Proceedings of the British Academy, **88**, 95–117

An Evolutionary and Chronological Framework for Human Social Behaviour

ROBERT A. FOLEY
Department of Biological Anthropology, University of Cambridge,
Downing Street, Cambridge, CB2 3DZ

Keywords: human evolution; social evolution; environment of evolutionary adaptedness; human behavioural ecology.

Summary. Human social behaviour is the product of millions of years of evolution. The details of the chronological and phylogenetic context in which human behaviour evolved can provide information about both the historical depth of specific behaviours and the reasons underlying their evolution. The chronological framework is described, and the ecological basis for human social evolution discussed. Eight key 'events' and time periods are identified: 35 million years ago (35 Myr), 25 Myr, 15 Myr, 5 Myr, 2 Myr, 300,000 years ago (300 Kyr), 100 Kyr and 30 Kyr. Critical developments occur in these periods when such attributes as compulsive sociality, male kin-bonding and changes in life history strategy and parenting behaviour occur. It is argued that a key factor in hominid social evolution is the conjunction of male kin-bonding and selection for energetically expensive offspring; that the shift to modern human behaviour occurs over a prolonged period in excess of 200 Kyr; and that the human evolutionary heritage (the EEA) is not unitary.

INTRODUCTION

TWO APPROACHES HAVE DOMINATED the research into the evolution of human social behaviour. One is primatology, and the extrapolation of the behaviour of extant non-human primates, and the principles underlying animal behaviour, to both humans and the ancestral hominids. The other is anthropology, and the inference of evolutionary history from either human universals or the specific behaviours of hunter-gatherers. In this paper I want to explore a third approach—the chronological and phylogenetic context for hominid evolution. The access that palaeobiology can provide to the timing and evolutionary context of changes in social behaviour can potentially fill the gap between living human and living ape. Palaeobiology can provide direct (albeit patchy) evidence for the path by which the baseline of primate social behaviour has been extended to the full modern human repertoire. In particular, I shall attempt to show that human social behaviour was not an inevitable evolutionary product, nor just a chance event, but the outcome of specific interactions between populations and their environments occurring cumulatively over millions of years. The aim will be to show that while the generalities of behavioural and ecological theory provide powerful models for social evolution, it is how these operate at particular times and in particular places that is paramount. The chronological pattern that will emerge will hopefully throw light on the nature of our evolutionary inheritance and the adaptive basis for human social behaviour. In the first part of the paper I shall present a phylogenetic and chronological context for human social evolution, while in the second I shall discuss the processes by which this occurred.

EVIDENCE FOR A TIMESCALE FOR HUMAN SOCIAL EVOLUTION

35 million years (35 Myr): the anthropoids and the origins of society

The 'origins of society' are often considered to be a classic problem in anthropology. Advances in the study of animal behaviour have, however, greatly modified this perception. Sociality, as distinct from a tendency to aggregate or gregariousness (Charles-Dominique 1977; Lee 1994), requires both the formation and the maintenance of relationships between members of a stable unit (Hinde 1976; Dunbar 1988). As such, a number of mammalian and avian groups can be considered to have maintained sociality, while the social insects fall outside this definition. Amongst the mammals, however, the primates exhibit the most flexible sociality. Out of the over 175 species of anthropoid primates, all but the orang-utan (*Pongo pygmaeus*) are social in the sense that individuals associate with each other for extended periods, interact in patterned ways and form relationships that can be defined by their qualities and intensity.

The orang-utan provides an interesting exception, which in itself demonstrates the ubiquity of primate sociality. While prolonged associations between members of the opposite sex are rare, there are affinities between males and specific females within discrete home ranges (Galdikas 1985). Associations between females have also been observed, especially when several mother-infant pairs congregate. It is not yet known if the females aggregate with the same other individuals over time. Orang-utans thus appear to be sociable within the context of solitary life, and their sociality is based on knowledge of individuals within a larger 'neighbourhood' where group size is limited to one for ecological reasons. In effect, orang-utan sociality could be considered as highly sophisticated, occurring as it does in the absence of visual and tactile reinforcement.

