Introduction

A succession of recent archaeological discoveries have challenged the notion that hominids remained in Africa until a mere 1 m.y.a.—the accepted wisdom up until the early 1990s. Following the re-dating of the Sangiran and Mojokerto *H. erectus* fossils to 1·8–1·6 m.y.a. by Swisher et al. (1994) and continuing with the publication of new skulls from Dmanisi dated to 1·7 m.y.a. (Gabunia et al., 2000; Lordkipanidze et al., 2000) it is now apparent that we have little understanding of how, when or why hominids colonized Eurasia (Figure 1). As the commentary in *Science* accompanying the announcement of the Dmanisi skulls put it, “Although the evidence from Dmanisi supports the idea that hominids got out of Africa fast and early—exactly where they went next and how they eventually got to Europe is a mystery” (Balter & Gibbons, 2000:950). Such understanding will develop, one hopes, largely from improvements in the archaeological data and an increase in the quantity and quality of dated archaeological sites and fossil localities. But to enable adequate interpretation of both existing and future discoveries the discipline also needs to improve its theoretical frameworks regarding hominid dispersal.

The literature is increasingly full of proposals about environmental barriers (deserts, mountains, plains), glacial/interglacial cycles, sea-crossing, land bridges and adaptive specializations, but lacks the means to evaluate their individual and combined impacts on hominid dispersal (see...
recent reviews of hominid dispersals by Larick & Ciochon, 1996; Bar-Yosef, 1998, 2000; Rolland, 1998; Arribas & Palmqvist, 1999; Straus & Bar-Yosef, 2001). Attempts at quantification and simulation modelling appear essential. It is striking that such methods play a central role in other disciplines dealing with long term change and dispersal patterns (such as climate modelling and epidemiology) but have been neglected in palaeoanthropology. The difficulties in establishing a manageable but sufficient set of variables and selecting appropriate parameter values hardly needs stressing. The rewards, however, can be substantial. These come partly from the development of a quantified simulation model by removing the ambiguities of language that hide behind terms such as “rapid dispersal” (how rapid?) or mountain barrier (how high?). Further benefits come from actually running simulations to appreciate the often unpredictable consequences of multiple interacting variables. To these ends, this paper introduces a computer simulation model called STEPPINGOUT which seeks to enhance the interpretation of archaeological and fossil data.

Developing models for hominid dispersal

As Rolland (1998) noted, systematic studies of human migration from methodological and theoretical perspectives have largely been confined to more recent chapters of prehistory [Gamble (1993) providing a notable exception]. Other than in the work of Turner (1992), topics such as adaptation and socio-ecology have received little attention in the context of dispersal and colonization even though they are otherwise
commonplace in palaeoanthropology. This is perhaps not surprising, as there is an evident clash of chronological and spatial scales: most models for hominid behaviour ultimately derive from studies of modern hunter-gatherers or nonhuman primates and relate to life-history and seasonal variation in behaviour—an ethnographic scale of analysis. When tackling hominid dispersals from Africa archaeologists need to think about quite different scales of time and space—hundreds of millennia and the continent of Eurasia from Boxgrove in the west to Java in the east. Moreover, H. ergaster, the species most likely to have first left Africa, is evidently quite different from both modern H. sapiens and the chimpanzee—bipedal and with modern human stature, but nonlinguistic and culturally constrained (for one cognitive and behavioural interpretation see Mithen, 1996).

The need to improve our current models of hominid dispersal has become particularly pressing due to the questions posed by the recent discoveries themselves. Most challenging of these is the claimed 1·8-million-year-old presence of H. erectus on Java (Swisher et al., 1994; Sémah et al., 2000). If this date is correct—or even if the true date is 1·6 or 1·4 m.y.a.—what does this imply for the “departure” date from Africa? If it requires a date prior to 2 m.y.a. this either implicates H. habilis (or A. habilis, Wood & Collard, 1999) or suggests that earlier discoveries of H. erectus in Africa remain to be discovered. Alternatively, would it have been feasible for H. ergaster/erectus to have dispersed from East Africa to S.E. Asia within no more than a few tens of millennia? Until issues of hominid evolutionary biogeography are addressed it remains quite impossible to evaluate these alternative possibilities.

The early dates from Asia, those from ‘Ubeidiya (Tchernov, 1995), Java, Longuppo Cave (Wanpo et al., 1995), Riwat (Dennell et al., 1988) and Dmanisi, have made the earliest hominid presence in Europe seem remarkably young—although serious doubts remain as to whether the anatomical remains at Longuppo are hominid (Wolff, cited in Culotta, 1995) and whether flaked stones from Riwat are artefacts or geofacts (Dennell et al., 1988). The most widely accepted earliest date in Europe at present is ca. 800 ka ago at TD6, Atapuerca (Carbonell et al., 1995, 1999) with settlement possibly not appearing outside of the Mediterranean zone until 500 ka ago (Dennell & Roebroeks, 1996; Roebroeks, 2001). If hominids were able to reach Java by 1·4–1·8 m.y.a. and were at Dmanisi by 1·7 m.y.a., the million-year delay in colonizing Europe appears extraordinary and, perhaps, illusory (Roebroeks & van Kolfschoten, 1994, 1995; Dennell & Roebroeks, 1996; Arribas & Palmqvist, 1999; Roebroeks, 2001). The contrast between early arrival in Asia and later arrival in Europe will become even more marked if the claimed lower Pleistocene artefacts from Dursunlu, southern Anatolia (Gulec et al., 1999) and ca. 2·0 m.y.a. artefacts from the Erq-el-Ahmar formation of the Jordan valley (Tchernov, 1995) are confirmed. One might ask: is it possible—from theoretical considerations alone—for both a very early hominid colonization of west and S.E. Asia and a very late colonization of Europe to be correct?

Orce, in southern Spain might provide a date for hominid presence in Europe equivalent to those from Asia with claimed 1·9 m.y.a. artefacts and much disputed hominid skeletal fragments (Roe, 1995; Palmqvist, 1997; Moyà-Solà & Köhler, 1997; Gibert et al., 1998a,b). This locality re-invigorates the claims that Europe may have been colonized from North Africa by a short (6·5–14·5 km) “boat” journey across the straits of Gibraltar (Roland, 1998; Arribas & Palmqvist, 1999; Straus, 2001). If that route had been available, how would the chronology and character of the Lower
Palaeolithic of Europe differ from that created by colonization from western or from central Asia alone?

