The southern dispersal hypothesis and the South Asian archaeological record: Examination of dispersal routes through GIS analysis

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Abstract

This research advances a model for coastal-based dispersals into South Asia during oxygen isotope stage (OIS) 4. A series of GIS-based analyses are included that assess the potential for expansions into the interior of South Asia, and these results are compared with known archaeological signatures from that time period. The results suggest that modern Homo sapiens could have traversed both the interior and coastlines using a number of routes, and colonized South Asia relatively rapidly. Use of these routes also implies a scenario in which modern H. sapiens, by either increased population growth or competitive ability, may have replaced indigenous South Asian hominin populations.

Keywords: South Asia; Human dispersals; Coastal routes; GIS; Modeling

Over the last decade, archaeological research has identified South Asia as a crucial new frontier in the study of human evolution. The presence of both fossil and lithic components throughout the region attests to Pleistocene colonization and occupation of the subcontinent by hominin populations (Kennedy, 2000; Misra, 2001). In terms of the region’s colonization by modern humans, the general assumption is that Homo sapiens came from the West, ostensibly from a Eurasian population that had its roots in the Levant (Klein, 1999; Straus and Bar-Yosef, 2001). This premise is largely implicit in maps of modern human expansions. Typically, the route is represented by a broad arrow that sweeps north-eastwards out of Africa ca. 45,000 years ago (kya), which then bifurcates into sub-branches that enter Europe, Siberia, and the northern portion of South Asia (Cavalli-Sforza et al., 1993; Foley, 1987). This route is purely illustrative, and is not the product of either paleogeographical or paleoenvironmental analysis. In contrast, it has been suggested that earlier dispersals of modern humans may have taken place between ca. 70 and 45 kya, or during the glacial conditions of oxygen isotope stage (OIS) 4 and the interstadial Stage 3 (Lahr and Foley, 1994, 1998; Oppenheimer, 2003; Stringer, 2000). These would have traced the coastlines of the Arabian Peninsula and the Indian subcontinent, and the
descendants of these people would have ultimately colonized Australasia and Island Melanesia by ca. 50 kya. The presence of sites dating to 42–47 kya in Australia (O’Connell and Allen, 2004) provide the calibration point for this ‘Southern Dispersal’, implying that modern humans must have left Africa prior to this date. The large numbers of sites across East Africa, the Arabian Peninsula, and South Asia that are broadly attributable to the Middle Paleolithic also hint at the potential for human dispersals through these regions (James and Petraglia, 2005; Petraglia, 2003; Petraglia et al., 2003).

Genetic studies support the colonization of South Asia by modern humans originating in Africa, and more specific studies highlight the importance of this region in the global expansion of particular lineages 50–70 kya (Forster, 2004; Kivisild et al., 2000; Macaulay et al., 2005). Recent GIS-based analyses have produced the first geographically explicit model of this ‘Southern Dispersal Route’ along the Indian Ocean rim, and also examined the environmental conditions that may have affected subsistence, migration speed, and demographic expansion had this route been employed in prehistory (Field and Lahr, 2005). This work highlights the attractiveness of South Asia to coastal foragers, and also suggests that portions of the route through this region would have compelled populations to move inland. Field and Lahr also suggest that the presence of the Indus and Ganges–Brahmaputra deltas would have served as full or partial barriers, keeping populations more or less within the confines of the South Asian subcontinent, and encouraging expansions into the interior. Recent genetic studies that indicate reduced gene flow between South Asia and the surrounding regions lend additional support to this hypothesis (Metspalu et al., 2004).

Moreover, preliminary studies of the genetic and phenotypic signatures of South Asian populations suggest that this region holds clues to understanding the evolution and structure of human diversity outside Africa. These signatures vary from the persistence of physical traits, such as skin color and body size, that may have originally developed in Africa, to unique genetic sequences that may have evolved in South Asia (Kivisild et al., 1999, 2003; Metspalu et al., 2004; Vishwanathan et al., 2004). Although it is likely that demographic factors shaped much of this diversity, the environment of the subcontinent, in particular geographical and ecological constraints, would also have influenced differential rates of population growth, the source and extent of demographic expansions, and the movement of populations within and beyond South Asia’s boundaries. Therefore, the paleoenvironment of the region and its relation to human occupation represents an important source of information on the factors affecting hominin evolutionary patterns in South Asia.

Over a century of archaeological research in South Asia has revealed a wealth of late Pleistocene sites (Misra, 1989, 2001; Paddayya, 1984; Pappu and Deo, 1994; Raju and Venkatasubbaiah, 2002). Unfortunately, fossils are extremely rare. In the Narmada Valley, a hominin calvarium has been classified as Homo heidelbergensis (Cameron et al., 2004; Kennedy, 2000; Rightmire, 2001), and dated via associated fauna to 250–300 kya. For the rest of prehistory in South Asia, lithic assemblages and a scattering of other artifacts have been used to define temporal units on the basis of technological sophistication, with refinement contributed by relative and absolute dating methods. Generally, Middle Palaeolithic industries (assemblages that are predominantly based on flakes and prepared cores) date to as early as 150 kya (Misra, 1995), occur in abundance throughout South Asia, and in a variety of topographic contexts (Jayaswal, 1978; Paddayya, 1984; Pal, 2002). Upper Palaeolithic industries, which contain a greater number of blades and microliths, appear as early as 45 kya (Dennell et al., 1992).

However, it must be noted that the Middle Palaeolithic lithic industries of South Asia are exceptionally diverse. A recent assessment by James and Petraglia (2005) outlines the regional diversity of such industries in South Asia, as well as general trends towards the inclusion of flake, blade and bladelet industries at a few key sites. Elsewhere, these characteristics are commonly associated with modern H. sapiens, however, James and Petraglia note that their sporadic occurrence in South Asia is more indicative of localized trends and independent invention, rather than the influx of a new population (or species) with a distinctive tool kit. The potential for a disassociation between H. sapiens and what is typically identified as Upper Palaeolithic/microlithic raises a number of important issues for human evolution (Foley and Lahr, 1997). In particular, the behaviors that scholars usually identify as ‘modern’, the timing of dispersals out of Africa, the demography of hominins and modern humans, and the utility of ‘Middle/Upper Palaeolithic’ typologies, become open to re-interpretation. Additional archaeological research in South Asia will undoubtedly clarify...
these issues, but at the moment it is impossible to discern a uniquely modern *H. sapiens* signature from any deposits prior to 28 kya. However, the hypothesis of a modern human occupation of the region in the early Upper Pleistocene remains entirely feasible.