Anthropoid primates can thus be considered as compulsively social, and to have exploited sociality as their core adaptation rather than morphological specialization (Jolly 1984; Dunbar 1988). If sociality occurs on all branches of the anthropoid clade, it is an ancestral or plesiomorphic trait for the group as a whole, or at least one which appeared early in anthropoid evolution. While the origins of this group are still far from clear, both the genetic and palaeontological evidence agree on the monophyly of the platyrrhines and catarrhines and places their last common ancestor at least 35 Myr ago (Kay & Fleagle 1994). Far from being a uniquely human phenomenon, sociality based on interactions, relationships and individual knowledge has a much deeper evolutionary heritage. This capacity for creating and maintaining social systems is likely to be an anciently embedded biological trait.

The anatomical and physiological correlates of social behaviour—the tangible evolutionary evidence—lies in the large brains and prolonged life history traits of the anthropoids. It can be argued that the hormonal and biochemical mechanisms mediating behaviour such as aggression, arousal, conciliation and so on, are similar across anthropoids, including humans (Keverne 1995). We can thus propose that humans are compulsively social as *anthropoid primates* rather than as humans. The primary inference to be drawn is that the origins of society, that hoary chestnut of anthropology, lie in the Eocene or Miocene, and not in recent prehistory or history.

25 Myr: finite social space and the kinship as the basis for social organization

While the capacity for social living may extend back over 30 Myr, the structure of those societies and associated behaviours have evolved over the subsequent periods. Foley & Lee (1989) have argued that social variation is based on two quantifiable elements: spatial association and kinship, and as a result only a finite number of social systems can occur (Figure 1). The Finite Social System model allows us to explore the range of variation that has occurred within the primates, relative to all potential states that can exist. Furthermore it allows for the specification of particular evolutionary

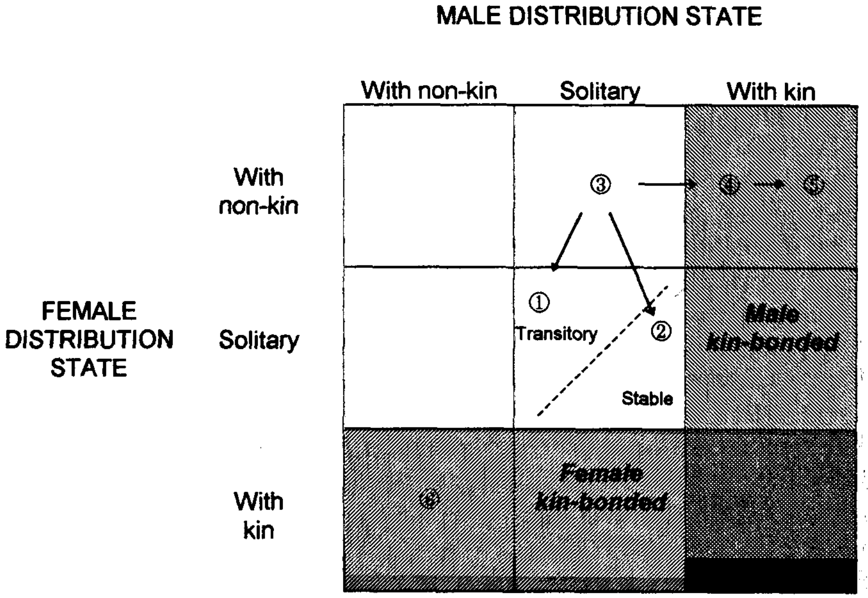

Figure 1. The finite social space model of social organization (Foley & Lee 1989). Social structure arises from the way in which males and females associate with members of their own sex—no association, with non-kin or with kin. Associations between males and females may be either transitory or stable (indicated by diagonal line, shown in central cell only). Where females associate with their own kin then female kin-bonding will occur. Where males associate with kin the group will be male kin-bonded. Associations between males and females may be either transitory or stable. The proposed basal hominoid social system is solitary males with stable associations with females who are not related to each other (3), as is found among gorillas. From this cell hominoids have evolved a diverse array of social systems—solitary (1) in orangs, monogamous (2) in gibbons, and male kin-bonded in chimpanzees (4). Humans have extended this with the presence of inter-generational lineages (5). It should be noted that all the hominoid social systems are evolutionarily adjacent to each other, in contrast to the female kin-bonded systems found in the cercopithecoids.

pathways in transitions between social states. When anthropoid sociality is considered, the non-random distribution of states is striking. Firstly, stable associations between males and females are the norm, in contrast to social states among ungulates and carnivores (Lee 1994). With the evolution of menstrual cycling among anthropoids, maintaining continual access to females becomes a male priority leading to a continual male presence irrespective of the female-female associations. Secondly, there is considerable congruence between social state and phylogenetic relatedness (Foley & Lee 1989). This can be interpreted in a number of ways. There may be phylogenetic inertia within social evolution with ancestral states being important determinants of subsequent evolutionary pathways (see below). Alternatively, since the model places states in relation to adjacency, shifts between states may follow pathways constrained by the plausibility or stability of intermediate states.

