The ecology of social transitions in human evolution

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We know that there are fundamental differences between humans and living apes, and also between living humans and their extinct relatives. It is also probably the case that the most significant and divergent of these differences relate to our social behaviour and its underlying cognition, as much as to fundamental differences in physiology, biochemistry or anatomy. In this paper, we first attempt to demarcate what are the principal differences between human and other societies in terms of social structure, organization and relationships, so that we can identify what derived features require explanation. We then consider the evidence of the archaeological and fossil record, to determine the most probable context in time and taxonomy, of these evolutionary trends. Finally, we attempt to link five major transitional points in hominin evolution to the selective context in which they occurred, and to use the principles of behavioural ecology to understand their ecological basis. Critical changes in human social organization relate to the development of a larger scale of fission and fusion; the development of a greater degree of nested substructures within the human community; and the development of intercommunity networks. The underlying model that we develop is that the evolution of 'human society' is underpinned by ecological factors, but these are influenced as much by technological and behavioural innovations as external environmental change.

Keywords: human evolution; social structure; social evolution; hominin behaviour; technological evolution

1. INTRODUCTION

The evolutionary, or Darwinian, study of society has a long and often controversial history, encompassing as it does the early days of social Darwinism and the sociobiological debate of the 1970s (Wilson 1975; Allen 1976). A number of things have perhaps made this a less contentious topic than it was. Of these, the most important is the fact that the phrase 'The Evolution of Society' is no longer synonymous with the evolution of human society. A century of research in animal behaviour has extended the social world well beyond humans (Wilson 1975; Trivers 1985; Runciman *et al.* 1996). Social animals can be found across all the major groups (Vos & Velicer 2006).

In the first part of this paper, we will consider what some of these key general social traits might be, as a basis for considering their evolutionary history and role. In other words, 'what distinguishes human society, from that of other animals, particularly, given the recency of the last common ancestor, from chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*)?'.

Additionally, advances have come in understanding the principles underlying variation in social behaviour (Crook 1970; Krebs & Davies 1984). Such principles range from the costs and benefits of cooperation (Clutton-Brock 1991), parental certainty (Davies

1991) to life history (Charnov & Berigan 1993) to the threat of predation (Van Schaik & Hörstermann 1994) to the costs of territorial defence (Lowen & Dunbar 1994). Key to all of these, however, is the general consensus that social structure is shaped by resources. The principles of socioecology provide a powerful framework for studying social evolution, and provide the basis for the main thrust of this paper—'that the major patterns of human social evolution have been shaped by changes in the environment or changes in the ecological relationships between humans and their resources, which can be tracked through time'.

As we shall argue, over the course of human evolution, changes in male foraging behaviour have led to them having increased control over resources, and influencing the distribution and behaviour of females. This shift represents not just a change in socioecology, but also in the underlying model of behavioural ecology, and may be one way in which we can understand the unique nature of human society (figure 1).

2. BASAL HOMININ SOCIALITY

At the most basic level, the parameters describing human society are the same as those for any other vertebrate group. The most obvious of these is the tendency to be social itself, namely to live in groups made up of known individuals (Hinde 1983). Other basic parameters that appear to be common across
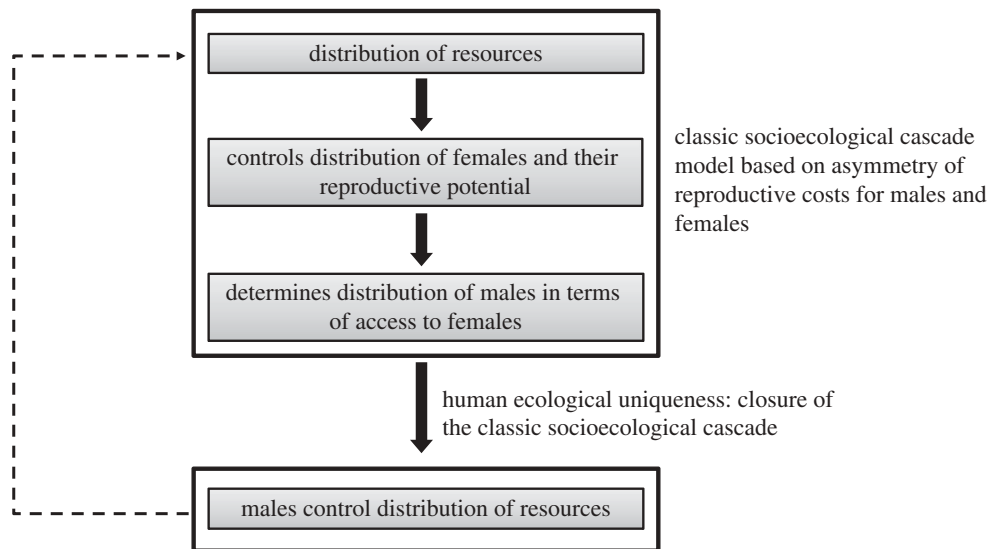
Figure 1. The classical model of socioecology, in which owing to the different costs of male and female reproduction, females are more strongly influenced by resources, and males by the distribution of females (Wrangham 1980). During the course of human social evolution, the increased ability of males to control resources has led to a closure of the cascade model, with males exerting control over female distribution through the control over resources.

humans and non-humans are more prolonged parental relationships, which might be either sex or both, kin-based relationships among resident adults, sex-based patterns of dispersal, more or less prolonged relationships between adult males and females, with one or more partners, some degree of tolerance of the presence of other members of the 'society', a lack of equivalent tolerance for members of another group (or at least a different pattern of behaviour) and some degree of structured or repeated style of relationship between individuals (e.g. dominance, submission, friendliness, aggression, etc.).

