snares, and nets for trapping small, fur-bearing animals would have been another innovation that provided furs for clothing and other means of keeping warm in subfreezing temperatures (see Hoffecker 2005).

Biological Considerations: Dispersal and Invasion

Biological dispersal is a neutral term that refers to the expansion of the range of a species into a new habitat. A biological invasion denotes “any process of colonization and establishment beyond a former range” (Davis 2009:3) but is often used to refer to a dispersal that has negative consequences on either indigenous species or humans. Because invasive species of pathogens, insects, and plants often have major ecological or economic costs, many invasion biologists concentrate on those species deemed harmful to humans either directly (e.g., pathogens) or indirectly (e.g., crop pests). Here, humans are seen as an invasive species, in that this species rapidly (relative to the rest of the Pleistocene) spread across Eurasia and had negative impacts on contemporary hominin species, all of which were extinct by the end of the Pleistocene.

The history of “Out of Africa 2” can therefore be discussed as a narrative about ourselves as an invasive species (see, e.g., Shipman 2015) or as a weed species that was able to flourish in unstable environments (see, e.g., Cachel and Harris 1998). Literature on the ecology of invasive species (e.g., Clobert

et al. 2013; MacDonald 2003; Shigesada and Kawasaki 1997) often focuses on plants, insects, and small mammals, sometimes under laboratory or experimental conditions, and inevitably has a very short time-depth. This literature is thus not directly applicable to the type of coarse data relating to a large mammal such as *H. sapiens*, with a complex set of behaviors and operating over timescales rarely shorter than millennia. These studies are useful, however, as a source of ideas on (i) the importance of the metapopulation as a demographic unit; (ii) differential responses to differences in resource availability; (iii) the effects of habitat loss and fragmentation, especially at the edge of the inhabited range; and (iv) competition with indigenous residents.

Populations and Metapopulations

A biological population is “all individuals of a given species in a prescribed area” (MacDonald 2003:15). Depending upon the choice of scale, this can be an individual settlement, a region, a country, or a continent. In a colonizing situation, a newly arrived population can expand radially outward by forming new colonies: a classic example is the radial dispersal of the muskrat from its point of introduction in Austria in 1905 (Elton 1958). Species capable of long-distance dispersal tend to behave differently in the way they colonize and subsequently use landscapes by forming a metapopulation, or “a group of spatially separated populations occupying a nexus of favourable patches” (Smith 2013:75). Those that interact infrequently are “loose metapopulations”: an example is subpopulations of arctic foxes inhabiting different islands. Others interact frequently and form “tight metapopulations,” such as birds nesting and living in different but nearby woodlands (MacDonald 2003:15). Under circumstances where the human skeletal record is sufficiently detailed, it may be possible to model tight metapopulations as paleodemes (Howell 1999), thereby providing a way of integrating human skeletal and archaeological data.

Humans are a prime example of a species that is extremely good at forming tight metapopulations (or alliances or networks; see Spikins 2015) that maintain cohesion through kinship, ideology, or other forms of corporate identity. Hunters and foragers, for example, typically live in groups within an area that maintain contact in order to share information, exchange and obtain scarce resources (such as furs, obsidian, or ochre), and find mating partners (Wobst 1976). As is evident from the distance over which items such as obsidian were exchanged in the late Paleolithic of East Asia (Ikeya 2015; Kuzmin 2006), these metapopulations could maintain contacts across the sea and over distances of up to 1,000 km; other examples are anthraxolite and amber at the Yana rhinoceros horn site that came from 600 km away (Pitulko et al. 2014).