In this model, kinship arises through sex-specific dispersal, while the costs and benefits of co-residing with kin are ecological or reproductive in origin (Wrangham 1979, 1980). Female kin-bonding is the most common independently evolved state, due to the ecological advantages of female kin co-operative control of resources among primates exploiting clumped, patchy, relatively large food resources. Male kin-bonding is infrequent and associated with control of females as a dispersed and patchy resource, when those females can be localized in time and space. Monogamy (a phylogenetic rarity among the anthropoids) appears to be associated with the inability of females to co-reside in relation to the resource base, as well as some significant and essential component of male contribution to infant survival. Monogamy may well be an unstable state, for if males can acquire more females then they will do so, mapping polygyny onto either female kin-bonded states or resulting in male kin states. The determination of core social states and the probability of different transitions between states have yet to be determined in a phylogenetically controlled analysis.

However, some interesting general patterns are apparent. The platyrrhines show considerable diversity in social state and indeed occupy the greatest number of different states. This diversity of social states may reflect both their early origin and their monophyletic radiation with subsequent niche separation within diverse New World habitats. Amongst the catarrhines, the number of states observed is lower. However, within these states are strong phylogenetic patterns which can throw light on the evolution of catarrhine social behaviour.

15 Myr: catarrhine social phylogeny and the evolution of male kin-bonding

That there may be a significant phylogenetic effect in patterns of social evolution provides an important avenue for investigating the timing and nature of human behavioural evolution. The phylogeny of the hominoids is now well established by molecular and anatomical evidence. Among living taxa, the hominoids are the sister clade of the Cercopithecoidea. Among the Hominoidea the hylobatids are the sister clade of all other hominoids, while among humans and the great apes, chimpanzees and humans appear to be the most closely related. Gorillas are the sister clade of the human/chimpanzee clade, and the orang is the sister group of all African apes and humans (Figure 2) (Williams & Goodman 1989).

The hominoids are remarkably diverse socially, as seen in Figure 2. The gibbons are primarily monogamous, the organ-utan solitary, the gorilla has single male groups, and the chimpanzee has a fission-fusion community

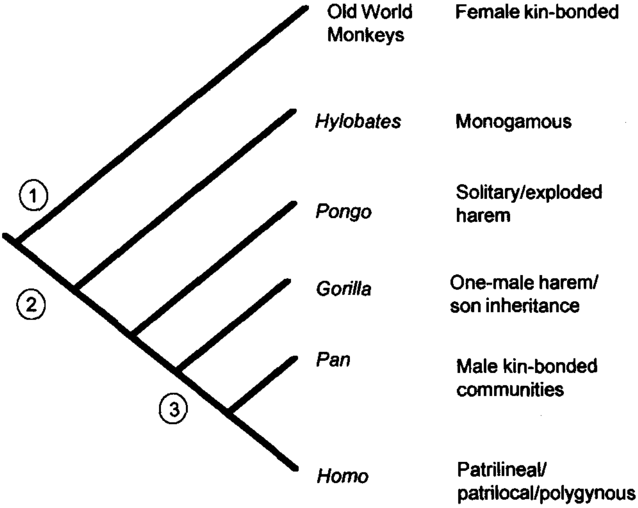

Figure 2. Evolutionary relationships of the catarrhines (Old World monkeys and apes), showing social systems. Female kin-bonding evolved only in the Old World monkey clade (1). Male residence appears to have become established among basal hominoids (2), while male kin-bonding evolved in the chimpanzee/human clade (3).

made up of related males and unrelated females. The bonobo or pygmy chimpanzee is less well understood, but also appears to be male kin-bonded with the addition of strong relationships between males and individual females (Smuts *et al.* 1987). Humans are socially variable, but a dominant pattern is patrilocality and unilineal descent groups, usually based on males. Despite this diversity, however, there are significant phylogenetic patterns; although the hominoids all occupy different cells within the finite social space model, they are all adjacent to each other, and as such it is possible to reconstruct the evolution of their social behaviour using phylogenetic techniques (Foley 1989; and see Rendall & Difiore 1995 for a recent analysis).