At this level, these basic parameters may be considered either as plesiomorphic traits that have evolved deep in vertebrate history or as forms of homoplasy common to all social animals. By looking more specifically at apes, especially the chimpanzee/bonobo as a sister clade, we can identify a number of basal traits which it is reasonable to assume were present in the earliest hominins.

Although it has been criticized (Sayers & Lovejoy 2008), the genus *Pan* serves as the most parsimonious basis for determining basal hominin social traits (table 1, column A). The assumption here is that the earliest hominins lived in multi-male, multi-female 'communities', and this is the fundamental unit of human social organization (Ghiglieri 1987; Wrangham 1987; Foley 1989). This is important, as much theorizing in anthropology has tended to place primacy on the family unit, but we see this as a trait that emerges during the course of our evolution. On the basis of comparison with the apes more widely, it is also probable that male residence and female transfer was the primary organizational principle for reproduction. What follows from this is an emphasis on relationships between males being mediated by kinship and between females by non-kin-based affiliation. A further inference, based on chimpanzee analogy, would be hostile relationships between communities. Finally, a key element of the community-based

socioecology of chimpanzees, and presumed here for the earliest hominins, would be the occurrence of a level of daily fission and fusion in foraging activities, with smaller parties forming the activity groups. Daily fusion would occur in the context of sleeping trees/shelter.

3. DERIVED HUMAN SOCIAL PATTERNS
Derived human traits can be divided into three categories—those that show little structural change and essential continuity from the basal hominin/last common ancestor, even if they have been elaborated (column B); those that are similar in form to the ancestral condition, but have changed significantly in quantitative terms (column C); and those that appear to be derived features that are more or less novel (column D). It is clear that a number of key traits develop during the course of human evolution, which alter the fundamental structure of society. In practice, these are underpinned by unique mechanisms associated with human cultural capacities, but, at a socioecological level, these are properties found elsewhere in the animal kingdom, and therefore can be considered to have evolved as behavioural traits in response to resource-based conditions—the massive extension of a fission–fusion system (elephants, *Loxodonta africana*) (Couzin 2006); much greater substructuring within multi-male, multi-female communities (hamadryas baboons, *Papio hamadryas*) (Kummer 1968); strong and persistent male–female relationships (many birds, for example) (Mock & Fujioka 1990); higher levels of paternal investment (primates, many birds) (Charpentier *et al.* 2008); and larger group sizes (Janson & Goldsmith 1995).

4. KEY TRANSITIONS IN HUMAN EVOLUTION
The increasingly complex pattern of hominin evolution (figure 2) contradicts previous models of a
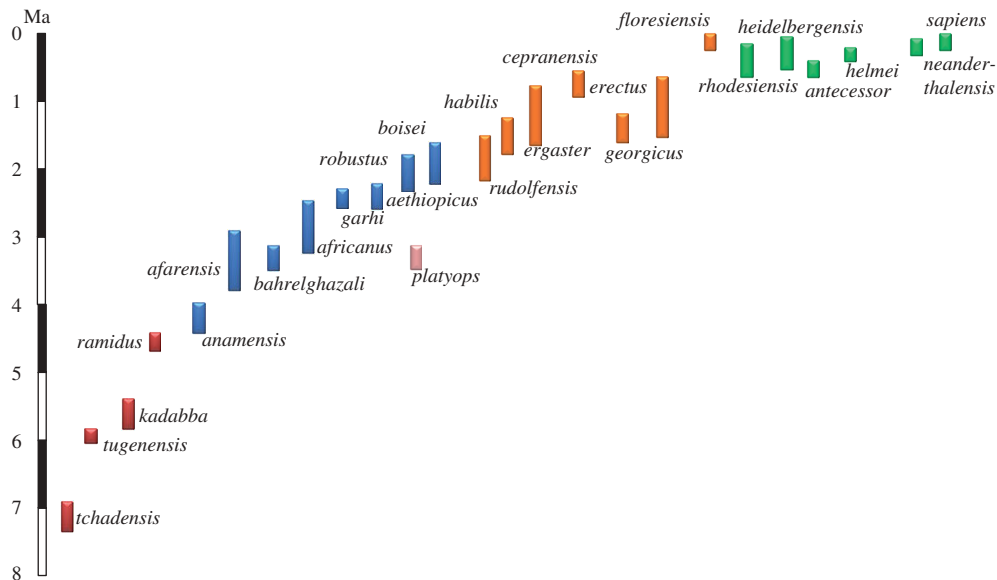
Figure 2. The pattern of hominin evolution. First and last appearance ages of recognized hominin taxa provide chronological ranges. The colour coding indicates major groupings that represent adaptive shifts discussed in the text. Red bars, earliest hominins; blue bars, australopithecines and allies; orange bars, smaller-brained *Homo*; green bars, larger-brained *Homo*.

Table 1. The development of key traits during the course of human evolution. The structure of the derived traits is underpinned by unique mechanisms associated with human cultural capacities, but at a socioecological level, these are properties found elsewhere in the animal kingdom, and therefore can be considered to have evolved as behavioural traits in response to resource-based conditions.

A (plesiomorphic traits)	B (derived hominin social traits)	C (derived hominin social traits)	D (derived features)
social characteristics of the basal hominins based on comparison with Pan *as model of last common ancestor*	*strongly continuous with basal hominins/last common ancestor*	*quantitative extensions of basal hominin/last common ancestor traits*	*human novelties*
multi-male, multi-female community structure	compulsive sociality	larger community sizes	strong male–female bonding and persistence of relationships
male resident, female dispersal on maturity	community structure at root of social organization	exploded or extended fission–fusion	higher paternal investment
weak male–female bonding	multi-male, multi-female communities	extension of kinship structures through generations and formations of lineages	development of affinal kin relationships
intercommunity hostility	male-kin bonding	organized (female) mate transfer	strong substructure within communities
male hierarchy	female transfer predominant		sex-based roles
female hierarchy	intergroup hostility		age-related dominance
			extensive parental investment and heritability of social status
			context-dependent intercommunity relationships
			male control of resources

continuous and gradual change towards the human condition. Rather, a summary of the archaeological and anatomical evidence (table 2 and figure 3) identifies a patchy pattern of change, especially when the different elements of the record are considered

independently. We argue that, within this patchiness, clusters of significant events lead us to determine five key transitions (figure 4).