A further set of questions arise concerning the continuity of occupation. Bar Yosef (Bar-Yosef, 1998, 2000; Bar-Yosef & Belfer-Cohen, 2001) assumes that the gaps in the archaeological sequences of Europe and Asia together with the variable technologies associated with the early Eurasian sites arise from the extinction of distinct *H. ergaster/erectus* lineages—presumably due to changing environmental conditions. Hence early dispersals from Africa may have little relevance to the long term establishment of Eurasian populations. One must also address the issue of historical contingency, its significance for human evolution having been considered by Bilsborough (1999) and Foley (1999). If we were able to re-run the Pliocene and Pleistocene with exactly the same sequence of environmental events and starting conditions, would the same pattern of hominid dispersal repeat itself? Or would we be asking why the first hominids arrived so late in Asia when compared to the particularly early settlement in Europe?

Computer simulation can help address such questions by improving the theoretical frameworks that currently exist for interpreting the evidence for hominid dispersal, as has been demonstrated for Holocene prehistory (e.g., Steele et al., 1998; Lake, 2001). We have no illusions that computer simulation is anything other than an imperfect tool, one for which the results are only as good as the data and procedures put into the programme. But by allowing (1) exploration of processes that happen across extensive ranges of time and space, (2) experimentation with different dispersal scenarios, and (3) examination of the implications of hominid ecological and evolutionary patterns, we feel that computer simulation has great potential for enhancing our studies of early prehistory and human evolution. Indeed, in light of its pervasive use in other disciplines that deal with long term processes, and especially its central role in reconstructing the Pleistocene climate, we feel that palaeoanthropology has sorely neglected this valuable research tool.

The computer simulation we have developed—referred to as STEPPING-OUT—is a powerful research tool. It enables one to model the dispersal of hominids across the Old World, from an East African origin at 2 m.y.a. until 500 ka ago. The simulation runs on time-steps of 250 years and allows one to experiment with different scenarios—whether these relate to colonization rates, palaeoenvironmental conditions, topographic barriers, land-bridges or hominid environmental and dietary preferences. In this paper we provide a summary of the key elements of the simulation and illustrate its use for addressing the contrasting arrival dates and occupation histories of Europe and East Asia. While we aim to provide sufficient technical details about the simulation for readers to evaluate the model, further information and an extensive set of simulation results are provided on the STEPPINGOUT web-page: www.rdg.ac.uk/archaeology/research/NERC.

**STEPPINGOUT: the basics**

STEPPINGOUT is a simulation programme that uses a grid of 7406 triangular cells arranged into 14 hexagons and seven pentagons that cover the globe excepting the Americas (Figure 2). This projection is the best compromise between achieving accurate distances and spatial areas within a matrix suitable for an iterative simulation study. Each triangle covers approximately 45,000 km² and may be defined as land or sea. For cells in coastal regions this designation will change as sea levels rise and fall during simulated time (as described below). A hominid population is defined as being either present or absent within each of the cells. At time \( t=1 \), a cluster of 21 cells in
East Africa is populated with hominids as the starting condition for the model (Figure 2). At each time-step the hominid population within each cell can do one or more of the following on a probabilistic basis: (1) change its characteristics in terms of ecological preferences; (2) colonize an adjacent cell; (3) become extinct. As such, this simulation is based on the principle of cellular models as have been used for examining issues of colonization and succession in population ecology (Hogeweg, 1988).

The probabilities for each event to occur are determined by the population’s characteristics, the spatial location of the grid cell (which influences its environmental conditions) and the current climatic state. The simulation provides no predetermined dispersal route out of Africa and through Eurasia; indeed hominids can just as easily spread back into Africa. Similarly we are not concerned with specific dispersal “events”; we believe that movement between Africa, Europe and Asia should be conceived as a continuous processes under the constraints of environmental factors. Our description of how the model is constructed refers to the set of parameter values that must be defined at the start of each simulation run and which are listed in Table 1.

### Hominid types and evolutionary events

STEPPINGOUT allows for six types of hominid populations, varying in their environmental and dietary preferences. With regard to the former, hominids can be either warm adapted, generalists or cold adapted, while with regard to diet they can be either omnivorous or game specialists. These preferences define survival probabilities for the each hominid type in each of the defined environmental regions and glacial/interglacial climatic stages, as described below. At time $t=1$, the founder East African population is designated as warm adapted omnivores. As such they have relatively high survival probabilities when in warm environments and relatively low probabilities when in cold environments. At each time step there is a probability (parameter TR, Table 1) that the population in any occupied cell may transform to another
hominid type not more than one evolutionary step away. Hence a warm adapted population may become a generalist, but not a cold adapted population. But once a generalist, it may then undertake a second transformation and become a cold adapted population. We do not specify whether such transformations are biological or cultural in character.

Colonization rates
At the start of the simulation a parameter value is set that defines the probability that a hominid population within one cell will