The present study, thus, aims to compare the Middle Paleolithic archaeological record with a hypothetical model of human dispersal and later demographic expansion, and discuss the implications of the model in relation to chronologies and prehistoric trends from particular areas. Although we will not be able to discuss the finer details of genetic and archaeological evidence in relation to the model, the broad patterns of convergence and mismatch will be used to formulate new hypotheses about South Asian prehistory that may be tested in future studies. Specifically, this paper uses GIS-based analyses to assess the potential for entry into South Asia via a northern terrestrial or southern coastal route. A second set of analyses suggests the most parsimonious routes around and through the subcontinent. A simple set of assumptions and constraints are employed in these analyses, and the resulting routes are those that demonstrate the most adherence to the model. GIS is used as an analytical engine in this respect, and we must stress that the results are a single outcome, but would not have been the only possible outcome had we chosen to include different or additional variables. We do not mean to imply that dispersals occurred in the precise way that our spatial maps portray, but rather that these maps serve as a hypothesis, and a heuristic device, for the discussion of South Asian prehistory.

Fundamentally, we assume that the first modern humans to enter South Asia were mobile hunter-gatherers, and in addition to hunting large game animals in a variety of terrestrial environments, they were also familiar with coastal resources and marine foods. This assumption stems from research in the African middle stone age (Henshilwood et al., 2001; Klein et al., 2004) that documents a generalized subsistence system that includes coastal organisms such as shellfish, fish, sea lions, and small rodents, as well as larger prey such as bovids and antelope. These findings imply that coastal resources, and perhaps more specifically aquatic resources such as fish and shellfish, may have encouraged dispersals via the coasts or along river valleys. To this end, we have weighted particular variables in our analyses (e.g., river corridors) in order to emphasize the attractiveness of these environments. However, movement through other regions is not prohibited, but varies according to relative measures of cost. In this study, topography is the primary controlling factor for dispersals, although the extent of other geographic features such as extents of sand seas or water gaps, also serve as barriers.

Our analysis of dispersal routes is followed by the investigation of locations known to have been colonized by hominins (but not necessarily by *H. sapiens*) in relation to dispersal routes and particular environmental conditions. The model anticipates that modern human populations would have encountered other hominins, most likely *H. heidelbergensis* or their descendants. Dispersals into the interior zones of the subcontinent undoubtedly put these two populations in direct competition with one another, perhaps in a similar fashion to the expansion of modern humans into Neanderthal-dominated Europe ca. 45 kya. Overall, our model suggests the manner in which modern human populations may have circumscribed and infiltrated South Asia, and ultimately expanded demographically to fill the subcontinent. Regions that would have served as corridors or barriers, or areas that would have been attractive in terms of fauna, water, or lithic resources are identified and discussed in relation to archaeological chronologies, artifact assemblages, and modern human diversity.

**Paleoenvironmental reconstruction**

In order to understand ancient dispersal patterns, it is essential to consider the role of palaeoenvironmental conditions. A full examination of the effects of climatic and tectonic change on South Asian prehistory is beyond the scope of the research summarized in this paper. However, a broad survey of some of the major palaeoenvironmental trends provides a framework for our model of dispersals and population expansions. South Asia is a large and complex region, and the modern climate and environments bear only partial resemblance to the conditions of OIS 4. Major terrestrial features, such as the Indus and Ganges Rivers and tributaries, have shifted their locations across the landscape (Chattopadhyaya, 1996; Schuldenrein, 2002), and produced extensive Holocene-aged deposits that overlie earlier Pleistocene-aged ones. Uplift and regional aridity have changed the activity patterns of fresh water sources, and either increased or decreased sediment loads in major drainages (Bhandari et al., 2005; Enzel et al., 1999; Kar et al., 2001; Srivastava et al., 2003). These and other changes
suggest that environmental dynamism and localized transitions are the norm for South Asia, and modern reconstructions must take these paleogeographic features into account as much as possible.

South Asia formed as a subcontinent after the collision of the India and Eurasian plates ca. 55 mya. Consequently, the region is flanked on the north by the Central Makran, Sulaiman, Hindu Kush, Punjab, Himalaya, and Arakan Mountain ranges (Fig. 1). The ranges are dissected by numerous streams and rivers, and can be crossed at specific points through high mountain passes. However, it is unlikely that these mountainous passes would have been open for much of OIS 4 due to the prevalence of extremely cold conditions and glaciers (Han, 1991). In broad outline, the conditions of OIS 4 are thought to approximate (although to a somewhat lesser extent in terms of extremes in temperature and aridity) what is known for OIS 2 (the last glacial maximum, 24–13 kya) (Adams and Faure, 1997). These studies indicate glacial conditions in northern latitudes (e.g., extremely dry and cool) during OIS 4, which resulted in the expansion of deserts in North Africa, Arabia, and Western South Asia (the proto Thar Desert) (Goudie, 1983), and the suppression of the monsoon system that normally results in seasonal rainfall patterns (Andrews et al., 1998; Overpeck et al., 1996). Analyses of river deposits from this period indicate that stream flow would have been reduced in all South Asian drainage systems, resulting in stream incision and thalwegs that reached depths of −80 m (R. Korisettar, pers. comm. to M. Petraglia). Global sea-level fall also lowered coastlines to approximately 80–88 m below modern levels (Cutler et al., 2003; Siddall et al., 2003). This would have exposed a considerable portion of the coastal shelf, in particular the Western side of the subcontinent.