(i) *African ape to terrestrial bipedal ape* (*approx. 4 Ma*). The date of this transition is uncertain,

Table 2. Summary of selected evidence for transitions in human evolution using five broad categories. The categories reflect the major ecological, life-history and behaviour aspects of hominin evolution and are by no means exhaustive. The evidence is drawn from the fossil and archaeological record. Dates are approximate estimates. Data relating to sexual dimorphism and brain size are shown in figure 3 and the overall distribution of hominin taxa in figure 1. The sum of these lines of evidence is used to propose five key transitions (given in italics in date column) (see also figure 4 and text).

date	lithic technology	locomotion	life history	foraging	dispersal
10 ka				domestication of plants and animals associated with increased sedentism	
15 ka				earliest domestication of plants	post last glacial maximum dispersals
20 ka				seed grinding technology/cereal exploitation	
60 ka					first evidence of *H. sapiens* outside Africa and adjacent zones
80 ka	modes 4 and 5 (enhanced prepared core technology with blade and microlith production; emphasis on lightweight composite tools)			intensive specialized hunting	
120 ka				exploitation of aquatic resources	earliest *H. sapiens* dispersal
150 ka			modern human life-history parameters		
250 ka					mode 3 (Neanderthal lineage) dispersals
400 ka	mode 3 (prepared core technology; emphasis on projectiles and earliest hafting)			systematic medium-sized ungulate hunting	
700 ka					larger brained *Homo* dispersals into Eurasia (*H. heidelbergensis, H. antecessor*)
800 ka	mode 2B (Acheulean biface technology with enhanced symmetry)			first evidence for fire (and cooking?)	
1.6 Ma	mode 2A (large flakes and Acheulean biface technology)				
1.8 Ma		human body shape shifts towards modern human condition	first shift in life history towards modern condition	increased evidence for regular meat-eating	first dispersals beyond Africa (Eurasian *H. erectus* dispersals)

(Continued.)

Table 2. (*Continued.*)

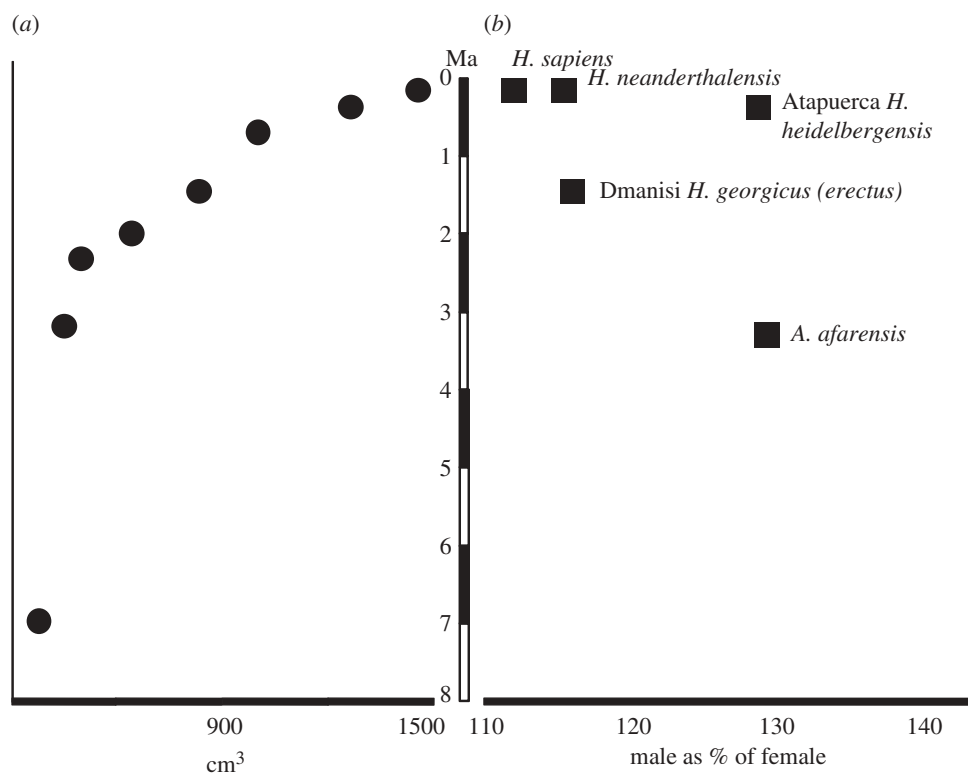| date	lithic technology	locomotion	life history	foraging	dispersal
2.6 Ma	mode 1 (flakes, pebble tools and the origins of percussive technology)			shift to carnivory	
3 Ma					australopithecine dispersals within Africa
4 Ma		unambiguous evidence for bipedalism			
6 Ma		first evidence for bipedalism?			

Figure 3. (*a*) Pattern of evolution in brain size and (*b*) sexual dimorphism as indicated by the fossil record. Points shown are approximate, and ranges and potential errors can be considerable, especially for sexual dimorphism.

depending upon whether the proposal that *Sahelanthropus* and *Ororrin* are bipeds is sustained (Brunet *et al.* 2002). The date of around 4.0 Ma is used here and broadly coincides with the emergence and radiation of the australopithecines (Leakey *et al.* 1998), the group that responded to the opportunities posed by bipedalism, and dispersed widely across Africa. However, the context in which bipedalism arose is more likely to be the early part of the Pliocene. There is little other relevant evidence, but there are many grounds for seeing the major shift in locomotion as a critical adaptive and ecological change.