<table>
<thead>
<tr>
<th>Name</th>
<th>Description</th>
<th>Range</th>
<th>Default value</th>
</tr>
</thead>
<tbody>
<tr>
<td>CR Colonization rate</td>
<td>Defines the probability of a population in a cell producing a colonist.</td>
<td>0–1</td>
<td>0.04</td>
</tr>
<tr>
<td>EX Extinction rate</td>
<td>Defines the probability of a population in a cell suffering extinction.</td>
<td>0–1</td>
<td>0.01</td>
</tr>
<tr>
<td>HB Altitude barrier</td>
<td>Defines the extent to which colonization rates are reduced for cells in the higher altitude categories.</td>
<td>Limited: colonization probabilities are reduced by 50% for &gt;3000 m; Moderate: colonization probabilities are reduced by 50% for &gt;1000 m, 66% for &gt;3000 m and 75% for &gt;5000 m; Severe: colonization probabilities are reduced by 75% for &gt;1000 m, and set to zero for &gt;3000 m and &gt;5000 m</td>
<td>Limited</td>
</tr>
<tr>
<td>TR Transformation rate</td>
<td>Defines the probability of a population in a cell changing one of its characteristics.</td>
<td>0–1</td>
<td>0.005</td>
</tr>
<tr>
<td>NZ Number of Zones</td>
<td>Defines the number of climate zones from 1 (uniform surface) to 11.</td>
<td>1, 4 or 11</td>
<td>11</td>
</tr>
<tr>
<td>S1 Cold/Warm adaptation</td>
<td>Defines the level of cold/warm specialization of hominids.</td>
<td>1 (most specialized)–3</td>
<td>2</td>
</tr>
<tr>
<td>S2 Diet adaptation</td>
<td>Defines the level of dietary specialization of hominids.</td>
<td>1–2 (most specialized)</td>
<td>2</td>
</tr>
<tr>
<td>GB Gibraltar land bridge</td>
<td>Allows a land bridge between Africa and Gibraltar</td>
<td>Yes or no</td>
<td>No</td>
</tr>
<tr>
<td>AF Afar route</td>
<td>Allows a land bridge between the East Africa and South-West Asia</td>
<td>Yes or no</td>
<td>Yes</td>
</tr>
<tr>
<td>AU SE Asia and bridge</td>
<td>Allows people to move between South-East Asia and Greater Australia during glacial periods (when the sea level is lower).</td>
<td>Yes or no</td>
<td>No</td>
</tr>
<tr>
<td>TC Temperate conditions</td>
<td>Decreases hominid survival probabilities in environmental zone (e) (temperate in interglacial conditions))</td>
<td>Yes or no</td>
<td>No</td>
</tr>
<tr>
<td>CA Coastal advantage</td>
<td>Defines the impact on the colonization rates for warm and generalist adapted populations when they are occupying coastal cells</td>
<td>1 Halved 2 Parity to inland rates 3 Doubled</td>
<td>2</td>
</tr>
</tbody>
</table>
produce a colonist population for an adjacent cell (parameter CR, Table 1). If colonization occurs, the parent population remains and a new population is created within one, randomly selected, adjacent cell. In this initial version of STEPPINGOUT the likelihood of colonization is not influenced by the prevailing environmental characteristics of each cell. As such characteristics influence the likelihood of extinction, there is nothing to be gained by having them also impact upon colonization as the significant factor for dispersal rates and patterns lies in the relationship between colonization and extinction. Account is taken, however, of altitude, as this may have provided a barrier to dispersal—the Taurus and Zagros ranges have been invoked as an explanation for the relatively late arrival of hominids in Europe (Rolland, 1998). Each cell is defined as being within one of four altitude categories (Figure 3). The probabilities of producing colonists can be adjusted for each altitude category by setting the value of parameter HB, as described in Table 1.

The simulation has the facility to either increase or decrease the colonization rates for coastally living hominids, i.e., for hominids within cells that are immediately adjacent to the sea. By changing the value of parameter CA (Table 1) when the simulation is initialized, the likelihood of producing a colonist for a coastally living warm adapted or generalist population can be either halved or doubled over that for an inland based population. To achieve an effective parity of colonization rates between inland and coastally based hominids, as in the default model (see below, Table 1), one has to set the likelihood for producing a colonist by a coastal population at double that for an inland population. This is because they are, on average, surrounded by only half the number of available cells when compared to an inland population, the rest being denoted as “sea”. The facility to manipulate coastal dispersal rates was partly introduced to explore whether the apparently different rates at which Europe and S.E. Asia were colonized may have arisen from behavioural differences between warm/generalist and cold adapted populations regarding coastal adaptation. Future versions of STEPPINGOUT might also apply the accelerated coastal dispersal to cold adapted populations.

The simulation does not allow two hominid population types to exist within one cell at any one time. Consequently if a colonist is produced for a cell already occupied by a
hominid population of another type, the simulation assumes competition takes place. A resident population will always “win”. We chose this rule as it is both the simplest and has the logic that hominids partly rely on a detailed knowledge of resource location for survival. Other rules are possible, such as the population with the highest survival probability for that environment wins, or hominid types could be given different competitive strengths. We hope to explore these in future versions of STEPPINGOUT. In the current version, if two arrive simultaneously in the same cell, that which has the highest survival probability for the cell, as defined below, is modelled as remaining, the other becomes extinct. If a colonist enters a cell where there is a resident population of the same hominid type no action is required as occupation within cells is simply recorded on a presence/absence basis.

Climatic change
Climate change is modelled to follow the scenario outlined by deMenocal (1995) with regard to the duration and amplitude of glacial–interglacial cycles. For the first million years of the simulation the cycle duration is set to 40 ka, and then extended to 100 ka for the final 500 ka. The climatic sequence of any one complete cycle is modelled in a series of ten steps designated as “0” for the height of a glacial period and “10” for a full interglacial (Figure 4). With regard to amplitude, for the first 300 ka of the simulation, when glacial cycles are only 40 ka long, only steps 4–9 of the climate scale are used and hence neither extreme glacial or interglacial conditions arise. Between 300 ka and 1·0 Ma steps 2–9 are used, and the whole scale is utilized for the remainder of the simulation. Along with these regular cycles we include a stochastic element to capture the phenomenon of fluctuations within cycles. Figure 4 illustrates a typical sequence of simulated climatic conditions.

Sea level change, land bridges, barriers and boat journeys
The simulation contains only two possible heights for sea levels, high and low (Figure 5). When the climatic cycle crosses step 4 on
the way to a full glacial phase the sea level is lowered; it is raised when it crosses step 6 on the way to a full interglacial phase. Hominid populations within land cells that are transformed into sea become extinct. The extent to which hominids were able to use “boats” (possibly unmodified natural rafts) to make water crossings is contentious. Stone artefacts from Flores island in S.E. Asia have been claimed to date to 0.9 m.y.a., suggesting that stretches of water amounting to at least 19 km had been crossed by *H. erectus* (Morwood et al., 1998). To examine the impact that this would make on dispersal patterns the simulation has a facility to provide hominids with an opportunity to make two “water crossings”—one across the straits of Gibraltar (GB), and one from the south-east Asian mainland into Greater Australia (AU), the latter only being made possible during periods of low sea level (Figure 5). These are created by simply making parameter values GB and AU (Table 1) either positive or negative.