The behavior of metapopulations is crucial when considering colonization. First, “at any given latitude or effective temperature the structure of the subsistence resource base can vary widely in terms of predictability, patchiness and density in space and time” (Ambrose and Lorenz 1990:9). Consequently,

dispersal into a diverse environment is more effective if these differences are dealt with by a metapopulation formed of several integrated groups rather than a single, nucleated population. Second, dispersal takes place at the edge of the inhabited range and thus in the least familiarized part of the landscape. A metapopulation can move into new territory on a trial and error basis, with “a group of spatially separated populations occupying a nexus of favourable patches. During the dispersal phase, demographic and environmental stochasticity eliminate small populations in some patches, but these are recolonized by immigrants from other nodes” (Smith 2013:75). One major advantage of this pattern of dispersal is that a large area can be occupied in a short space of time provided that groups maintain sufficient connectivity with each other to ensure that each (or most) survives. Smith (2013:75), for example, estimates that the arid interior of Australia could have been occupied by only 25,000 people in 150 years, starting with a donor population of ~500 that doubled every 25 years. Collectively, a species organized into metapopulations can also acquire far more knowledge of their environment as an information network than any group could obtain singly.

Sinks and Sources

The dynamics of metapopulations can also be modeled as “sources and sinks” along the lines proposed by Eller, Hawks, and Relethford (2004), Hawks (2009), and Pulliam (1988) and developed in an early Paleolithic context by Dennell, Martín-Torres, and Bermudez de Castro (2011) and Martín-Torres et al. (2016). To quote Hawks (2009), “a population sink is a region where the average rate of reproduction is below replacement levels. This region can remain populated only if individuals migrate in from other places. The places that reproduce above replacement are called population sources.”

At a continental scale, the main source populations are in refugia. At a regional scale, source populations will tend to be south of the northern limit of expansion and/or in areas where resources are more abundant and predictable; new subunits of a metapopulation would be created from members of a source population. Population sinks would be at the limits of the current range and/or in areas where resources are less abundant and predictable. These groups within a metapopulation would require the import of members from other groups, and probably the import of mating partners, to remain viable (see fig. 4). Demographic expansion thus depends greatly upon (i) extinction rates in sink populations at the edge of the inhabited range and (ii) the ability of the main source populations to support sink populations, especially those at the edge of the range. This becomes difficult when population densities are low and intergroup distances are high.

Resource Variability

As Ambrose and Lorenz (1990) pointed out, the resources in a landscape can vary enormously in terms of availability,