(ii) *Terrestrial bipedal ape (australopithecine) to 'early* Homo' (*approx. 2.0 Ma*). Between 2.5 and 1.8 Ma, there is an enormous amount of change in the hominin lineage and its associated behaviour. In the early part of this period, the genus *Homo* evolves, and there is the first evidence for meat-eating and lithic technology (modes 1 and 2a) (Prat *et al.* 2005). From shortly after 2.0 Ma, the hominin body plan is reorganized from the 'bipedal ape' posture of the australopithecines to something very similar to modern humans (Walker & Leakey 1993); brain size increases substantially, and patterns of dental development indicate a delayed process of maturation (i.e. a shift in the life-history strategy) (Smith 1994). Perhaps most significantly, the impact of these changes can be seen in the rapid dispersal of hominins across Africa, and, for the first time, beyond.

(iii) *Early* Homo *to* Homo heidelbergensis (*1.0– 0.8 Ma*). Between 1.0 and 0.8 Ma, another major
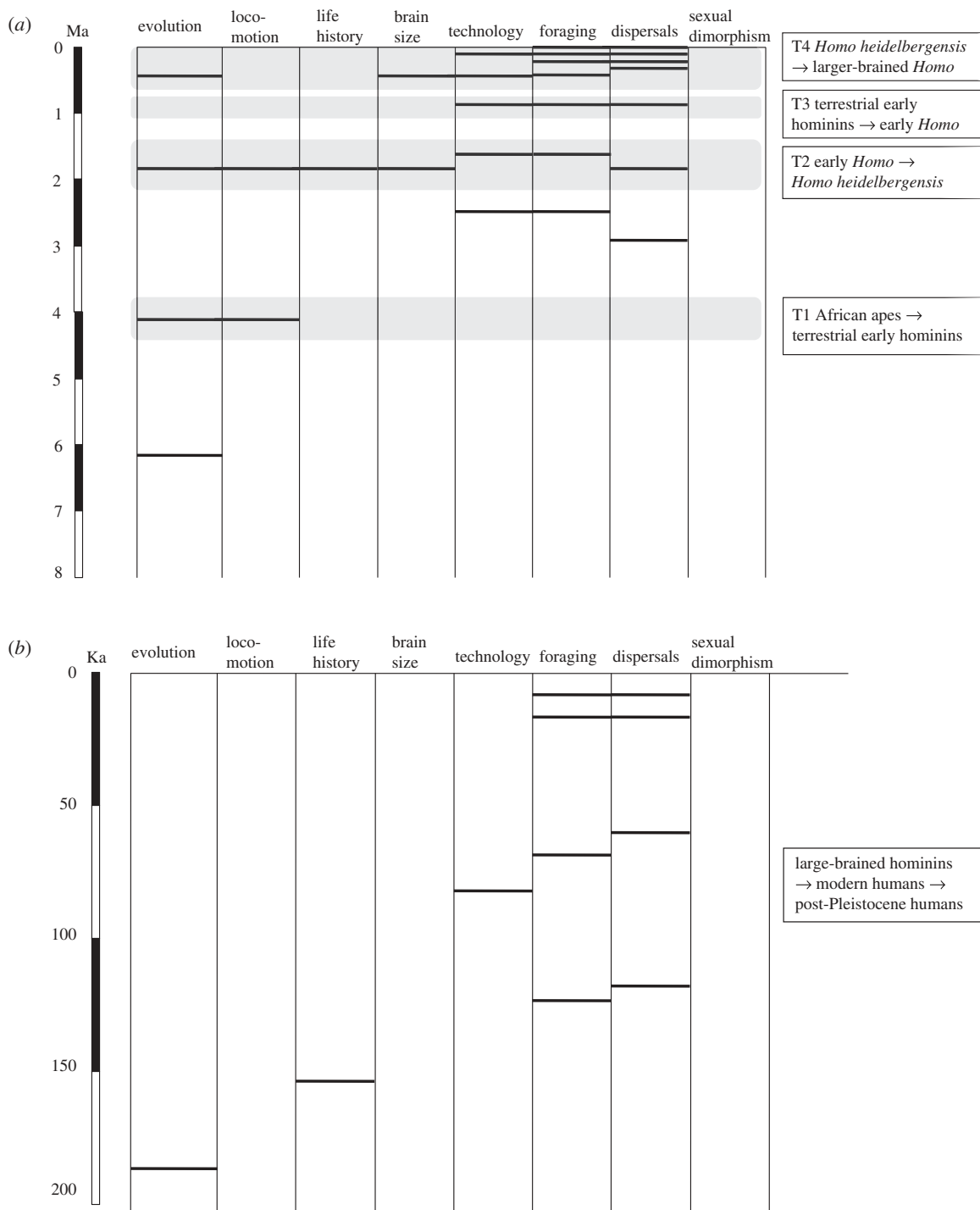
Figure 4. The timing of the five key transitions discussed in the text, based on archaeological and palaeontological evidence (table 2). (*a*) The first four transitions occurring on a time scale of millions of years; (*b*) the fifth transition on a time scale of thousands of years.

change occurs. Although the fossil record is particularly poor, this is when *H. heidelbergensis* (derived from *Homo erectus/ergaster* depending upon terminology) evolves. However, more significantly, it is when the true 'Acheulean' stone technology develops (mode 2B), and spreads across much of Eurasia, providing the first significant colonization of more northerly environments (Gamble 1993). A number of shifts, perhaps including the extensive use of fire and even cooking (Wrangham *et al.* 1999), may provide the basis for a major change in hominin socioecology at this time, albeit at a regional scale.