Figure 2 also shows the phylogeny of the hominoids with the inferred points of key elements of social evolution superimposed. The key observation is that while the cercopithecoids show extensive female kin-bonding, this is absent from the hominoid clade. The inference would be that among stem hominoids sociality was not characterized by large groups with a kin-based organization. As is evidenced by the gibbons, orang and gorilla, the fundamental social niche of the hominoids is likely to have been small social units made up of one male, one or more females, and young. The period of early diversification or the Hominoidea, from 25 to 10 Myr, perhaps established the small core units of hominoid social life. Gibbons, orangs and gorillas all represent variations on this theme.

The main shift in this pattern occurs on the stem hominid/chimpanzee clade. Kin-based social organizations develop with the establishment of larger communities. These, though, in contrast to those found in the cercopithecoids, are male based. Both common chimpanzees and humans, while maintaining the characteristic sub-units of small groups, have organized above them a larger community. The cores of these communities are the residential males. Females leave these communities at maturity and join other ones.

If this reconstruction is the case, then the phylogenetic context for human social evolution consists of small 'family' units as part of a general hominoid ancestry, and male kin-bonding, male residence, and female dispersal as an African ape ancestry, established in the late Miocene, between 8 and 5 Myr.

5 Myr: savanna socioecology

The divergence of the ancestors of humans and chimpanzees is thought to have occurred between 7 and 5 Myr, and there is sound fossil evidence for the existence of bipedal hominids by around 4 Myr. In all probability any differences between these early hominids and other apes in terms of behaviour were likely to have been at the level of variation displayed between extant hominoid groups, rather than being significant differences in 'grade'.

General socioecological principles might allow some predictions to be made about the social behaviour of the australopithecines. The primary characteristics of the early hominids, and the difference between them and other apes, lies in their bipedal locomotion. This has generally been associated with the occupation of more open environments, environments that became more widespread in eastern Africa during the later Miocene and Pliocene. Although it is likely that the early hominids retained considerable levels of arboreal activity, especially in feeding (Susman *et al.* 1985), the ecological implications of foraging in more savanna conditions are profound. Resources are more spatially patchy, seasonally variable, more dispersed and overall less abundant than those in forests (Foley 1987a). Time for foraging, day range length, and home range area are all likely to increase. The implication would be that while communities may remain large and a significant element of social organization (due at least in part to increased predator pressure, but also as a consequence of inter-group competition and the advantage of male coalitions), the actual foraging and day-to-day functional groupings may also have been smaller (Foley 1993). This may have led to a strengthening of the ancestral hominoid sub-units. It is interesting to note that among humans and bonobos there is an intensification of the strengths of attachment within the smaller social units, essentially the formation of something approaching a family structure. From an evolutionary point of view it is unclear whether this is an independent evolution in the bonobo and hominid lineage or whether it reflects the ancestral condition from which the common chimpanzee has departed. A strong case can be made for the former, and that stronger association in sub-units occurs in response to food occurring in larger patches (White & Wrangham 1988; Foley 1989). If this interpretation is correct, the social organization of the bonobo may be considered of interest less because it represents that of the last common ancestor, as some have claimed, but because it is convergently derived in two lineages in response to similar selective pressures.

There is an increasing consensus that the australopithecines are closer in behaviour to the African apes than to modern humans; in 'grade' terms, their level of organization is likely to have been similar to that of the apes, and the array of australopithecines are likely to have exhibited a range of variations on social behaviour, but variations that would have been little more than a variant on that seen in chimpanzees today.

2 Myr: expensive offspring and the socioecological basis for encephalization

It has been suggested that one response to the seasonality of the more open environments of eastern Africa would have been a greater reliance upon meat-eating, particularly as a dry season response to the movements of large, herbivorous mammals (Foley 1987a). For many populations such a response may not have been possible, due to the absence of herds of ungulates as they underwent seasonal migrations. These surviving, or even thriving, populations of australopithecines, between 3 and 1 Myr, would have maintained the ancestral and conservative patterns of social behaviour. In contrast, those able to invest more foraging effort into meat or other high quality resources, would have entered a new resource structure, and some life history and social changes would have occurred.