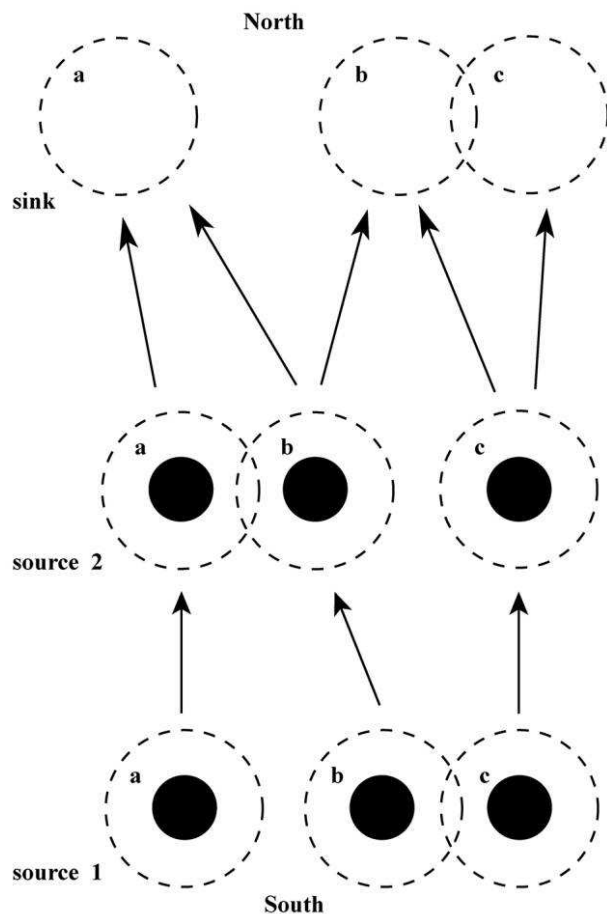


Figure 4. The dynamics of source and sink populations. The solid circles denote source metapopulations during cold periods when populations contract into refugia; the dashed circles indicate interglacial or interstadial conditions when expansion from them is possible. Here, the bottom row indicates three metapopulations in refugia; each is separated in glacial conditions, but in interglacial conditions, metapopulations *b* and *c* overlap. The middle row indicates how each expands in interglacial times and becomes a source population: here, demes *2a* and *2b* overlap, but *2c* (derived originally from demes *b* and *c*) remains isolated. The top row indicates sink populations at the maximum expansion during an interglacial; here, metapopulation *3a* (derived from *2a* and *2b*) is isolated, but *3b* and *3c* overlap, although each has a different ancestry. These sink groups are highly vulnerable to short-term climatic and mortality changes and would probably need recruitment from source populations farther south. Adapted from Dennell, Martínón-Torres, and Castro (2011), figure 6.

predictability, and patchiness, and they require different responses from a colonizing metapopulation. With humans, two broad strategies can be identified. Meltzer (2009:234–238) has usefully developed Beaton’s (1991) categories of transient explorers and estate settlers to suggest how North America was colonized. He renames these as the cautious and the bold. “Cautious” groups are ones that remain anchored to patches of high year-round productivity. Over time, some may seek

similar locations nearby and develop those in turn, but generally, dispersal rates are slow; such groups “moved only slowly across the latitudes and longitudes, each daughter colony being spawned by the overflow of a saturated estate” (Beaton 1991:220–221). An example in Asia of such a process might be the Levant, with its rich coastal plain and inland lakes. Rather than envisaging human settlement there after 100–125 ka as a “failed dispersal” (Shea 2008), it might instead be an example of how cautious colonizers made the most of a rich environment, beyond which resources in the deserts and semiarid plains to the east were more scattered, harder to obtain, and a disincentive to dispersal.

“Bold” colonists are ones that move when productivity declines. These colonists inhabit areas that will not support long-term residence of the kind favored by cautious colonists, so they have a high incentive to move, and especially to “jump” across areas that are low in productivity (such as steppe or deserts; see fig. 5a). During sudden environmental downturns, for example, water resources might diminish and game become less plentiful; onward movement to new areas thus becomes risky, but it is nevertheless less risky than clinging to a declining resource base. Bold colonists tend to use mobility to explore and become familiar with large areas (Veth 2005); as an example, judging from where different types of stone were obtained, the occupants of Puritjarra at 35 ka in western Australia were probably familiar with ~10,000 km² of territory. Bold colonists also have a characteristic method of expansion “in which migrants generate new satellite colonies rather than simply expanding the occupied area from its periphery” (Smith 2013:75). They thus form a metapopulation of spatially separate groups, some of which may fail, but which can be replaced by colonists. An Asian example might be the colonization of the North China Plain, where resources were scarce, winters harsh, and few areas allowed intensive long-term occupation. Bold colonists are also ones that seek out naive prey that is unfamiliar with humans and thus easier to hunt; when the animals become more wary and vigilant, bold colonists will move to new areas where the prey is naive (Dennell, forthcoming).¹

It is here that the contrast between short-term visitors and long-term residents (Dennell 2003) becomes important. In areas where resources are subject to fluctuations in availability, settlement is likely to have been intermittent and confined to moister and warmer intervals, punctuated by periods of settlement contraction or even abandonment during climatic downturns. In semiarid and arid areas where rainfall is highly variable, settlement records are likely discontinuous, as is also the case in high-latitude regions where winter temper-

1. Spikins (2015) points out that jump dispersals by bold colonists may be forced rather than voluntary. In metapopulations with strict norms of behavior, transgressors may be forcibly expelled. Although difficult to demonstrate from Paleolithic evidence, her suggestion is worth noting when considering instances of short-term human presence in areas such as off-shore islands or the Arctic that were far from the main areas of settlement.