(iv) *Homo heidelbergensis to larger brained* Homo (*from 500 ka*). From around half a million years ago,

there is an increase in the rate of evolution of the brain. This can be seen in two lineages (*Homo sapiens* and *Homo neanderthalensis*), and may be a single evolutionary event, followed by later divergence (Foley & Lahr 1997) or convergence (Stringer & Hublin 1999). Among the changes that can be seen in this period are shifts in life history, the development of mode 3 technology and changes in subsistence behaviour (Stiner *et al.* 2000).

(v) *Larger-brained* Homo *to* H. sapiens (*200–0 ka*). The final transition is the evolution of modern humans (Stringer 2002). This has often been considered a speciation event, as part of the 'Out of

Africa' model, with morphological and behavioural change. However, the fossil, genetic and archaeological evidence suggest that these were cumulative changes spread over a period of more than 200 000 years (figure 3b), and continue through to the development of agriculture. The finer resolution of the archaeological and palaeontological records points to the multiple character of transitions (Foley & Lahr 1997; Foley 2005), a feature that is obscured in earlier examples (figure 3a). Evidence exists for the exploitation of aquatic resources, more specialized hunting behaviour, greater use of complex technology, the appearance of symbolic material culture as well as massive demographic growth (d'Errico *et al.* 2003; Marean *et al.* 2007; Atkinson *et al.* 2008).

5. TOWARDS AN ECOLOGICAL MODEL FOR THE EVOLUTION OF HUMAN SOCIETY: EXPLAINING KEY TRANSITIONS

Having briefly described the evidence available, and inferred some key points in hominin evolutionary history, we can now turn to their explanation in terms of the relationship between ecological conditions and behavioural or social outcomes.

6. TRANSITION 1: BIPEDALISM AND RANGE SIZE

The significant factor that is key to understanding the emergence of the early bipedal hominins is the change in climate and environment that occurs at the end of the Miocene and into the Early Pliocene. At this time, there was pronounced global cooling. The effect of this varied regionally, but there is general consensus that in Africa there was increasing aridity, a decline in closed forest habitats and a spread of more wooded, bushed and grassy environments, often with pronounced seasonality. There is a general trend towards terrestriality among the catarrhines during this period (Fleagle 1999), and the hominins in one sense represent the hominoid extreme in this context. Although there is debate about the environment in which bipedalism evolved, there is none concerning the extent to which it provides the basis for adaptation to terrestrial environments. In terms of behavioural ecology, there is a change towards more dispersed and patchy plant resources, many of which would have been of relatively poor quality. The key shift, and one likely to have played a major part in the selection for bipedalism, is towards longer day ranges. Furthermore, the more patchy environments are likely to have promoted a greater degree of fissioning behaviour in feeding parties, and this may also have become more extensive if sleeping sites were both more dispersed and less suitable for larger communities. One of the bases for later human social behaviour, extensive fissioning and fusing may have had its roots in this change. A further implication might also have been, through the fissioning, a greater tendency for the formation of substructuring within the larger communities.

Derived from general models, a further expectation would be that there was a decrease in community size (counter to later trends in human evolution) (Foley 2001). One of the interesting but uncertain implications of this concerns the nature of intergroup relationships under these circumstances. Smaller communities would have been vulnerable to attack, and also more reluctant to patrol borders. The costs of hostility may have been high, and it is possible that, compared with chimpanzees, these communities may have had more variable intergroup encounters. However, although there are shifts in the socioecology of these early australopithecines, the basic changes that are likely to have occurred would be well within the normal expectations for ape social behaviour and organization, and there is little evidence for any marked shifts in the direction of human sociality. Bipedalism, though, with its implications for both ranging and carrying (Foley & Elton 1998), is one of the building blocks for later adaptive changes.

7. TRANSITION 2: TOOLS AND MEAT

The transition occurring around 2.0 Ma involves many traits changing, although the evidence is insufficient to determine a particular sequence or coevolutionary relationship. Many of these features are correlated in that they are all strongly associated with both later *Homo* and modern humans—larger brains, delayed and elongated life-history parameters and the use of technology as a part of behavioural adaptation. This more 'human' package is to some extent confirmed by the more modern body proportions, including a reduced gut (Aiello & Wheeler 1995). These are not fully modern humans—the brain size is around two-thirds of modern humans, the rate of maturation is more rapid and there is evidence that they were incapable of speech production.

The period prior to 2.0 Ma is characterized by a continuation of the trend towards cooler and drier environments, and there is some suggestion that at this time there was an expansion of grasslands and grazing faunas (Bobe & Behrensmeyer 2004). It is a period of extensive evolutionary change across a range of mammals, with high levels of lineage diversity. However, while environmental change is important, it can also be argued that there was a more direct impact on hominin evolution driven by its own adaptive change. The two critical events are the development of more extensive meat-eating (as indicated by cut marks on bones and faunal assemblages in association with artefacts) and the use of tools. It is probable that, while earlier hominins made use of some level of technology, the use of a percussive technology, which produces strong cutting edges, provided a major advantage in terms of access to animal carcasses. Within a behavioural ecological model, the implications of this change would be a more reliable access to high-quality resources, especially during dry seasons, and a smoothing out of seasonal variation This change led to a greater availability of energy for mothers, and a relaxation of the constraints on the energetic costs of larger brains, especially when tied to a delayed life-history strategy (Foley & Lee 1991). It has also been argued that this may have involved

greater bonding between males and females, greater male investment in offspring as well as a divergence in male and female economic roles (Hill & Kaplan 1993).

In sum, around two million years ago, *Homo* lived in communities in which the relationships between males and females and the reproductive tactics of each in terms of a more expensive offspring were changing. This change, we would argue, is directly related to greater access through technology to meat. That it was a significant change is suggested by the massive expansion of geographical range of hominins shortly after this time.