The next major event in the evolution of human social behaviour is the increasing brain size that occurs within genus *Homo*. Among the australopithecines there is very little increase in brain size, when body size is taken into account. Maximum Encephalization Quotient (EQ) for extant apes is little over 2.0, and australopithecine EQ ranges from 2.4 to 3.1. An increase to 3.3 can be observed for *Homo ergaster* at 1.6 Myr (McHenry 1992). Thereafter brain size increases steadily, if not spectacularly, over the subsequent million years.

It has been widely argued that increased social complexity underlies this increase in encephalization (Humphrey 1976; Dunbar 1992). However, while sociality might be a major selective force, it does not explain the conditions under which this selection can lead to evolutionary change (Foley 1995a). The key question with this particular part of hominid evolution is what enables early *Homo* to have larger brains, given that these are highly expensive tissue that impose great energetic costs on mothers and infants alike. Foley & Lee (1991) have calculated these additional costs as up to 9% of an infant's nutritional requirements, while Leonard & Robertson (1992) have estimated that the additional size of the human brain means that brain metabolism for humans accounts for 22% of BMR, whereas for the chimpanzee it would only be 8%. In view of the additional costs involved in encephalization, there must not only be positive selective pressure in favour of larger brains, but also a more secure ecological basis. It can be inferred that the social evolution implied by encephalization is dependent upon energetic changes.

Meat-eating may be proposed as a significant part of the change in hominid energetics (Foley & Lee 1991). Meat is a high quality resource, providing both ample energy and protein. As such it can be an important contribution to the additional costs of larger brains. As various authors have shown, there is a link between large brains and high quality food supplies, and in the case of early *Homo* meat rather than plant foods may well be the critical resource added to the early hominid diet breadth. There is certainly evidence for *Homo ergaster* of an increase in hominid involvement in animal butchery, although whether this is through hunting or scavenging is a matter of debate. However, from the point of view of evolutionary ecology the fact that meat is acquired is of greater significance than the means by which it is acquired.

If meat is a means by which higher levels of encephalization can be sustained, then a number of questions about the means by which this occurred can be considered. One such means, as pointed out by Martin *et al.* (1985) and Aiello & Wheeler (1995), is that less gut tissue is required with greater levels of carnivory. As gut tissue is also very metabolically costly, then higher levels of meat-eating can also lead to reduced overall growth and maintenance costs as the gut becomes smaller. Smaller gut size is a corollary of larger brains and higher levels of meat-eating. To this could also be added two further observations: first, that data show that with *Homo* at 2.0 Myr, and *Homo ergaster* between 1.5 and 1.2 Myr, stone technology both develops and is greatly enhanced (Schick & Toth 1993); and second, that with *Homo ergaster* thorax shape, and by implication gut size, shifts to the pattern found in humans rather than apes (Ruff & Walker 1993). Together with the dietary and anatomical evidence, this all points to a change in the way energy was acquired and metabolized by early hominids, and in turn an implied change in the way the hominids were organized socially.

The argument here is that a shift to more open and seasonal environments under local ecological conditions where animal resources were abundant, especially in the dry season, led to greater levels of meat-eating. This was the essential cause, through different populations living in different environmental conditions, of the divergence of the genus *Homo* from the trends found among the australopithecines (Foley 1987a). Greater meat-eating provided more energy, allowed for reduced energy expenditure, and acted as a selective pressure leading to greater levels of sociality. As a corollary of this, during the period 2.0 to 1.0 Myr the expected shift in social organization might well have been towards more intense and extensive male alliances. The phylogenetic heritage of male kin-bonding, evolved for reasons related to longevity and male access to females, provided a premium in terms of foraging behaviour under these new ecological conditions. Females associated with male groups that were numerically larger and effective at acquiring, and probably protecting, resources.

300,000 years (300 Kyr): the 1000 gram brain and evolution of human life history strategies

The period between 1.6 and 0.3 Myr has often been viewed as one of evolutionary stasis (Rightmire 1981). The stability of both morphology and technology lends considerable credence to this view in terms of overall grade of biological organization and behavioural adaptation. However, it should be noted that during this time the hominid range expanded very markedly, and there was considerable evolutionary divergence between populations. Such divergence is likely to have incorporated behavioural and social diversity, at least at the level known for chimpanzee populations today (McGrew 1992), and more likely on a greater scale.