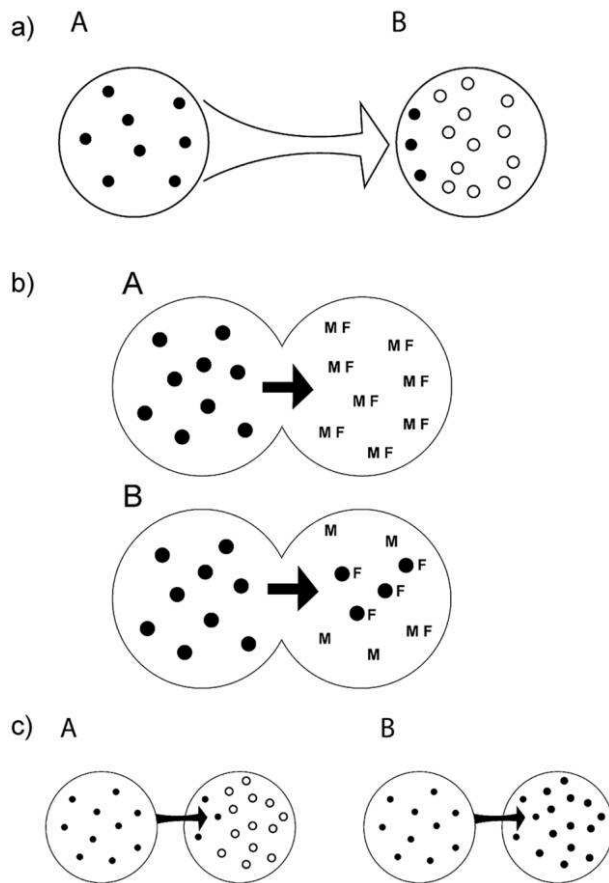


Figure 5. Three scenarios of colonizing metapopulations. *a*, Bold colonization by jump dispersal. Here, some groups (black circles) at the edge of a metapopulation take the risk of jumping across an area of low productivity (e.g., a desert or open sea) to find a better area than their present location. Although the risk of failure is high, success means that a new region can be colonized by descendant groups (white circles). *b*, Colonization and assimilation. In this scenario, part of a metapopulation (*A*; black circles) begins to invade an area occupied by a different type of hominin, shown as MF, with M = males and F = females. The invasive metapopulation then proceeds to assimilate the females of reproductive age (*B*), thus degrading the previous viability of the indigenous population. This type of scenario is indicated by evidence of gene flow from Neanderthals and Denisovans into *Homo sapiens* outside Africa and may also help explain the evidence for hybridization in the East Asian skeletal evidence for *H. sapiens* between marine isotope stage (MIS) 5 and MIS 3. *c*, Colonization and population replacement. Here, a metapopulation (black circles) begins to invade an area already occupied by other groups (open circles). In *B*, the indigenous occupants are replaced. This process may have been violent but may also have occurred because the incoming population outcompeted the local population for key resources and locations and destroyed their connectivity between groups. This scenario is one explanation for the replacement of Neanderthals by *H. sapiens* in western Eurasia.

atures are the key variable. Two related points are that the first appearance of humans in these types of unstable environments should not be mistaken for the onset of colonization: these might indicate, in Shea's (2008) words, a "failed dispersal" (or a

forced expulsion; Spikins 2015); and second, these areas are demographic "sinks" that could only be sustained by being replenished from an external source population in a refugium (Dennell, Martín-Torres, and Bermudez de Castro 2011).

Habitat loss and fragmentation. The dispersal of *H. sapiens* into and across Asia began in MIS 5 and was completed mostly in MIS 4 and 3, both of which experienced a considerable degree of climatic and hence environmental change. The climatic instability of MIS 3 has been identified as a major reason why Neanderthals became extinct (see, e.g., d'Errico and Sánchez Goñi 2003); by implication, *H. sapiens* was able to better cope with such changes. The key factor here is how humans responded to habitat disruption or, specifically, loss and fragmentation.