8. TRANSITION 3: FIRE, FAMILIES AND FOCUS

The geographical range of *Homo* now ranged from the tropics to 55°N, but across such ecological diversity, stone technology stayed remarkably constant and formed two major provinces. In China and southeast Asia, technology remained as mode 1 (Moore & Brumm 2007). By contrast, in India, southwest Asia, Europe and Africa, mode 2 bifaces came to dominate, although mode 1 was still common. These bifaces now displayed greater symmetry and precision in knapping skills than the earlier examples. This is the classic Acheulean that continues in Europe to at least 300 ka. It is in this second province that we can track this transition, while in the former, stasis and conservatism occur. Hominins followed familiar environmental conditions to achieve a northern distribution. At the eastern English site of Pakefield (Parfitt *et al.* 2005), dating to 750 ka, soil carbonates indicate a Mediterranean environment. Major glaciations had not yet occurred, but even so the population ebbed and flowed into the northernmost parts of its range according to local ecological conditions. This suggests a constrained pattern of fission and fusion that was as yet unable to adapt to the seasonal shortages of higher latitudes by more fluid social arrangements.

One possibility is that cooking, rather than stone technology, may have been the critical adaptive change at this point, especially as there may have been a link between the control of fire and the ability to survive in colder environments. It also radically changed hominin socioecology. Wrangham (Wrangham *et al.* 1999; Wrangham & Conklin-Brittain 2003; Boback *et al.* 2007; Wobber *et al.* 2008) has argued that cooking is essential as a means of making meat in larger quantities energetically viable within a time budget and that it also massively increases the digestibility of plant foods. The control of fire, evidence for which becomes stronger at the period, is essential for this, and would have had a major impact on interdependence of individuals, the spatial structure of social interactions and the roles of males and females in subsistence. The Jordan Valley site of Gesher-Benot-Ya'Aqov (Goren-Inbar *et al.* 2002, 2004; Madsen & Goren-Inbar 2004), dated to 780 ka, has evidence for small hearths in which nuts and seeds were processed as well as an advanced mode 2B stone technology.

The critical question is how a change in ecological energetics through fire and cooking shaped social evolution. One possibility is that it placed a greater emphasis on bonding between individual males and females, which strengthened smaller family units within the larger community structure. Cooking, spatial patterns shaped by hearth structures and specialized roles by sex were factors that both changed male–female relationships and produced the nested social structures that characterize humans (i.e. family units embedded within larger kin-based communities). Indirect evidence for this type of change may be provided by the very marked increase in the symmetry and quality of mode 2B Acheulean bifaces. The knapping skills indicate not only novel cognitive skills (Wynn 1988) when compared with mode 1 or mode 2A (and now demonstrated by neuroimaging; Stout & Chaminade 2007), but also the human skill of focused attention. The ability to focus attention so single-mindedly on the making of an object, and its constant repetition across three continents and many millennia, is testament to a high level of attention in practical operations. However, it may also allow us to infer the coevolutionary development of close male–female bonding at this time supported by a similar focused attention, most commonly expressed psychologically as our propensity for infatuation, the love-struck gaze.

But this Acheulean gaze was not the only derived human trait that appeared at this time. Using the correlation between brain and community size, Dunbar (2003) has proposed that hominins in this period possessed a theory of mind and accompanying orders of intentionality. Gamble (2009) has argued for the importance of behaviours that amplified the strength and persistence of social bonds in such an advanced hominin cognition. These would include social laughter and crying as well as other mood enhancers such as collective dance and music.

9. TRANSITION 4: SOCIAL BRAINS AND TECHNOLOGIES

At around 300 ka, there is a further change in technology, the abandonment of the hand-axe, which was a consistent part of Afro–Eurasian populations for a considerable period of time, and the elaboration of a lithic technology based on prepared core technology (mode 3). There are a number of significant aspects of this technology; first, it can be argued that it involves a considerable level of planning in its production, suggesting greater cognitive competence. Second, it is a means of mass production of flakes and blades of a predictable shape. And third, it is the basis for a projectile technology. Its appearance is poorly understood, and some argue that it arose several times and was prefigured in the Acheulean giant core/flake technology (McNabb *et al.* 2004). However, it broadly correlates with the evolution of two large-brained hominin lineages (Neanderthals and modern humans) and an acceleration in the rate of encephalization. It is during this period that hominin brain size becomes equivalent to that found in living humans, and on occasion exceeds it.

There is little doubt that both Neanderthals and modern humans are significantly different from other hominins. Indeed, despite the many arguments about how they differ from each other, what they share is far more striking when compared with any other hominin. Both for tens of thousands of years had a basic mode 3 Middle Stone Age/Palaeolithic technology, with the emergence of distinctive regional traits. They had similar but not identical life-history schedules; both probably had speech and language (MacLarnon & Hewitt 1999), and the capacity for considerable cultural variation.

The ecological basis for this proposed transition is that effective and relatively replicable projectiles provided access to medium-sized ungulates, at a time when other more easily obtainable prey were declining (possibly in response to human pressure; Stiner *et al.* 2000). Well-fashioned wooden spears were used to hunt herds of horses at the German site of Schöningen, dating to 400 ka (Thieme 2005). These are associated with several lakeside hearths. It is possible that during this period, prior to the evolution of modern humans in Africa, these archaic hominins were undergoing major changes in two aspects of their social life. The first is that there was a greater degree of demographic packing, with populations now competing more severely for space and resources. The greater regionality of the archaeological record may suggest this is taking place, with material culture at least one line of evidence for stronger signals of community affiliation. In other words, this period sees a much greater emphasis on groups as units. This may have been the critical pre-condition for the evolution of cultural capacities that would enforce social norms more effectively, and which set the basis for modern humans with their broader cultural repertoire. It may also be the case that at this point, with an emphasis on group affiliation, the importance of strong clan/lineage-based kinship systems became a major adaptive facet of their social life. Furthermore, such strong affiliation might also indicate the existence of hostile relationships between groups. Some support for this local group model of later Middle Pleistocene hominins comes from the evidence for small effective population sizes (based on palaeogenetics and modern genetics) for both Neanderthals and modern humans—in other words, a highly structured population.