Increased aridity suppressed vegetation in the higher elevations, resulting in a topographic mosaic of polar deserts and montane tundra throughout the Himalayas and Hindu Kush ranges (Adams and Faure, 1997). Palynological cores and faunal remains from the south coast of India indicate that much of the interior of South Asia was covered with dry savannahs and grasslands during glacial periods (Erdelen and Preu, 1990; Kotlia and Sanwal, 2004). These conditions would have extended longitudinally from the Deccan Plateau to the northern Gangetic Plain, changing into dry scrublands at the foothills of the eastern and Western Ghats. Dry tropical woodlands are thought to have existed in the eastern portion of the region, in addition to a thorny scrubland and mangrove environment around the Ganges–Brahmaputra Delta (Adams and Faure, 1997). More recent palynological investigations suggest the presence of a wet evergreen forest refugium in the extreme southern end of South Asia (i.e., the southern tip of India, and also Sri Lanka), perhaps in combination with tropical woodlands in the southern ranges of the Western and Eastern Ghats (Prabhu et al., 2004). Mangroves would have been present at times along the Western coastal shelf, with increases and decreases in mangrove expanses signalling variations in monsoonal rains and discharges of outflow (Kumaran et al., 2005, 2004; Narayana et al., 2002).

The dynamic fluctuations of the monsoon system are thought to have had a major impact on hominin populations throughout South Asian prehistory (An et al., 2001). Seasonal and spatial fluctuations are known to have occurred episodically in the past, opening up some of the more extreme environments to habitation during brief periods (Korisettar and Ramesh, 2002; Von Rad et al., 1999). Archaeological sites in the Thar Desert demonstrate periods of wet conditions (Andrews et al., 1998; Deotare et al., 2004; Kar et al., 2001; Misra, 1995). Episodic monsoon activity had a variety of effects on the river systems of the subcontinent. The drainages that originate in the Himalayan Ranges would have experienced more instances of lateral shift and abandoned channels due to increased sediment load and post-monsoon discharge, whereas the rivers of the south (Peninsular India) would have maintained broad shallow valleys on a rocky landscape, with little instance of braiding (R. Korisettar, pers. comm. to M. Petraglia). However, discharge in these regions was enough to form large lakes in the broad shallow valleys, which transitioned into dry basins as aridity returned (Korisettar, 2004).

Lastly, a period of punctuated change that occurred within the time frame of the Southern Dispersal may also have had an impact on hominin populations and the expansion of modern human populations into South Asia. Ash and tephra deposits located throughout the region are known to be the product of a volcanic eruption, specifically the super-eruption of the Toba volcano in Indonesia between 71 and 74 kya (Acharyya and Basu, 1993; Shane et al., 1993; Westgate et al., 1998). It has been suggested that the after-effects of this eruption resulted in a population crash for all terrestrial organisms, including hominin popula-
Fig. 1. Palaeoenvironmental model for South Asia during OIS 4. Based on reconstructions summarized in Adams and Faure (1997) (2005 website), and also personal comments from Dorian Fuller in 2005. Extent of Thar Desert derived from Glennie and Singhvi (2002).
Asian prehistory is currently under scrutiny (Jones, in preparation). The magnitude of this event and its effects on hominin populations in South Asian prehistory is currently under scrutiny (Jones, in preparation).

A GIS-based model of dispersals across South Asia

A geographic information system (GIS) was employed to better understand dispersal routes across South Asia. Although there is good knowledge about the location of archaeological sites thanks to numerous surveys, the actual routes that hominins may have undertaken has not been a subject of serious study. The current study employs GIS methodologies in order to examine the likeliest routes for dispersals. While GIS has become a standard tool in archaeology (Church et al., 2000; Wheatley and Gillings, 2002), there have been relatively few studies which attempt the kind of analyses portrayed here (for an exception, see Anderson and Gillam, 2000). However, we must stress that our methodology is derived from a very simple model and set of assumptions, some of which have been discussed elsewhere in studies of the colonization of the New World (Dixon, 1999, 2001; Grün, 1994; Mandryk et al., 2001; Mosimann and Martin, 1975) and Australia (Birdsell, 1977; Bowdler, 1977; O’Connell and James, 1998; O’Connor and Chappell, 2003; Wild, 1985). In our model, we assume that the first modern humans to colonize South Asia were mobile hunter-gatherers, and that these groups may have relied upon, or at least been familiar with, subsistence strategies that included coastal resources. We also assume that regions that were mountainous, at high elevation, or with steep slopes would not have been included as part of major routes of colonization. Montane environments and resources were undoubtedly important to early colonizers; however, when considering human dispersals these regions are less likely to have served as major routes, as they are more costly to hunter-gatherers in terms of energy expenditure, and less attractive in terms of the availability of game and collectable foods. Thus, our focus is on coastlines, plains, and river valleys, and more generally on corridors that connect the interior of South Asia with the coasts.

Methodology I: friction surface

The generation of routes into and through a paleoenvironmentally adjusted model of South Asia was performed with ArcGIS 8.3 software, and utilized a rasterized model of the landscape of South Asia (i.e., the features of the landscape were represented as a cellular grid). Each of the cells in the model was coded to a particular value, thus creating a ‘friction surface’ that could be used to analyze portions of the landscape for the least costly routes between particular points. In this case, rasterized slope data from the HYDRO1K and ETOPO2 (LPDAC, 2003; NGDC, 2004) data sets supplied the founding layers for the friction surface. These data were merged to produce a composite terrain for the region, with a resolution of 1 km for the HYDRO1K terrestrial surfaces, and 3.7 km for the ETOPO2 bathymetric surfaces (i.e., portions of South Asia exposed by the 80–88 m sea-level fall). The act of merging these rasters produced a resolution ‘edge’ along the coastlines. This edge was not mosaiced (i.e., the difference between resolution of the rasters was not generalized) in order to preserve the quality of both data sets in the coastal areas. The presence of the edge did present some problems, as route segments that were plotted through the ETOPO2 data were of lower resolution than those of the HYDRO1K dataset. However, an ‘edge effect’ in which the routes followed the merged edges of the data sets occurred only rarely, due to the use of the wandering method outlined below.