Ecologists have paid considerable attention to the consequences of climatic and environmental change on plant and animal populations. Given current concerns over global warming, most of these studies consider the effects of increased temperatures: Pleistocene researchers, of course, have to consider also the consequences of climatic downturns involving lower temperatures. Climatic changes involve habitat fragmentation and loss that is most keenly felt at the edges of the inhabited range. Regarding habitat fragmentation, Baguette et al. (2013:381) point out that "habitat fragmentation is an inherent consequence of habitat loss: the progressive disappearance of a given habitat entails changes in both the area of remnant fragments and their spatial configuration, with consequences on the structural connectivity among remnants." They emphasize that, when suitable habitat has fallen to <40% of its original extent, the distances between fragments suddenly increase, with significant consequences: "By increasing the distance among such patches, landscape fragmentation is expected to increase dispersal costs, including loss of time and energy and the risk of getting lost" (Baguette et al. 2013:385). Dytham and Travis (2013:400) stress that "it is not the loss of habitat per se that is the most important element of fragmentation . . . it is loss of 'connectivity' that can be crucial for the survival of a species. This effect will be non-linear as there will be a threshold of habitat loss that will break the connectivity of a region." There are clear implications here for the importance, for widely dispersed groups in a metapopulation, of maintaining connectivity when habitats become fragmented.

Because *H. sapiens* as a colonizing species invaded areas containing indigenous resident populations, the crucial factors are how each was able to respond most effectively to habitat loss and fragmentation during climatic downturns, the opportunities offered by periods of climatic amelioration, and the extent to which *H. sapiens* disrupted the connectivity of the indigenous population. These points bring us to the subject of competition with resident populations.

Competition with Resident Populations

Unlike *H. sapiens* in Australia and the Americas, *H. sapiens* in Eurasia colonized a continent that was already occupied.

At the time of potential contact with *H. sapiens* (i.e., after MIS 5), Neanderthals were resident in Southwest and Central Asia, southern Siberia as far east as Okladinov Cave in the Siberian Altai (Krause et al. 2007), and perhaps even farther east. *Homo erectus* sensu stricto was present in China and perhaps also Southeast Asia (although it may already have become locally extinct by the time of contact), and *Homo floresiensis* was present on Flores, Indonesia, until 50 ka (Sutikna et al. 2016) and perhaps was present on other islands in the region. Two unknowns are an unknown resident population in South Asia that does not appear to have been *H. erectus* sensu stricto or *Homo heidelbergensis* (Athreya 2007) and the “Denisovans,” known only from the gene sequence extracted from a finger phalanx and two teeth from Denisova Cave, in Siberia (Krause et al. 2010; Reich et al. 2010; Sawyer et al. 2015), that is also present in modern populations in Melanesia (Reich et al. 2011) and Tibet (Huerta-Sánchez and Casey 2015).

Little is known about how incoming metapopulations interacted with indigenous metapopulations across Asia at and after contact. Some geneticists argue that there was interbreeding between *H. sapiens*, Neanderthals, and Denisovans. As an example, Kuhlwilm and colleagues (2016:429) propose that there was “admixture among archaic and modern human populations, including gene flow from Neanderthals into modern humans outside Africa, Denisovan gene flow into the ancestors of present-day humans in Oceania and mainland Asia, gene flow into the Denisovans from Neanderthals, and, possibly, gene flow into the Denisovans from an unknown archaic group that diverged from the other lineages more than one million years ago.” We may never know the nature of these encounters between *H. sapiens* and Neanderthals. However, when looking at colonial and imperial history, sexual relations between colonizer and colonized were overwhelmingly between European males and native females (see, e.g., Hyam 1991; Walter 2010). As a speculation, interbreeding between *H. sapiens* and Neanderthals and Denisovans may also have been largely between invasive male *H. sapiens* and indigenous female Neanderthals and Denisovans (see fig. 5*b*).