With regard to dispersal from Africa into south-west Asia two possible routes exist: one from North Africa into modern day Negev—the Nile Valley Route—and one from East Africa into modern day Yemen—the Afar Route (AF, Figure 5). The former is frequently assumed to be the key due to the early dates for ‘Ubeidiya, but Larick & Ciochon (1996:548) stress the significance of the latter as being “the best departure point for eastward travel” and is supported by geological and palaeontological evidence (Rolland, 1998; Tchernov, 1995). To examine the relative importance of these two routes STEPPINGOUT has a facility to “block” the Afar route into Asia by changing the value of parameter AF (Table 1).

Environmental preferences and extinction rates
In addition to their altitude designation, each land cell is classified as belonging to one of a predefined number of regions. The default number used is 11, which maps on to environmental zones of the present day [see Figure 6(a)] (defined by setting parameter NZ to 11, Table 1). It is possible, however, to utilize a simplified geographic map employing only four regions, as in Figure 6(b). This enables us to explore Dennell’s (1998) argument that Plio-Pleistocene hominid dispersal to eastern Asia was facilitated by an extent of

![Figure 5. High and low sea levels used in STEPPINGOUT, possible sea crossings and the Afar exit route that can be either included or removed from a simulation (see parameters GB, AF, AU, Table 3).](image-url)
Figure 6. (a) Environmental zones used in STEPPINGOUT (based on information in Park, 1977). (b) Reduced number of environmental zones (based on Dennell, 1998) (see parameter NZ, Table 3).
grasslands that has been unknown during Quaternary.

The environment of each region will change as the climate passes through glacial and interglacial cycles. Those in northern latitudes, for instance, which are designated as temperate or continental [regions (c), (d) and (e)] at the present day (i.e., in a full interglacial state), will become transformed into tundra or even sub-arctic regions as a full glacial approaches, whereas those in low latitudes defined as steppe (h) or savannah (j) during an interglacial will become desert. Rather than explicitly modelling the environmental changes of each region we simply define whether they become more or less amenable to the survival of hominid populations of each of our six types. Hence warm adapted hominids will have relatively high chances of survival in, for instance, region (g), designated as Mediterranean during an interglacial, when the simulated climatic cycle is passing through steps 10–6, and a relatively low chance of survival when passing through stages steps 5–0 during which that region is assumed to approach desert conditions.

In this regard each hominid type is defined by a two dimensional matrix of survival probabilities, with each entry defining the probability of survival from time=\( t \) to time=\( t+1 \) in any of the regions at any of the steps of the climatic cycle. The survival probabilities are derived from informed estimates of the relative likelihood of survival of the six alternative types of hominids in each type of environmental zone and an overall extinction rate for hominids (parameter EX, Table 1). There is, of course, some degree of arbitrariness in assigning these survival probabilities and we have simply drawn on literature regarding the likely environmental preferences and tolerances of hominid species; the advantage of a simulation model is that these can be easily amended in future versions of STEPPINGOUT. For the current version, the selected survival probabilities for two hominid types—warm adapted omnivores and cold adapted game specialists as used for the default run of the simulation (see below and Table 1) are illustrated in Figure 7(a),(b).

The simulation allows one to manipulate these values in three ways. (1) The values as a whole can either be increased or decreased, thus making all hominid types either more or less prone to extinction. This gross change is undertaken by changing the values of parameter EX, Table 1. (2) The simulation has a facility to make the hominid types either more or less similar to each other by changing the value of the S1 parameter (Table 1). If this is increased the cold adapted hominids become even more prone to extinction when the climate is passing through the warmer steps (5–10) of the glacial–interglacial cycles, while the converse is true for the warm adapted hominids. Similarly one can change the S2 parameter to make the hominids either more or less similar with regard to their dietary preferences. (3) STEPPINGOUT is currently designed with a further variable, TC, which allows one to reduce the survival probabilities of hominids in environmental zone (e), defined as temperate at an interglacial. We use this when exploring possible reasons for a relatively late colonization of Europe.

Running, recording and calibrating the simulation

Running the simulation simply involves defining the values for each of the twelve parameters defined in Table 1, which is done interactively, and then letting the hominids disperse from Africa (if they do at all) under the constraints of those values. As the simulation has a stochastic element, any two runs with the same parameter values will produce different results. The stochastic element simply impacts upon the outcome of probabilistic events (e.g., producing a colonist, surviving in a cell); we do not
Figure 7. (a) Survival probability matrix for cold adapted game specialist for each climatic step and environmental zone. (b) Survival probability matrix for warm adapted omnivore.
included perturbations to parameter values in this version of the model. Consequently for any one set of parameters we normally make 30 runs to examine the variability in dispersal patterns that can arise from chance alone (this number of runs having been assessed as providing a representative range of the results from any one single set of parameter values). A substantial quantity of data is recorded from each run, allowing us to address numerous issues raised about the history of hominid dispersal. The results of interest in this article are the dates of first arrival at six selected localities—Ubediya, Dmanisi, Longuppo, Java, Atapuerca and Boxgrove (Figure 1).

With the number of parameter values that must be defined, and the range of values that are available, a very large number of simulation runs creating a vast array of dispersal patterns, could be undertaken. It is quite possible, for instance, to create extremely rapid global colonization (within a few thousand years of the start date) simply by ensuring that colonization probabilities are set at high values and extinction probabilities at relatively low values. Conversely it is quite possible to set parameter values so that hominids are quite unable to ever disperse from Africa. Neither of these scenarios would be of great archaeological interest as the record itself imposes constraints on what dispersal patterns may have existed, and therefore what parameter values are useful to explore.

The one constraint we have chosen to adopt is the date of arrival at Dmanisi at ca. 1·7 m.y.a., which seems to be the most widely accepted of all the early Pleistocene dates in Eurasia. Hence when selecting a range of colonization and extinction rates to use as our default values we have constrained these (by prior exploration of the model) to values which produce first occupation at Dmanisi at dates that centre upon 1·7 m.y.a.—an exact date is impossible due to the probabilistic nature of the simulation. This, in effect, acts to calibrate the simulation model to feasible colonization and extinction rates.

The default simulation

To illustrate STEPPINGOUT we begin by describing a single run which uses what we term the default parameter settings (Table 1) and the climatic sequence in Figure 4. Other than ensuring that the defined colonization and extinction rates provide an appropriate arrival date for Dmanisi, these parameter values are largely arbitrarily defined. They serve to provide a baseline simulation against which other simulations can be compared by a process of experimentation with parameter values.