The second impact is the explosion of the scale of fission–fusion in response to these ecological changes. It is generally accepted (table 1) that fission–fusion is an important element of chimpanzee social organization and that it may have been enhanced among the earlier hominins (transition 1). However, among modern humans, fission–fusion occurs at a different order of magnitude. Individuals, families, bands, etc. can split up for very long periods of time, and disperse over large distances, while still maintaining a common social network. The ecology and demographic structure at the time of this transition may have been the spur to this exploded form of fission–fusion. Projectiles and the exploitation of mid-sized ungulates, for example, imply more seasonally variable foraging patterns and might correlate with greater

fission–fusion. A further indication of a significant change in ranging patterns comes from the evidence that lithic raw materials were extracted and transported over greater distances than before.

It is during this period that almost 30 per cent of hominin encephalization occurred (figure 2a). This has been related to an increase in community size, but it may also have been selected for by the greater cognitive demand of maintaining social relationships over distance and time.

10. TRANSITION 5: ECOLOGICAL INTENSIFICATION

Three features stand out in this transition. First, there is the appearance of our current anatomical and genetic characteristics in Africa (Stringer & Andrews 1988; Noonan *et al.* 2006). Second, there is the global dispersal of these characteristics allied, in many cases with a novel technology, to the previously uninhabited 75 per cent of the globe. This occurs late, beginning with the sea crossing to Australia some 60 ka ago. It concludes with the settlement of remote Polynesia within the last millennium. Third, there is the rapid increase in population numbers following the retreat of the last glaciation that began some 16 ka ago (Lowe *et al.* 2008).

In transition 3 nested complexity arose within groups and in transition 4 the spatial and temporal extension of that pattern was associated with greater fission–fusion. Now further change resulted from the emergence of intergroup complexity based initially on a more energy-rich ecology. This involved the use of aquatic and smaller animal resources, the exploitation of which was made possible by specialized technologies (modes 4 and 5) and domestic units of production. During the course of this transition (after 30 ka), it also becomes clear that human populations were able to exist at much higher densities and to intensify their foraging strategies of seed-harvesting, cereal agriculture and animal domestication.

The evidence for complexity in intergroup relationships takes several forms. A rise in the quantity and diversity of cultural forms, including composite tools, art and architecture, is matched by widespread distributions of distinctive cultural markers that signal group affiliation at a large geographical scale. Mobility ceases to be the key foraging tactic as more long-lived settlements occur in response to greater demographic packing. Territorial markers appear in the form of cemeteries and defended settlements, while extensive networks of exchange are now found through which items such as shell, obsidian, amber and other localized resources are channelled.

At this point, a fundamental shift that goes beyond the normal range of the socioecological model occurred. Technological dependence, spatially restricted and controlled staples such as domesticates, defended flocks, fields and stores, opened the possibility for greater male control over access to resources at local, regional and inter-regional scales. If we take it as axiomatic to the model that female reproduction is dependent upon access to resources, and males by access to females,

Table 3. Summary of the ecological basis for, and social consequence of, the five transitions in hominin evolution discussed in the text.

transition	time	ecological change	social implications	key structural shifts in human social evolution	hominin taxon with derived social behaviour
T1 (bipedalism, range size and fission fusion)	6–4 Ma	terrestriality and longer ranging distances	more dispersed social communities and greater fission and fusion	fission–fusion	australopithecines
T2 (tools and meat)	2.6–1.6 Ma	greater access to animal resources (technology); more reliable food supply; smoothing of seasonal variation	more prolonged male–female bonding	male–female relationships	early *Homo*
T3 (fire, families and focus)	800–700 ka	more energy-rich-food sources through cooking and technology	more stable male–female bonds; establishment of nested units within community structure (family units)	nested hierarchical community structures	*H. heidelbergensis*
T4 (social brains and technologies (projectiles))	~400–300 ka	more reliable food resources across greater range of environments (projectiles); greater demographic packing	greater fission–fusion and development of stable social life at a distance greater regional differentiation of communities and beginnings of structures beyond the level of the community	exploded fission–fusion and supracommunity structures	*Homo helmei*, *H. neanderthalensis*, *H. sapiens*
T5 (ecological intensification)	200–10 ka	energy-rich ecology through aquatic resources, cereal harvesting, hunting and domestication of animals.	intergroup and regional social structures and networks male control of resources and thus of female distribution	regional social systems and networks social structure dominated by resource ownership, defence and control	*H. sapiens*

then the open-ended model becomes closed when males themselves control the resources. Complex social structures that interweave marriage patterns and resources, which characterize all human societies, represent an entirely novel socioecology that is uniquely human.

Transition 5 is classically the origins of *H. sapiens* and modern human behaviour. Recent contributions to this topic have tended to focus on such a transition being relatively chronologically constrained. In contrast, we would argue here that it is a prolonged and cumulative transition, stretching from the biological changes over 150 ka to the emergence of a fully sedentary, agricultural and ethnically complex world in the last 15 ka (table 3 and figure 5).