The merged surface was then reclassified, and the values of individual increments of slope recalibrated using a scale that has been adjusted to reflect human energy expenditure (Bell and Lock, 2000; Gorenflo and Gale, 1990; Llobera, 2000; van Leusen, 2002) (Table 1). In this scaling, the relative energetic cost of crossing slopes increases with slope grade. We acknowledge that slope is only one aspect of topography that affects biogeographical processes, however, it allows for a relative assessment of energy expenditure for movement across long distances, and is fairly sensitive to topographic constraints such as cliffs or rugged topography, which may have directed population movements in one direction or another. Equating slope grade with travel cost also parallels a basic assumption of biological theory, which proposes that routes up and across steep slopes are more costly in terms of energy expenditure and foraging time than across flat landscapes, and are less often pursued by mobile organisms (Krebs and Davies, 1993).

Our friction surface also utilized barriers, which we defined as features of the landscape that would effectively block or re-direct travel, such as lakes, sand seas, wide rivers, coastlines, and continental ice
likely to have provided permanent water location during glacial periods. They are also more likely to have persisted in their present location during these drainages are of significant size and volume, and more likely to have persisted in their present location during glacial periods. They are also more likely to have persisted in their present location during OIS 4.

Stream order (Strahler, 1964) was used to select streams of order 3 or higher, as these drainages are of significant size and volume, and more likely to have persisted in their present location during glacial periods. They are also more likely to have provided permanent water flow. Riparian areas that were wider than 5 k were set as impermeable barriers, but rivers and streams of lesser size were presumed to have been crossable. The location of the coastline at OIS 4 was projected as an impermeable boundary line on top of the friction surface using a topographic algorithm within ArcGIS. We employed −88 m as the coastline for our model, which exposed a significant portion of the coastal shelf. However, this boundary designation is only a rough estimate of the coastline at OIS 4, as this method does not take into account other factors that would have affected sea levels at that time, such as continental uplift.

The location of sand seas during OIS 4 was estimated for South Asia using models generated by geologists (Glennie and Singhvi, 2002) and the modern extent of the Thar Desert from the Global GIS Database (USGS, 2000). Sand seas were not classified as impermeable boundaries, but were given a value that was high in relation to other slope costs in the study (15°), but not high enough to completely preclude the possibility of crossing the narrower portions (Table 1). Other GIS-based studies that utilized friction surfaces have identified the importance of partial barriers such as sand seas, as they can also re-direct movement, and slow down traverse rates (Ray et al., 1999; Steele et al., 1998; Surovell, 2003; Young and Bettinger, 1995).

Lastly, we also assume that during the glacial conditions of OIS 4, riparian areas that would have provided water and habitat for a variety of animals would have been most attractive to hunter-gatherers. To this end, riparian areas that flank major river courses were assigned relatively low values (or no cost) in order to emphasize their attractiveness on the rasterized landscape (Table 1). We acknowledge that privileging these features in the landscape will have the effect of driving route generation towards a particular outcome; however, in the context of a slope-based friction surface, riparian areas along river courses were already of extremely low cost. By emphasizing these areas, we are attempting to construct a model that is relevant to the needs of hunter-gatherers at OIS 4. Other variables that relate to human subsistence and mobility (e.g., vegetation types, the density of game animals, and rainfall averages) were not included in analyses that result in route generation, as precise empirical data concerning their presence and character is lacking for this time period. Rather, the effect these conditions may have had on populations as they moved along the topographically derived routes will be

<table>
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</tr>
<tr>
<td>Sea level</td>
<td>Impermeable</td>
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a Slope calculations were obtained from ancillary slope data sets of HYDRO1K and calculations based on the topographic coverage of ETOPO2.

b Slope energy values were derived from the following calculation: tan slope x tan (1°) (Bell and Lock, 2000, pp. 88–89).

c The location of major rivers likely to have been present during OIS 4 was calculated from the HYDRO1K stream data set. Stream order (Strahler, 1964) was used to select streams of order 3 or higher, these drainages are of significant size and volume, and more likely to have persisted in their present location during glacial periods. They are also more likely to have provided permanent water flow.
d The extent of aeolian sand deposits is derived from the Global GIS Database (USGS, 2000) and published data by Glennie and Singhvi (2002) for the extent of desert sands during glacial episodes in Arabia and South Asia. The value of 15 prohibits crossing by least-cost pathways in nearly all circumstances, but does allow for crossing of short stretches (i.e., 90 km).

e As discussed previously, global sea levels for OIS 4 were given an average of −80 m. The location of this level on the ETOPO2 data set was calculated for the study area, and this line was then reclassified as an impermeable barrier.

sheets. In this study, the location of major rivers likely to have been present during OIS 4 was calculated from the HYDRO1K stream data set. Stream order data included in the data set was used to select streams of order 3 or higher (Strahler, 1964), as these drainages are of significant size and volume, and more likely to have persisted in their present location during glacial periods. They are also more likely to have provided permanent water flow. River
discussed in terms of their impact on foraging, demography, and settlement patterns.

**Methodology II: least cost routes**

Our model assumes that migrating populations generally follow the “easier”, or least costly, route across a terrain. A route may be defined as a linear course of travel through a physical landscape, which includes the crossing of flat plains, river banks, or at times crossing of mountain passes. This study employed two discrete analyses: a ‘direct route’ analysis and a ‘wandering route’ analysis. The direct route analysis sought to examine the most parsimonious route into South Asia from points to the west; the wandering route analysis aimed to produce hypothetical routes within South Asia that were not driven by a destination, but would have led to the distribution of modern human populations in different regions, and perhaps at different times. Both of these analyses rely upon a least-cost algorithm housed within the GIS. This analysis determines the pathway of least-cost between two points by measuring the value of adjacent and intervening cells in the analysis field (Madry and Rakos, 1996; van Leusen, 2002). In the direct route analysis, an expansive ‘origin’ that lies to the west of South Asia was used to simulate the entry into South Asia from either a northern terrestrial route, or a Western coastal route. This origin was a line that stretched 2200 km across nearly all of southwest Asia, from the Pamir Mountain Range that lies to the west of the Tibetan Plateau, to the banks of the Euphrates River in Eastern Arabia (Fig. 2). This area was chosen as the origin based upon the consensus view that modern humans dispersed out of Africa, rather than a source from the northeast, such as Eastern Asia. Points were set up along this line at an interval of every kilometre. Using the friction surface described above, and a destination point set on the southernmost tip of South Asia, the least costly ‘direct’ route from each of the points along the line was calculated.