Having begun with a population cluster in East Africa (Figure 2) the population disperses throughout Africa and into Eurasia as illustrated by the three maps in Figure 8 showing hominid distributions at 1·7, 1·5 and 0·5 m.y.a., illustrating the whereabouts of the three categories warm (red), generalist (green) and cold adapted (blue) hominid types (for the purposes of this paper we have combined the two dietary specialisms; the STEPPINGOUT web page provides details for all six hominid categories). Figure 9 illustrates the growth and fluctuations of their population numbers (in terms of the number of cells occupied), showing the impact of both dispersal into high latitudes the climatic cycles.

Table 2 provides dates for arrival at our six selected localities. The Dmanisi date of 1·78 is a sufficiently realistic estimate for that site and, as described above, is simply a construct of the parameter settings. None of the other dates has been predetermined in this fashion and they show a marked discrepancy with those currently available from the archaeological and fossil records, with arrival at Boxgrove at 1·65 m.y.a., and Java at 1·18 m.y.a. The latter agrees, however, with arguments that the Swisher et al.
Figure 8. Distribution of hominids at three time steps of a single default simulation run. Blue = cold adapted, green = generalist, red = warm adapted.
(1994) dates are unrelated to the Java fossils themselves and that the true date for hominid arrival in Java is around 1 m.y.a. (Langbroek & Roebroeks 2000).

Figure 10 shows the history of occupation at these localities, that being the specific triangular grid cell within which the site is located. This shows that once hominids have arrived at Boxgrove or Atapuerca they are effectively permanently present from that date. In contrast, occupation at the other localities is more sporadic, especially at 'Ubediya. The European sites also have a relatively stable type of hominid present; the Asian sites are quite variable, especially that of Dmanisi which has no less than five different types present at some time during its occupation history.

The distribution of hominids with regard to environmental zones for the whole course of the simulation is illustrated in Figure 11. Each pie chart summarizes three different categories of zones: (1) those for which cold adapted hominids are favoured over others at all stages of the climatic cycle; (2) zones in which the most favoured hominid varies with the stages of the climatic cycle; (3) zones in which warm adapted hominids...
Figure 10. Simulated occupation history at six localities by the six hominid types, for single run of the default simulation.
are always favoured. As the pie charts illustrate, the nonfavoured hominids always have a presence within each of these three groups of environmental zones. Even in the environments which range from subarctic to temperate at a full interglacial 5% of the total number of hominid occupations is by warm adapted types.

The results in Figures 8–11 and Table 2 (column 3) are from one single run of STEPPINGOUT; as a stochastic element is involved a second or third run with the same parameter settings will produce different results. To explore what range of variability arises 30 runs were made with the default parameter settings. In seven (23%) of those runs, hominids remained in Africa for the whole duration of the simulation. In the runs in which hominids left Africa, the six localities are almost always reached during the duration of the simulation run. The results with regard to the arrival dates at the six localities for the remaining 23 runs are illustrated in Figure 12 and summarized in Table 2. That for Dmanisi is normally distributed around 1·7 m.y.a., as expected in light of the model design. Those for Java range from 1·5 to 0·8 m.y.a., while hominids have always reached Atapuerca by 1·3 m.y.a. and there are only three runs in which they arrive at Boxgrove after this date. The shape of the distributions vary between the localities: that of Java is notably broad reflecting its distance from Africa which allows historical chance a greater role in determining when hominids arrive.

Experiments in hominid dispersals

The results from the default parameter settings are evidently quite out of accord with the currently available evidence (Table 2), although the simulated arrival dates in Europe are compatible with the arguments from Arribas & Palmqvist (1999). To explore what parameter values (if any) will lead to a chronology of dispersal that matches that currently available from the empirical evidence, as well as to sample the behaviour from STEPPINGOUT in general, we have undertaken 32 simulations (almost 1000 runs), as summarized in Table 3. Each simulation involves 30 runs with the same parameter values. With regard to this
Figure 12. Distributions of arrival dates at six localities from 30 runs of the default simulation.

- **Ubeldiya**
- **Dmanisi**
- **Longgupo**
- **Java**
- **Atapuerca**
- **Boxgrove**

Proportional representation of number of occurrences in 30 runs.

Legend:
- Proposed date on basis of archaeological & fossil evidence (Table 2)
<table>
<thead>
<tr>
<th>No.</th>
<th>Aim.</th>
<th>Differences in parameter values from default (Table 1)</th>
<th>% of runs ((n=30)) in which hominids exit Africa</th>
<th>Summary of results</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Default model</td>
<td>None</td>
<td>77</td>
<td>Mean and range of arrival dates are as follows: ‘Ubeidiya: 1·82, 2·0–1·5 m.y.a. Dmanisi: 1·61, 1·9–1·6 Longgupo: 1·34, 1·7–1·0 Java: 0·97, 1·5–0·9 Atapuerca: 1·45, 1·7–1·4 Boxgrove: 1·42, 1·8–1·0</td>
</tr>
<tr>
<td>2</td>
<td>Decreased rate of coastal movement</td>
<td>CA=1</td>
<td>70</td>
<td>Arrival at Boxgrove is substantially delayed with 50% of arrivals occurring after 1·0 m.y.a. Arrival at Atapuerca and Java is delayed, the latter only being reached in 23% of the runs.</td>
</tr>
<tr>
<td>3</td>
<td>Increased rate of coastal movement</td>
<td>CA=3</td>
<td>93</td>
<td>Shifts arrival dates earlier at all sites, with runs reaching Java by 1·4 m.y.a. and Boxgrove by 1·7 m.y.a. Arrival at Java adopts a bimodal distribution, with modes at 1·4 and 0·8 m.y.a. Limited impact on arrival dates at other sites; that at ‘Ubeidiya appears slightly earlier while there is a greater spread of arrival dates at Longgupo.</td>
</tr>
<tr>
<td>4</td>
<td>Reduced evolutionary potential (i.e. likelihood of population transformation)</td>
<td>TR=0·0001</td>
<td>100</td>
<td>In comparison with the default all arrival dates are earlier, largely as a consequence of the increased rate of coastal movement (as in simulation 3). This is, however, enhanced for Java with 80% of runs now arriving by 1·5 m.y.a.</td>
</tr>
<tr>
<td>5</td>
<td>Reduced survival probability in temperate zone</td>
<td>TC=Yes</td>
<td>57</td>
<td>No impact on arrival dates.</td>
</tr>
<tr>
<td>6</td>
<td>Increased rate of coastal movement and reduced evolutionary potential</td>
<td>CA=3 TR=0·0001</td>
<td>100</td>
<td>In comparison with the default all arrival dates are earlier, largely as a consequence of the increased rate of coastal movement (as in simulation 3). This is, however, enhanced for Java with 80% of runs now arriving by 1·5 m.y.a.</td>
</tr>
<tr>
<td>7</td>
<td>Increased rate of coastal movement and reduced survival in temperate zone</td>
<td>CA=3 TC=Yes</td>
<td>97</td>
<td>Arrival dates appear identical with those from increased rate of coastal movement alone (simulation 3).</td>
</tr>
<tr>
<td>8</td>
<td>Increased rate of coastal movement, reduced evolutionary potential and reduced survival in temperate zone</td>
<td>CA=3 TR=0·0001 TC=Yes</td>
<td>100</td>
<td>Results are very similar to that with increased rate of coastal movement alone (simulation 3), but with slightly earlier arrival dates at ‘Ubeidiya, Dmanisi and Java.</td>
</tr>
</tbody>
</table>
Table 3  continued.