The long-term consequences of these encounters may have been negative (such as male hybrid infertility; Sankararaman et al. 2014) or positive if leading to “hybrid vigor,” enhanced immunity (see Stewart and Stringer 2012), and the acquisition of beneficial genes such as those that facilitated life at high altitudes (Huerta-Sánchez and Casey 2015) or in cold environments.

At least four other scenarios of human-indigenous interaction can be envisaged: (1) taking over the indigenous species’ habitat by, for example, more effective hunting of prime animals, preemptive use of key locations, and aggressive behavior toward the inhabitants (see fig. 5*c*); (2) coexisting but with little interaction; (3) occupying parts of the landscape (such as coastal regions) that were seldom used by indigenous groups (see Shigesada and Kawasawki 1997:104); and (4) introducing new diseases into Asia that were lethal to indigenous residents (Bar-Yosef and Belfer-Cohen 2001), just as, in recent times, smallpox decimated the indigenous Americans after Spanish contact.

Discussion

As argued above, the colonization of continental and island Asia by *H. sapiens* was likely a lengthy and complex process. One key aspect that underpins this process—particularly the colonization of the rainforest and the islands of South and Southeast Asia and Japan as well as colonization of the Arctic, Siberia, Central Asia, and North China, with their long sub-freezing winters—is the importance of tight metapopulations or networks. In other words, groups within a defined human metapopulation were able to establish and maintain social links with each other and with other groups for sharing information, exchanging valued items (e.g., obsidian, ivory, and furs), obtaining mating partners, and maintaining genetic viability through recruitment or assimilation. By 40 ka, it is probable that such groups were defined and sustained by language, kinship, and perhaps ideology. Tight metapopulations were highly effective ways of colonizing new environments, particularly those as challenging as Siberia, the Arctic, and rainforests. “Modern” behavior is evidenced less by the type of artefact or the evidence of symbolism as by the ability to operate as part of a network with strong links between groups. “Trait lists” (or “shopping lists”) of items of material culture deemed to indicate “modern human behavior” are clearly inoperable in Arabia, India, Southeast and Central Asia, China, and Australia, although they have some utility in the Levant and parts of Siberia. The underlying problem is that no single item or group of items is both unique to *H. sapiens* and universal across its range. A different perspective is acquired if one thinks of mental technologies expressed in ways of maintaining connectivity within networks over long distances, especially in challenging environments. Colonization of new habitats (e.g., the rainforest and the Arctic) is probably one of the clearest indicators of this type of mental technology, exhibited in solving problems and being adaptable. *Homo sapiens* may have been simply better at maintaining tight metapopulations as an invasive colonizing species than its predecessors.

As stated in the introduction of this paper, the intention here is to focus on the process of human dispersal from Africa, rather than on the outcome as a series of (often speculative) arrows that show little more than some of the routes that may have been taken and when these had been undertaken. The constraints of landscape and climate, the behavioral thresholds that were overcome in dispersal across Asia, or the likely behavior and impact of an invasive species have not been given the attention they deserve. In a similar vein, insufficient attention has been paid by Old World prehistorians to how colonization has been treated by those researching the Americas or Australia. For example, the contrasts between cautious and bold colonists or the importance of naive faunas are important themes that could be imported from Americanists, and Australian notions of corridors, barriers, and refugia are similarly capable of useful employment in discussions of the Asian evidence. The literature on the biology of dispersal and invasion also has great potential for investigating how *H. sapiens* extended its range across the largest continent.

The quality and quantity of archaeological and fossil skeletal data on the Asian story of “Out of Africa 2” is now far outstripped by the quality and quantity of climatic and environmental evidence on Asia during the last glacial cycle. This presents obvious incentives to archaeologists to improve the dating and calibration of their evidence, to venture beyond a cultural approach based almost entirely on lithic evidence, and to integrate their evidence with other disciplines. It is hoped that this volume will mark an important step in this process.

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