The wandering route method employed a 60 km search radius and a starting point on the friction surface (the location of the starting point is described below). Analysis of the values of the cells surrounding the starting point determined the least costly path, which could proceed in any direction towards the boundary of the search radius. Thus, each wandering route was generated as a culmination of 60 km path segments; following each calculation, the search radius was moved to the newest endpoint, and the path was calculated from that point onwards. Analyses of routes by segment leg continued until the culminated route reached a cul de sac, such as a high mountain valley, or joined with a least-cost wandering route that had already been plotted. At this point, the route was started again from a new origin. It is important to note that the wandering route technique is distinctly different from the ‘origin’ and ‘destination’ driven routes exemplified by Anderson and Gillam’s (2000) analyses of colonization routes into the New World. Their technique plots the least costly routes from origin points to sites in the interior that are known to have been occupied by Paleoindians. This does not emphasize any particular environment as more attractive or habitable, but indicates a potential sequence for colonization of the continent via a direct route. The wandering method employed in this study eliminates the problem of having a destination, and more closely mimics the movement of colonizing populations, who would not have known what lay before them. However, it should be noted that these GIS routes remain hypothetical, and should be recognized as predicted outcomes from the range of possibilities identified above in the discussion of the friction surface. Additional analyses that incorporated other variables, such as the attractiveness of lithic resources, or seasonal migration routes for herds of large mammals, would have produced alternative outcomes in the wandering analysis.

**Result of the direct routes analysis**

Approximately 2200 separate sub-routes were generated from the points along the origin line, which overlapped into three major routes that proceeded around or through the Zagros Mountains (Fig. 2). These sub-routes united near the Straits of Hormuz, and then headed east along the Makran Coast into South Asia. The linear origin analysis suggests that the most economical routes into South Asia cross through the lower elevations of the Zagros Mountains, or follow a predominantly riparian corridor along the Euphrates River and onto the Makran Coast. This indicates that populations originating in the Levant, Northern Africa, or other points to the west would have been more likely to enter South Asia if they took a southern route. This also holds true for dispersals originating along the southeast edge of the Eurasian Steppes (the farthest
eastern point of the line). Analyses of least-cost routes from this region encounter the steep terrain of the Hindu Kush and Pamir Mountains, and when they cannot proceed south they turn back, in a westward direction. Of note, the least-cost routes do not cross the Hindu Kush Mountains into the northernmost headwaters of the Indus Valley. Not only were these regions rugged and steep, but during OIS 4...
they would have been partially ice-bound (Paterson, 2003), and less likely to have attracted hunter-gatherers that were moving eastwards. This does not preclude the possibility that populations entered and occupied these regions, but implies that these areas were not major routes into South Asia for the bulk of the population.

The potential sub-routes also offered markedly different resources. The routes through the Zagros Mountains cross the arid Naomid Plain and Lut Basin, which during OIS 4 consisted of windswept yardangs and expansive salt flats (Selivanov, 1982) (Fig. 2, inset). Although wet phases could have supported small populations of ungulates and birds, during dry periods this region would have been a very harsh environment. In contrast, the Tigris–Euphrates route would have crossed through riparian areas and marshes, providing an expansive environment with both water and game (Aqrawi, 2001). It is more likely that this region could have supported a dispersing population during OIS 4, and thus led them directly towards the Straits of Hormuz and the Makran Coast. Once in this region, migrating populations would have encountered an arid coastline that provided a variety of marine foods (e.g., molluscs, crustaceans, birds, and turtles) (Hopner et al., 2000), and with further travel eastwards would have reached the rich ecosystem of the Indus Delta (Meadows and Meadows, 1999).

**Result of wandering routes analysis**

The initiation point for the wandering routes begins on the Western bank of the Indus Delta (Fig. 3). This location was selected from the results of the direct route analysis, which passed through this region. We also realize that caution needs to be exercised in placing the wandering origin here, given that the bed of the Indus and its tributaries has repeatedly changed its course over the Holocene. The Indus Valley is an ancient riparian landscape that has been carrying outflow from the Himalayas to the Indian Ocean throughout the Pleistocene (Schuldenrein, 2002). It may have been one of the first of several diversions into the interior, as the river itself could have proved a barrier during OIS 4, and the flat alluvial terraces of the valley bottom would have drawn hunter-gatherer populations northwards. Indeed, this was the result of the first analysis; the wandering route reached a cul de sac between the coastline and the wide Indus Delta, and the placement of a new starting point a few kilome-
Fig. 3. Results of the wandering path analyses into and through South Asia. Least-cost routes are indicated by the grey lines. Costly areas, including sand seas and areas of high slope are indicated by the color grade. Inset shows detail of Cape Rama diversion.
and game. Archaeological survey in this region has, in fact, indicated an abundance of sites (Pappu and Deo, 1994), although at least a proportion of this abundance is due to the ease of surveying in this region. Additional wandering indicated a diversion northwards into the Krishna Basin, which eventually turned southeast and followed the Penner River Valley to the Coromandel Coast.