<table>
<thead>
<tr>
<th>No.</th>
<th>The simulation explores the impact of:</th>
<th>Differences in parameter values from default (Table 1)</th>
<th>% of runs ((n=30)) in which hominids exit Africa</th>
<th>Summary of results</th>
</tr>
</thead>
<tbody>
<tr>
<td>9</td>
<td>Entry into Europe made possible via Gibraltar straits</td>
<td>GB=Yes</td>
<td>97</td>
<td>Arrival at Atapuerca is shifted substantially earlier with 87% of runs arriving prior to 1.5 m.y.a. Arrival at Boxgrove is made slightly earlier with 63% of runs arriving prior to 1.5 m.y.a. Arrival at other sites remain very similar to that of the default.</td>
</tr>
<tr>
<td>10</td>
<td>Entry into Europe made possible by Gibraltar straits and increased rate of coastal movement</td>
<td>GB=Yes, CA=3</td>
<td>90</td>
<td>Arrival at all sites are shifted earlier from the default but the predominant influence on all sites except for Atapuerca is accounted for by the enhanced coastal movement. Arrival at Atapuerca is made slightly earlier than in simulation 9. For those in which hominids do leave Africa arrival dates are very similar to those of the default.</td>
</tr>
<tr>
<td>11</td>
<td>Absence of dispersal via Arabia</td>
<td>AF=No</td>
<td>50</td>
<td>Arrival at Java, Longgupo, Atapuerca and Java is delayed.</td>
</tr>
<tr>
<td>12</td>
<td>Reduced degree of hominid climatic specialization</td>
<td>S1=3</td>
<td>77</td>
<td>Arrival at Java, Longgupo, Atapuerca and Java is delayed.</td>
</tr>
<tr>
<td>13</td>
<td>Increased degree of hominid climatic specialization</td>
<td>S1=1</td>
<td>47</td>
<td>Arrival dates are very similar to the default.</td>
</tr>
<tr>
<td>14</td>
<td>Reduced degree of hominid dietary specialization</td>
<td>S2=1</td>
<td>13</td>
<td>Although hominids never get out of Africa, they survive within that continent.</td>
</tr>
<tr>
<td>15</td>
<td>Increased degree of hominid climatic specialization and reduced dietary specialization</td>
<td>S1=1, S2=1</td>
<td>0</td>
<td>Arrival dates are very similar to those with enhanced coastal movement (simulation No. 3), but in no cases is there entry into Greater Australia.</td>
</tr>
<tr>
<td>16</td>
<td>Reduced degree of climatic and dietary specialization</td>
<td>S1=3, S2=2</td>
<td>23</td>
<td>Arrival dates are very similar to those with enhanced coastal movement (simulation No. 3), but in no cases is there entry into Greater Australia.</td>
</tr>
<tr>
<td>17</td>
<td>Increased rate of coastal movement and possibility of entry into Greater Australia during low sea levels</td>
<td>CA=3, AU=Yes</td>
<td>90</td>
<td>Arrival dates are very similar to those with enhanced coastal movement (simulation No. 3), but in no cases is there entry into Greater Australia.</td>
</tr>
<tr>
<td>18</td>
<td>Reduction to four environmental zones</td>
<td>NZ=4</td>
<td>100</td>
<td>Arrival at all sites shifted earlier.</td>
</tr>
<tr>
<td>19</td>
<td>Reduction to a single environmental zone</td>
<td>NZ=1</td>
<td>100</td>
<td>Arrival at all sites shifted earlier.</td>
</tr>
<tr>
<td>20</td>
<td>Increased colonization rate</td>
<td>CR=0.05</td>
<td>90</td>
<td>Arrival at all sites is slightly shifted earlier, with the mean for Dmanisi becoming 1.68 m.y.a.</td>
</tr>
<tr>
<td>21</td>
<td>Decreased colonization rate</td>
<td>CR=0.03</td>
<td>17</td>
<td>With only five examples outside Africa no arrival pattern can be discerned.</td>
</tr>
<tr>
<td>No.</td>
<td>Aim.</td>
<td>Differences in parameter values from default (Table 1)</td>
<td>% of runs ((n=30)) in which hominids exit Africa</td>
<td>Summary of results</td>
</tr>
<tr>
<td>-----</td>
<td>-------------------------------------------------------------------------------------------------------------------------------------</td>
<td>--------------------------------------------------------</td>
<td>--------------------------------------------------</td>
<td>------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------</td>
</tr>
<tr>
<td>22</td>
<td>Increased colonization and extinction rates</td>
<td>CR=0·05&lt;br&gt;EX=0·15</td>
<td>73</td>
<td>Slightly earlier arrival at Dmanisi and Atapuerca but no apparent difference elsewhere.</td>
</tr>
<tr>
<td>23</td>
<td>Decreased colonization and extinction rates</td>
<td>CR=0·03&lt;br&gt;EX=0·005</td>
<td>40</td>
<td>Arrival dates are very similar to the default.</td>
</tr>
<tr>
<td>24</td>
<td>Reduced survival probability in temperate zone and increased colonization rate</td>
<td>TC=Yes&lt;br&gt;CR=0·05</td>
<td>87</td>
<td>Arrival dates at all sites are shifted earlier with the increased colonization rate having the predominant effect (as in simulation 20).</td>
</tr>
<tr>
<td>25</td>
<td>Reduced survival probability in temperate zone, increased colonization and extinction rates</td>
<td>TC=Yes&lt;br&gt;CR=0·05&lt;br&gt;EX=0·15</td>
<td>70</td>
<td>Arrival dates are all very similar to the default.</td>
</tr>
<tr>
<td>26</td>
<td>Moderate altitudinal barrier to dispersal</td>
<td>HB=moderate</td>
<td>77</td>
<td>Arrival dates at Longuppo and Java are delayed—50% at the latter site occur after 0·9 m.y.a. Boxgrove has two examples of late arrivals occurring after 0·7 m.y.a.</td>
</tr>
<tr>
<td>27</td>
<td>Moderate altitudinal barrier to dispersal and enhanced coastal movement</td>
<td>HB=moderate&lt;br&gt;CA=3</td>
<td>93</td>
<td>Arrival dates appear very similar to simulation with enhanced coastal movement (No. 3), with exception of those for Longuppo which are delayed.</td>
</tr>
<tr>
<td>28</td>
<td>Severe altitudinal barrier to dispersal</td>
<td>HB=severe</td>
<td>77</td>
<td>Arrival at all sites is delayed, with the most notable impact at Java and Longuppo.</td>
</tr>
<tr>
<td>29</td>
<td>Severe altitudinal barrier to dispersal and enhanced coastal movement</td>
<td>HB=severe&lt;br&gt;CA=3</td>
<td>90</td>
<td>Arrival dates appear very similar to simulation with enhanced coastal movement (No. 3), with exception of those for Longuppo which are delayed.</td>
</tr>
<tr>
<td>30</td>
<td>Severe altitudinal barrier and possibility of entry into Europe via Gibraltar straits</td>
<td>HB=severe&lt;br&gt;GB=Yes</td>
<td>80</td>
<td>Arrival dates for Europe and West Asia are similar to the default; those of Longuppo and Java are delayed.</td>
</tr>
<tr>
<td>31</td>
<td>Altitudinal barrier and reduced evolutionary potential</td>
<td>HB=moderate&lt;br&gt;TR=0·0001&lt;br&gt;CA=3</td>
<td>90</td>
<td>Arrival dates are substantially delayed for Atapuerca, and delayed for Longuppo, Java and Boxgrove with six examples at the latter site after 0·8 m.y.a.</td>
</tr>
<tr>
<td>32</td>
<td>Altitudinal barrier, reduced evolutionary potential and enhanced coastal movement</td>
<td>HB=moderate&lt;br&gt;TR=0·0001&lt;br&gt;CA=3</td>
<td>100</td>
<td>Arrival dates at Java are made substantially earlier, but limited impact elsewhere. One example of arrival at Boxgrove after 0·7 m.y.a.</td>
</tr>
</tbody>
</table>
Figure 13. Distributions of arrival dates at six localities from 30 runs of the default simulation (solid) and 30 runs of simulation No. 2 (hashed) which inhibits coastal movement (see Table 3).
paper, the key interest is to examine how the adjustments made to the default parameter settings affects arrival dates at the six localities. In Figure 13, for example, we illustrate the arrival dates from simulation run No. 2 in which we have inhibited the hominids’ ability to disperse in the coastal zone (as specified in Table 3). Arrival dates at all sites other than 'Ubeidiya and Dmanisi have been substantially delayed, the effect being particularly marked in Europe.