Nonetheless around 300 Kyr, in addition to various biogeographical and behavioural (archaeological) changes, there is an important shift in the rate of encephalization (Aiello & Dunbar 1993). Over the following 250 Kyr brain size increases from a nominal '*Homo erectus*' baseline of around 1000 grams, to one that overlaps with the range found in modern humans. Archaic *sapiens* and Neanderthals both have high levels of encephalization, comparable with those found in anatomically modern humans.

The ecological and social conditions that gave rise to the selection for this acceleration in trend are hard to pinpoint. Certainly there are some significant archaeological changes, principally associated in Africa and Europe with the development of prepared flake technologies (the Middle Palaeolithic / Middle Stone Age) (Schick & Toth 1993), and there is also the possibility that fire may be systematically used at this point. According to Aiello & Dunbar (1993), at this stage group size reaches a critical threshold where grooming is insufficient for the maintenance of social relationships within a group, and language supplants grooming as the primary means of social lubrication, resulting in rapid evolutionary and social changes. Alternatively, Foley & Lee (1991) have argued that 1000 grams represents, in terms of brain energy expenditure, the point at which modern human growth rates and developmental strategies would be necessary to sustain the very high metabolic costs of brain growth. Essentially it can be argued that the energy needed by both mother and infant during development would be so high that the principal means for solving this problem lie in slower growth rates. This change in life history strategy—the well-known shift from more rapid ape growth patterns to the extended and delayed pattern of maturation found in modern humans—would have profound social and demographic consequences: a longer period of infant altriciality and dependence, longer inter-birth intervals, delayed onset of first reproduction. A corollary of this might also be an extension of longevity, with profound consequences for competition between males and mating strategies.

It can perhaps be argued that the period between 300 Kyr and 200 Kyr was of critical importance in the evolution of human social behaviour. The energetic costs of reproduction associated with larger brains resulted in a change in life history strategies, leading to new patterns of social behaviour and organization. Underpinning both social and life history changes might be changes in foraging pattern associated with technology or some other extractive strategy. The consequences of this change could well have been either directly, or indirectly through group size, selection for much greater levels of communication, and hence the evolution of language. Such a timing for what might broadly be considered the origins of language functionally equivalent to that found in modern humans would be consistent with the morphological data, with the acceleration of brain size evolution that occurs at this time, and the apparently 'modern' behaviours associated with Neanderthals (Mellars 1996) who would be as much descendants of these archaic groups as *Homo sapiens* itself.

100 Kyr: dispersal, group size and territoriality

Anatomically modern humans—*Homo sapiens*—are present in Africa from around 140 Kyr. Both morphological and genetic evidence support the view that the origins of modern humans lie within Africa, and that they disperse from their area of endemism to other parts of the world over the subsequent 60 Kyr (Lahr & Foley 1994). By and large both the evolution of anatomically modern humans and their dispersal are not associated with any markedly visible evidence for a change in behaviour, although within Africa temporary changes in technology do occur at various points (Foley

1987b; Klein 1992; Brookes *et al.* 1995). These, however, are transient, and the first 80 Kyr of the existence of anatomically modern humans do not appear to be characterized by any behaviour that is significantly different from that of contemporary archaic populations such as the Neanderthals. Significant changes of behaviour occur from around 40 Kyr, but these are regionally variable. The most dramatic shift occurs in Europe and the Mediterranean, where Upper Palaeolithic blade industries occur; other regions, such as Australia and eastern Asia do not undergo any apparent change during the later Pleistocene (Mellars 1991; Klein 1992). Furthermore, the European evidence, which is the most abundant, shows that there is as much change between early and late Upper Palaeolithic as there is between the Middle and Upper Palaeolithic (Clark & Lindly 1989). This is indicated morphologically with the loss of skeletal robusticity that occurs (Lahr 1996), or the relatively sudden flowering of art during the Magdalenian.

Technologically, anatomically modern humans appear to be highly variable, with very distinct regional and temporal patterns occurring (Foley 1987b). It is hard to sustain the view that on behavioural grounds the appearance of anatomically modern humans was a rapid or dramatic revolution in the hominid world. Events occurred cumulatively and multiply over a period of 100 Kyr, culminating in the full colonization of the world and the shift to agriculture during the period 15 to 5 Kyr. Indeed, it is the high potential for dispersal itself, rather than any specific behaviour, that seems to characterize modern humans (Gamble 1993).