However, if a fifth origin was placed on the southern side of Cape Rama, a wandering route was predicted that ran southwards towards the tip of peninsular South Asia. At Cape Comorin, the wandering route headed northwards, and crossed the Sri Lankan isthmus. The route continued to flank the coastline for the next 2500 km, occasionally dipping into low lying river deltas. The route ultimately entered the Penner Delta, and then upon reaching the Ganges–Brahmaputra Delta crossed into the Damodar Valley. As with the Narmada and the Indus, the size of the Ganges–Brahmaputra river system, as well as the expanse of mangroves and marsh around the delta, implies a region that would have impeded colonization to the east. Based on this, and also the attractiveness of the riparian corridor connecting the Damodar River with the coastline, our analyses suggest that populations would have been diverted, at least initially, into the Ganges Valley, rather than continuing eastwards into the Pleistocene Sundarbans. The remainder of the wandering route analysis predicted travel westward, flanking the southern side of the Ganges–Brahmaputra Delta. Continued wandering along the south bank of the Ganges River produced four final bifurcations: two routes crossed the river at a narrow point and headed northwards into the valleys of the Arun and Sun Kosi Rivers, which flow out of the Himalayas. Two other routes continued westward and followed the Ganges and the Ghaggar Rivers. The routes were allowed to terminate at this point.

**Proposed routes, colonization issues, and the archaeological record of South Asia**

The least-cost routes suggest that the coastlines could have provided major migratory corridors into and within South Asia, and these regions should bear evidence for human occupation. However, an archaeological signature that could be linked to coastlines remains elusive. Perhaps one of the obvious, but salient, explanations for this is that many Pleistocene sites along the proposed coastal routes would have been submerged following the rise in sea levels after the last glacial maximum. This is apparent in a comparison of Fig. 4 with a modern map of South Asia. Our study suggests that submerged sites should exist along both coasts of India as well as between India and Sri Lanka, although to date no detailed examination of potential underwater deposits has been attempted (Flemming, 2004). A few sites are known that are adjacent to coastal regions, such as Ramayogi Agraharam (Rath et al., 1997), Borra (Vijaya Prakash et al., 1995), Attirampakkam (Pappu, 2001), the Konkan complex (Gudzer, 1980), and the Hiran Valley (Baskaran et al., 1986; Marathe, 1981), and these sites contain assemblages that are categorized as Middle Paleolithic. The Hiran Valley deposits have associated dates within the range we suggest for the Southern Dispersal (56–69 kya), although which hominin species made the artefacts found remains unknown.

If the lack of sites along the coast is not a product of survey effort, another explanation could be the speed of dispersal. It is possible that coastal movements occurred relatively rapidly, and left little in the way of a recognizable archaeological signature. Such a scenario has been suggested by wave of advance models of colonizing populations, such as Hazelwood and Steele’s (2004) and Steele et al.’s (1998) analyses for pioneer expansions into continents. Their work outlines the actual mechanisms of wave dispersals in detail, suggesting that ‘broad’ wave profiles, in which population density is low and dispersals are rapid, leave only remnant deposits and no clear pattern of decreasing age from the ‘origin’ to the outer edges of the expansion. We suggest a similar scenario for South Asia, with the added twist that its coastlines would have initially funnelled the dispersals south and eastwards. The Makran Coast and the coastline of the Thar Desert, which appears as the most likely entry point into South Asia in our analyses, were extremely arid during OIS 4, and consisted of a narrow coastal corridor backed by rugged desert hills (Singhvi and Kar, 2004). The intertidal zones would have provided a variety of marine foods, such as molluscs, sand dwelling shellfish, nesting sea turtles, and crabs (Hopner et al., 2000), although the lack of water and narrowness of this corridor implies that populations would have had to move through quickly (Field and Lahr, 2005). Further south, coastal dispersals may have encountered brackish marshes and salt flats, and perhaps also expanses of mangroves (Kumar et al., 2004). Subsistence in this region may also have relied exclusively upon marine resources, as these environments provide few terrestrial ones.
This scenario of an initial coastal occupation for South Asia has also been suggested for the Americas, where several early dates for human occupation appear in South America, rather than near the presumed origin point in Beringia (Dillehay, 2000; Dixon, 1999; Roosvelt et al., 1996). Dixon has suggested that this pattern relates to an initial expansion along the coastlines of the Americas by populations utilizing coastal resources and watercraft. He also hypothesizes that a generalized coastal foraging strategy is advantageous in colonizing scenarios, as it does not require a complex tool kit or access to lithic resources, nor large populations of terrestrial mammals. Rather, such dispersals may have relied on simple gathering of intertidal animals, such as shellfish, which require few tools. The initial colonization of South Asia by modern *H. sapiens* could have followed a similar pattern, with less investment in complex lithics that are associated with terrestrial hunting (e.g., blades and composite tools), and a highly developed suite of tools associated with coastal foraging, such as wooden spears, shell and bone hooks, fiber nets and baskets.

In terms of dispersals into the interior of South Asia, the route analyses identify deltas as the initial portals inland. The Indus River is the first encountered in these analyses, and although increased aridity during OIS 4 would have significantly reduced the size of the river, in the midst of the surrounding desert the estuary would have provided a crucial habitat for migrating birds, as well as contained fish and shellfish. Larger animals that were common to the savannahs of South Asia, such as elephant, buffalo, wild cattle, horse, deer, and rhinoceros may have been present (Badam, 1979). These conditions suggest that populations could have remained in this region for longer periods, and probably expanded upriver as indicated by the wandering route analyses (Fig. 3). The occurrence of Site 55 in the foothills of the Hindu Kush Mountains, which is dated to 45 kya, is the only Pleistocene site in this part of South Asia that may correspond with this dispersal route. Dennell and colleagues document the presence of stone blades at the site, and also suggest that the activities included habitation and lithic procurement in the high foothills (Dennell et al., 1992). Although the high rate of sedimentation has resulted in a poorly known Paleolithic archaeological record for the rest of the Indus, we hypothesize that other sites are likely to be found in abundance in future. In addition, the fact that the region is flanked by the Thar Desert and the mountains of the Sulaiman and Hindu Kush ranges implies a degree of isolation for these populations, although networks of exchange and interaction may have episodically moved people and materials out of the region.