The complete set of results from all 32 simulations (960 individual runs) are available on the STEPPINGOUT webpage and are summarized in Table 3. Here we comment upon several of the key issues regarding hominid dispersal in light of these results.

**Leaving Africa**

The simulations have indicated that exiting from Africa is the most sensitive aspect of the model and, by implication, the most important event in the whole history of hominid dispersal. The simulations suggest that it might easily not have happened at all (Table 3, column 4), as occurred in approximately one-third of the total number of simulation runs. We found that slight adjustments to the default parameters, such as those controlling adaptive specialization (simulations 13–15) and colonization rates (simulation 23) severely reduced the frequency of runs in which hominids left the continent, even though when they did exit they still reached Dmanisi at dates that accord with existing evidence. In those runs in which hominids did exit Africa, colonization of Eurasia tended to be extremely rapid. Such findings strengthen the arguments about the impact of the “desert” barrier on the chronology of dispersal (Rolland, 1998).

We also note that in almost all cases when hominids did successfully exit from Africa, this had happened by 1·7 m.y.a. (86%). This suggests that the increased duration and amplitude of the glacial–interglacial cycles after this date is a major constraint on hominids leaving Africa. If, as is frequently argued, there were multiple dispersals from Africa into Eurasia, STEPPINGOUT suggests that the majority, perhaps all, would have occurred prior to 1·5 m.y.a.

**Relative dates of arrival in Europe and S.E. Asia**

We found that several parameters in the model could be manipulated from their default values to enable hominids to reach Java by the date of 1·6 m.y.a. as proposed by Swisher et al. (1994). The most effective means was by enhancing the likelihood that populations in coastal cells would produce a colonist, i.e., by providing hominids with a specialized coastal adaptation (simulation 3), Figure 14. This made it likely that Java would be colonized by 1·4 m.y.a. Similarly, we also found it possible to manipulate variables to delay the arrival at Atapuerca and Boxgrove from the values in the default simulation to approach those for the “mature chronology” of Europe—arrival not before 1·0 m.y.a. (Arribas & Palmqvist, 1999). Figure 13 showed how this can be achieved by inhibiting coastal adaptation (simulation 2), while Figure 15 illustrates the same result by reducing the rate at which hominids can adapt to new environments (simulation 4) and imposing topographic barriers (simulation 26)—the Taurus and Zagros ranges for Europe. While both of these provided examples of a relatively late arrival at Atapuerca and Boxgrove, the majority of runs still created occupation prior to 1·0 m.y.a.