11. EVOLUTION OF HUMAN SOCIETY: TRENDS AND PRINCIPLES

All too often, the reconstruction in both popular and scientific accounts of how human social behaviour evolved is mere speculation. This unsatisfying situation arises when the archaeological and fossil data that exist to test competing hypotheses are ignored and mishandled. Our strategy in this paper has been to maximize the points at which reconstruction articulates with archaeological and paleobiological data, thereby ensuring consistency with general principles drawn from neo-behavioural ecology. There is much to learn still, but some general points can be made. One such point is that if the 'community',
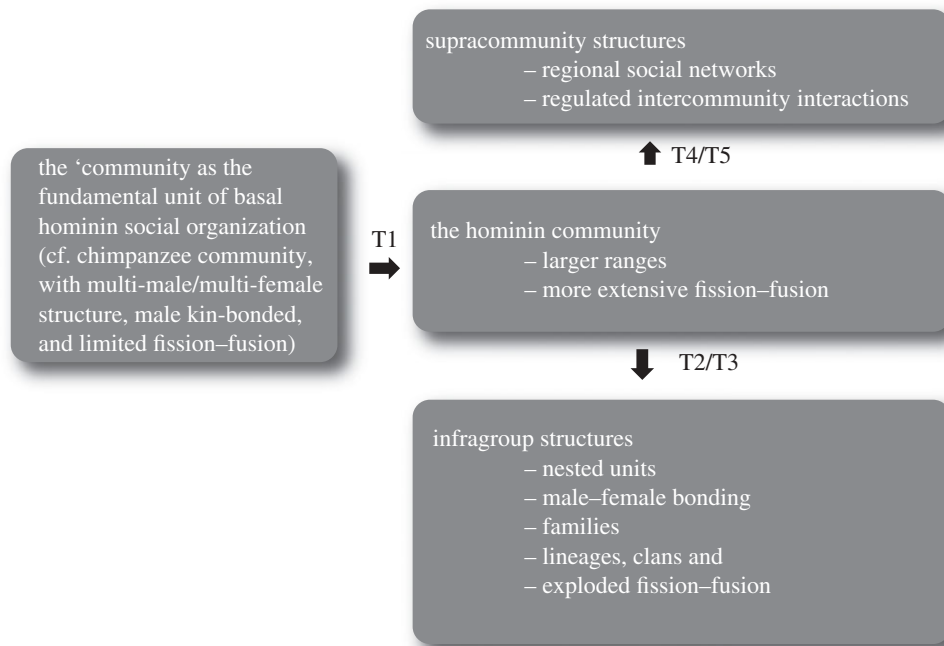
Figure 5. The community is the fundamental hominin and African hominoid social unit, and during the course of hominin evolution, it has been elaborated by increased fissioning and fusion (transition 1 and later transitions), greater infracommunity structure (transitions 2 and 3) and greater supracommunity networks and associations (transitions 4 and 5). See text for discussion.

in the sense used to describe both chimpanzee groups and human social units (Foley & Lahr 2001), was present from the last common ancestor to the emergence of modern humans, the key development is the addition of social structures both below—families and descent groups—and above—shared political systems, segmentary lineage systems and trade networks. The community, however, remains the core and the basis for elaboration.

A second point is that across the course of human evolution, one of the strongest trends is that human 'society' has evolved to cope with more and more 'fissioning'. If the community is one of the most basic building blocks of human society—a group with shared dialects, kin bonds and political organization—then it is clear that humans have the capacity to maintain these in the absence of close social proximity, and with long periods where there is no contact. The social and cognitive apparatus that has evolved provides the mechanisms for this. However, from a socioecological perspective, the fissioning potential (which may become permanent as groups do diverge and form new ones) provides ecological flexibility to human communities and to individuals pursuing their reproductive and other goals. Human society is essentially a chimpanzee community with exploded fission–fusion; a society that has achieved release from the constraints of proximity (Rodseth *et al.* 1991) that dominate the negotiation and often daily affirmation of social bonds and hierarchies among primates. Social extension in time and space was not achieved by all hominins. It appeared late in human evolution, as indicated by overwater dispersal to Australia and then throughout Polynesia as well as

coping in the extreme continental environments of boreal Siberia with longer periods of fission, and very low population densities owing to highly seasonal resources.

A third important implication is that kinship runs like a thread through the course of human evolution, from the beginnings of the last common ancestor through to the present day. The maintenance of kinship through several generations (descent groups) is both a truly unique development and also fundamental to the way in which communities both hold together and ultimately divide. This may be as recent as the global dispersal 60 ka ago (Gamble 2008). The complexities of other kinship systems are probably superimposed on top of this, but lineage systems have the power to enhance the deployment of larger groups of individuals for both economic and military advantage. This provides expandability to human society, and is likely to have been essential to the process of global colonization.

The fourth general point relates to the role of the environment. Most of the major changes of human behavioural evolution coincide with climatic and environmental changes (although there are other phases of climatic change with no such evolutionary response). However, some of the changes that occurred also involved the consequences of more endogenous elements of the hominins themselves—including technology, fire and cultural mechanisms for maintaining larger groups. In this sense, there is a strong feedback element in the links between ecological and social factors in hominin evolution, which helps to account for the rapid acceleration in social change in the last 60 ka.

Finally, the specific aspects of human social evolution may change the principles of socioecology, and thus in turn help produce a different type of evolution. It is generally accepted that female reproductive success is more closely tied to access to resources, and in that sense, female distribution in relation to resources plays the fundamental role in shaping social systems and strategies. Males, more constrained by access to females, adapt to the distribution of those females. However, over the course of human evolution, it is probably the case that male behaviour has meant that males have had increasing control over resources and have defended such resources extensively. This is particularly the case with animal domesticates, and lies at the heart of most pastoralist societies, for example. This means that females have increasingly had to adapt to a distribution of resources that is itself controlled by males—closing the socioecological loop. The consequences of this for human society, social behaviour and cultural practice, have probably been very marked.

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