A similar environment would have been associated with the Narmada Delta. If, as hypothesized, populations of mobile foragers were moving down the Western coastline of South Asia, the expanses of riparian areas associated with the Narmada Delta would have provided a welcome refuge from the aridity of the desert coastlines to the north. In addition, the Narmada Valley would have provided a rich terrestrial habitat for ungulates, birds, and other wildlife, and mobile foragers that used this valley as a route into the interior would have encountered savannahs and grasslands. These landscapes would have supported terrestrial fauna of similar composition to sub-Saharan Africa, including horse, rhino, boar, deer, antelope, wild cattle, pygmy hippo, elephant, stegodon, and buffalo (Badam, 1979). The archaeological sites of Bhimbetka rockshelter (III F-23) and Adamgarh occur along this route, occupying either side of the Narmada River. The deep deposits (over 3 m, and ranging from the Late Acheulean to the Mesolithic) of both sites indicate the presence of populations in the region in the Late Pleistocene (Joshi, 1978; Misra, 1985). Aridity in this environment would have required populations to be mobile, yet tied to crucial environmental zones that contained water and lithic resources. However, if a relative abundance of terrestrial fauna is assumed, then there is the potential for demographic expansion in this region, with additional geographic expansions to the grasslands of the north and south.

A third interior dispersal is hypothesized by the crossing of the Western Ghats at Cape Rama. Populations that entered this portion of the subcontinent would have first encountered the hills of the Western Ghats, which during OIS 4 supported dry woodlands and scrublands. Once in the interior of peninsular South Asia, migrants would have encountered grassy country in the Deccan Plateau, which was broken occasionally into hilly terrain with a vegetation of scrub and dry deciduous forest. This region also contains a number of basins, such as the Kaladgi and Cuddapah. Archaeological investigations in this region indicate a high density of sites and a range of lithic assemblages (Murty and Reddy, 1975; Pappu and Deo, 1994; Petraglia et al., 2003; Raju, 1988). Excavations in the Kurnool Caves have revealed Upper Pleistocene deposits, which include
lithic artifacts and the remains of horse, rhino, boar, gazelle, deer, antelope, and wild cattle (Murty, 1979; Prasad, 1996). As with the grasslands to the north, human populations are expected to have expanded demographically in this environment, and eventually filled the various tributaries with small, mobile groups.

If the least-cost routes are viewed as a hypothetical “distribution scheme” for South Asian populations, it is important to note the instances where routes seem to result in convergences. For example, continued migrations via the Narmada Valley would eventually reach the Ganges Plain, which could also be reached through separate movements across the Potwar Plateau, and along the Western side of the Ganges–Brahmaputra Delta. This suggests that the eastern end of the Gangetic Plain could have experienced a higher frequency of dispersals, and perhaps also accumulated a more diverse population as a result. This region may have also acted as a partial cul-de-sac, as further expansions eastwards would have been slowed down by the expanse of the Ganges–Brahmaputra Delta acting as a potential spatial ‘bottleneck’. A number of sites exist in this region, with sequences that range from the Acheulean to the Mesolithic. The Son River Valley and the Belan Valley are particularly rich areas with stratigraphic sequences and palaeoecological information (Ahmed, 1984; Blumenshine et al., 1983; Clark and Williams, 1990; Sharma and Clark, 1983). Dispersals in the south suggest the convergence of routes in and around the Coromandel Coast and the isthmus of Pleistocene Sri Lanka. Increased interaction in this region may have also resulted in a more diverse population, and higher frequency of exchange concerning technology and ideas.

There are a number of instances in which the archaeological record seems unrelated to the least-cost routes emerging from this study. For example, a series of important sites in the Thar Desert: the sites of Didwana (Misra et al., 1982), Luni Valley (Mishra et al., 1999), and Hockra (Allchin et al., 1978). Although the simulations did not suggest dispersals into the Thar Desert under the palaeoenvironmental conditions stipulated, the area would have been attractive during wet periods, even if of short duration. Indeed, archaeological sites in the area are often associated with riverine and lacustrine settings (Mishra et al., 1999; Misra, 1995). In such circumstances, this region may have been reached via dispersals along the Ghaggar River, or perhaps by the intermittent streams that flow southwards out of the desert. Also missed by the predicted routes are the late Pleistocene sites of Badatombalena and Fa Hien on Sri Lanka (Deraniyagala, 1992). The earliest known remains for modern H. sapiens and shell beads in South Asia come from this region, dating to ca. 31–28 kya (Kumar et al., 1988). If these dates indeed indicate the earliest occupation of Sri Lanka by modern humans, then a late settlement date for the isthmus (and later island) is predicted.

Discussion

Current understanding of our evolutionary history suggests that South Asia must have played a pivotal role in the expansion of modern humans out of Africa (Lahr and Foley, 1994; Stringer, 2000). As the mid-way point between Africa and Australia, and as a large region that supported a savannah environment similar to that of Sub-Saharan Africa, it seems a prime candidate for early colonization by modern H. sapiens, as well as a potentially major locus for subsequent expansions of human populations. Such a pivotal role is also suggested by the pattern of non-African mitochondrial DNA (mtDNA) diversity, showing that populations in the region today carry lineages that are part of one of the two first clades to derive from African diversity (namely M* lineages). More recent genetic analyses indicate that certain geographically isolated populations in Southeast Asia retain unique mtDNA lineages with time-depths of 44,000–63,000 years, suggesting that lineage divergence occurred very early in the region (Macaulay et al., 2005; Thangaraj et al., 2005).