What appeared impossible to achieve, however, is a simulation in which hominids arrive in Java relatively early and Europe relatively late. We found that the impact of providing a coastal adaptation, and hence enabling hominids to reach Java by
1·6 m.y.a., overrides the impacts of topographic barriers and slow rates of adaptation that had otherwise delayed arrival in Europe (simulations 6, 27), Figure 16. In other words the history of hominid dispersal may have either led to a particularly early arrival in S.E. Java, or a relatively late arrival in Europe—but these are mutually exclusive possibilities. We are inclined to the first of these scenarios, our simulation results supporting the arguments for an "Old Europe Chronology" of occupation prior to 1·5 m.y.a. that Arribas & Palmqvist (1999) propose on palaeontological grounds. We appreciate, however, that there may be further constraints of entry and survival into Europe that are currently absent from the model, notably intense levels of competition from carnivores as proposed by Turner (1982, 1992). Finally, it should be noted that the most common occurrence from the simulations is for a late arrival in Java (c. 1 m.y.a.), which supports doubts about the relevance of Swisher et al's (1994) dates (Langbroek & Roebroeks 2000).

**Bridges and barriers**

When the Afar route out of Africa was removed from the default model (simulation 11), the likelihood that hominids would leave that continent was halved, although there was no impact on arrival dates at any of the localities. We have so far been unable to undertake further simulations that lacked the Afar bridge but STEPPINGOUT has led us to favour arguments that this route was of greater significance than the Nile Valley for hominid dispersal. Nevertheless a substantial portion of dispersals did occur via the Nile Valley route. This leads some
support to the arguments that Lower Palaeolithic sites such as el-Abassieh in Cairo may reflect the ability of hominids to live and migrate through this region (Tchernov, 1995) rather than this route being closed to hominids until 500 ka (Rolland, 1998).

When we provided hominids with the possibility of entry into Europe via the Gibraltar straits—which assumes they were able to make a water crossing—this was used with equal frequency as the East African dispersal route (simulation 9). It led to a much earlier arrival dates at Atapuerca but made little impact on those for Boxgrove, Figure 17. This result was found even when severe topographic barriers for dispersal were introduced (simulation 30).

The Australasian “bridge” remained unused by hominids (simulation 17). This provided entry into Greater Australia, again assuming that hominids were able to make water crossings. It was only present, however, at glacial maximums when sea level was at a minimum. We have so far undertaken only one simulation to explore this; apparently the necessary combination of hominids in the right place, at the right time, and the element of chance allowing them to colonize the appropriate cells, did not arise in any of the 30 runs.

We have already commented upon the significance of the North African desert barrier, especially after 1·5 m.y.a. when the glacial/interglacial cycles increase in magnitude. Topographic barriers of both a moderate and severe nature were shown to delay entry into Europe; but as we have noted above that effect was easily negated if hominids were also given a specialized coastal adaptation. East Asian arrival dates remained delayed, however, in comparison with the default model (Figure 18). This suggests that topographic barriers may have had a more significant influence on dispersal into Asia than Europe.
Conclusion

STEPPINGOUT is designed to help formulate theories, ideas and scenarios for the study of hominid dispersal, in the same manner that simulations of atmospheric circulation facilitate the study of Pliocene/Pleistocene environmental change. It remains a relatively simple model, one needing considerably more exploration and development; indeed we invite interested parties to propose further “experiments” with STEPPINGOUT, perhaps using parameter values and combinations that they feel are more appropriate than those we have so far selected. In its present form, however, in which colonization and extinction rates are calibrated to conform with occupation at Dmanisi at 1.7 m.y.a., it has served to strengthen some arguments in the current literature and weaken others:

- The intermittent nature of initial hominid occupation in western Asia has been stressed, supporting Bar-Yosef’s (1998, 2000) arguments for multiple dispersals and extinct lineages. This has been shown to vary with a more continuous presence, implying cultural and biological continuity, in Europe. STEPPINGOUT suggests that the hominid fossil record in Western Asia is likely to be more variable in terms of environmental and physiological adaptations than that of Europe due to the number of different hominid types that were present during its entire history of occupation.
- Although multiple dispersals are likely to have taken place, STEPPINGOUT suggests that it is more likely that these would have occurred prior to 1.7 m.y.a., as increasing amplitude of glacial/interglacial cycles appears to inhibit hominid ability to leave the African continent.
- STEPPINGOUT suggests that rapid colonization of S.E. Asia by 1.6 m.y.a.

Figure 16. Distributions of arrival dates at Java and Boxgrove from 30 runs of the default simulation (solid) and 30 runs of simulation No. 6 (left, hashed) which enhances rate of coastal movement and reduces likelihood of cold adapted populations arising, and simulation No. 27 (right, hashed) which enhances rate of coastal movement and imposes moderate altitude barriers to dispersal (see Table 3).
could have arisen if hominids were able to disperse relatively rapidly in coastal regions. This, of course, creates an archaeological dilemma due to the absence of the Pleistocene coastal zone within which sites might be located. It stresses, however, the importance of lower Palaeolithic material that comes from current coastal plains, such as that from Evron Quarry, Israel (Tchernov et al., 1994), and the need to develop models of coastal adaptation for human ancestors.

- With regard to dispersal routes the significance of the Afar landbridge was affirmed, hence supporting the arguments made on palaeontological and geological grounds (Tchernov, 1995, Rolland, 1998). STEPPINGOUT suggests that chronology of hominid occupation in Europe, especially in northern regions, is unlikely to be significantly altered by access into Europe via the Gibraltar straits.

- STEPPINGOUT supports the “Old Europe Chronology” of occupation prior to 1·5 m.y.a., as argued by Arribas & Palmqvist (1999) on palaeontological grounds. Although a ‘Mature Europe’ chronology can be derived (no occupation prior to 1·0 m.y.a.) the vast majority of simulations resulted in substantially earlier occupation.

- The simulations have also shown the immense influence that historical contingency may have had on the arrival of hominids at localities outside of Africa. Even when the arrival dates for ‘Ubeidiya and Dmanisi are relatively constrained around narrow windows between 1·9 and 1·5 m.y.a., as in the default, those for sites at greater distances from Africa are spread

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Figure 17. Distributions of arrival dates at Atapuerca and Boxgrove from 30 runs of the default simulation (solid) and 30 runs of simulation No. 9 which enables entry into Europe via Gibraltar (see Table 3).
over extensive periods by chance factors alone (i.e., in runs with the same parameter values). It may simply have been chance alone that determined whether hominids arrived in Europe at 1.5 or 0.8 m.y.a.

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References