The extensive evidence of a lack of genetic diversity of living humans (including South Asians) also strongly suggests that modern humans replaced, rather than intermingled with the archaic populations that already resided outside of Africa (Cann, 2001; Cann et al., 1987; Currat and Excoffier, 2004; Eswaran et al., 2005; Forster, 2004; Relethford and John, 1995; Watson et al., 1997). Currently, the lack of hominin fossils makes it difficult to determine exactly what these populations were in South Asia—either Homo erectus, H. heidelbergensis, Homo neanderthalensis, or a yet undescribed species of Homo. From extensive archaeological deposits it appears that they enjoyed a lengthy history, with their own trends towards more diverse and sophisticated lithic assemblages (James and Petraglia, 2005). However,
the fact that these populations went extinct with the influx of modern humans suggests that \textit{H. sapiens} had some competitive advantage over pre-existing South Asian hominins, perhaps in terms of increased rates of population growth, more flexible subsistence strategies, or more extensive social networks. Moreover, the absence of a distinctive lithic assemblage that can be linked to modern \textit{H. sapiens} may be more telling than previously realized. If these populations relied upon generalized coastal hunting and gathering strategies similar to those that have been documented for Blombos Cave and Ysterfontein (Henshilwood et al., 2001; Klein et al., 2004), then the search for microliths or points which are usually associated with specialized terrestrial hunting and equated with modern \textit{H. sapiens}, may be a false trail. A generalized tool kit, and an accompanying subsistence system that could rapidly traverse coastal and riparian environments may have provided one of the crucial advantages that allowed modern humans to move into regions that may have already been inhabited by South Asian hominins. Moreover, this flexibility may have meant that they were less constrained by broader ecological regions, and could move freely between them without a lengthy period of technological adjustment. We also stress that the search for a parallel to the European Upper Paleolithic (e.g., blades, carved bone points, beads, effigies, etc.) in South Asia enforces a particular model of human behavioural evolution (Klein, 1999), and precludes the usage of broader definitions of modernity. Research of modernity in Africa (Foley and Lahr, 1997; McBrearty and Brooks, 2000) has shown that early modern human behavior appears to follow multiple development trajectories, rather than a single progression.

In addition, the least-cost routes suggested by the analyses presented in this paper indicate that modern humans would have been able to follow natural corridors deep into the countryside, and establish populations within the heart of South Asia. At a minimum, if modern humans were able to maintain a higher rate of population growth after their entry into the interior, then outward population expansions from these regions may have placed additional pressure on indigenous South Asian \textit{Homo} by forcing them out of the most productive savannahs and into the marginal areas. Based on the results of least-cost route analysis, the most likely loci for the expansion of anatomically modern human populations within South Asia were the Son, Belan and Upper Narmada Valleys, as well as the Krishna and Godavari drainages. These regions appear to have been major loci for hominin populations in antiquity, as evinced by the abundant Middle Paleolithic and Late Acheulean assemblages. Further population growth would probably have spread modern humans north and south, to the limits of the savannas. Such demographic growth and expansion across South Asia may be reflected in the increased complexity of the archaeological record after 45 kya (James and Petraglia, 2005).

Additional aspects of South Asian prehistory are not well articulated in the model of South Asian dispersals presented here. For one, the importance of lithic sources in the hominin choice of habitats was not included in the analyses. Discovery of quarries or other lithic sources may have provided the impetus for additional expansions into parts of South Asia, while the absence of these resources, such as in the Ganges Valley, may also have played a role in the lack of sites in this region. The impact of the Toba eruption on South Asian hominins is also unknown. If, as has been suggested (Ambrose, 1998), the eruption and its associated ashfall had a significant and negative impact on hominin populations in South Asia, modern \textit{H. sapiens} may have led a relatively unchallenged invasion of the region after 70 kya. As the dating for the initial entry into Australasia is at a maximum 50 kya, this leaves plenty of time for populations to have dispersed into and through South Asia in the millennia following the Toba eruption.

Conclusion

The results of GIS-based analyses of least-cost routes predicts that entry into Asia during OIS 4 is more likely to have used a coastal corridor that originated to the west, as opposed to a northern montane corridor through the Hindu Kush Mountains. Once in South Asia, populations may have followed a number of routes, which included both coastal and terrestrial contexts. Diversions into the interior are suggested via the Indus River and Narmada River valleys, and also through a break in the Western Ghats. The analyses also indicate that dispersals along the coasts of South Asia would have eventually turned inland at the Ganges–Brahmaputra Delta, and that this feature may have blocked or slow populations attempting to move eastwards. The identification of archaeological sites and site complexes along these corridors indicates some concurrence with these hypotheses in several cases,
although their absence is notable for the coastal regions. The rise in sea levels since the Last Glacial Maximum may explain this absence to some degree, although we also suggest that the subsistence technologies employed by coastal foragers, such as perishable nets or collecting equipment, or expedient tools used for collecting shellfish, may not have preserved into the Holocene. Moreover, dispersals through arid coastal regions may have been very rapid, and left little in the form of archaeological deposits. In terms of the Southern Dispersal Hypothesis, the analysis of routes described here suggests that dispersals into South Asia could have happened very rapidly, and either expanded through the interior or along the coastal perimeter. However, there is also the potential for a relative deceleration out of South Asia (i.e., south and eastwards into Asia) as populations expanded demographically into the varied environments of the region, and also met the barrier of the Ganges–Brahmaputra Delta.

What is known for the paleoenvironment of South Asia suggests that both the coasts and the interior would have been attractive to mobile parties of modern hunter-gatherers. If the use of coasts and riparian corridors allowed for rapid dispersals into South Asia, and movement between these environments was not a problem in terms of subsistence and subsistence related technologies, our analyses suggest that populations could have expanded rapidly into the heartland of South Asia. Reasons for the extinction of non-modern hominins, if still present in these regions, are discussed. Later expansions that led to the extinction of indigenous hominins are also surmised. This hypothesis has further support from genetic data that suggests lineage divergence in South Asia ca. 44,000–63,000 years ago, as well as archaeological evidence for increasingly modern behaviors in South Asia after this time period.

In conclusion, the prehistory of South Asia will be further uncovered in future years through study of the archaeological and fossil record, and the genetics of modern populations. The assessment of the potential routes of dispersal through the region allows for an examination of the paleoenvironmental factors that may have shaped or directed prehistoric use of the South Asian landscape, and also provides a model and a series of hypotheses that may be tested against others. Undoubtedly, future work and exploration in the region will further develop and refine this model, and lead to new hypotheses concerning the dispersal of modern humans throughout the world.

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