The question this raises is—what is the basis for these dispersals? In the light of what has already been established in hominid social evolution, it can be argued that the ancestral social condition for modern humans consisted of moderately large communities, with coalitions of males linked by kinship, and unrelated females attached to specific males or possibly several males. Given the evidence for changes in life history parameters, particularly the slower growth, delayed maturation and increased longevity, such groups are likely to have at least an element of inter-generational lineage structuring (patrilineal, given the pattern of male residence). Assuming conditions of net local population growth, two significant characteristics would arise from this ancestral social organization. The first is that with male kin-bonded groups, communities would be at least partially closed to each other and hostile, resulting in some form of territorial or agonistic behaviour between communities. A consequence of this would be that overall group or community size would be an advantage, particularly in terms of numbers of males within a coalition. The competitive advantages that would arise from this would, however, also lead to both social and ecological pressures. As group size goes up, competition for both resources and reproduction would increase. This would lead to the second of the two ancestral tendencies occurring—demographic fission of communities. Primate social groups tend to split into two when they reach group sizes that are greater than can be socially or ecologically maintained (Dunbar 1992, this volume). Fission of groups would in turn be a factor promoting geographical dispersal and leading to the colonization of new regions and localities, whether or not they might already be occupied by hominids.

The overall effect would be to produce kin-based communities, benefiting from a tendency towards larger size, but ultimately with limits on that size. Fission of male kin-bonded groups would in effect lead to a segmented lineage structure dispersed and dispersing across the region as a whole, and thus producing larger-scale networks of cultural groups, and a regional pattern of ethnic differentiation. An important element in this model is that it explains why there should be such regional and chronological variation in the appearance of what has been referred to as modern behaviour, or at least its archaeological manifestation. Art, 'symbolic behaviour', blade technology, and so on (such as those found in the European Upper Palaeolithic), are not so much manifestations of a radically different form of behaviour but of specific demographic and ecological conditions arising from the successful dispersals of the descendants of the middle and early Upper Pleistocene African hominid populations.

30 Kyr: demography and the agricultural revolution

A case may be made that the appearance of anatomically modern humans heralds the end of genetically-based evolution, and the Upper Palaeolithic the end of long term behavioural evolution. As it is clearly not the case that social evolution was terminated at these points, it may be that at this time models based on Darwinian evolution should be abandoned in favour of alternative ones drawing on theories derived from the social sciences. However, some suggestive observations can be made that might indicate that neo-Darwinian principles may still be of use in understanding more recent social evolution.

The first of these might be that the new chronology for the evolution of 'modern' human anatomy and behaviour brings the development of agriculture into a new relationship with these major evolutionary events. The orthodox chronology denotes hunting and gathering as a stable adaptation over periods of hundreds of thousands of years, if not millions, with agriculture as a short and recent aberration over the last 10 Kyr. However, if modern human behaviour is more recent in origin, then so too is what is generally referred to as the hunter-gatherer adaptive lifestyle—the suite of traits associated with small flexible bands of bilaterally related individuals, with a sexual division of labour and food-sharing (Foley 1988). More significantly, there will be considerable regional variation, with, for example, modern hunter-gatherers being present in Africa over a period of 100 Kyr, in Australia over perhaps 60 Kyr, and in Europe only 35 Kyr, while in the New World the figure may be less than 20 Kyr. These timescales undermine the major evolutionary contrast between hunting and gathering and agriculture.

In view of the fact that modern humans dispersed into most parts of the world during the late Pleistocene, and that these dispersals were repeated many times (including during the process of agriculture itself), it would appear that human demography over this period would have been far more dynamic than traditionally perceived. The shift from small mobile hunter-gatherer groups to larger and more sedentary farming communities should be seen as an interaction between the basic social structures described above as the adaptations and heritage of the last 100 Kyr, and the new and more packed demographic conditions.

This perspective has implications for considering the process of ecological intensification that occurs at the end of the Pleistocene in many parts of the world. It has traditionally been thought that hunter-gatherer adaptations are essentially homeostatic, with either dispersal or reduced fertility acting to keep populations within the level of carrying capacity. The apparent stability of hunter-gatherers over very long periods of time would be cited as evidence of this (Lee & DeVore 1968). However, under this new chronology for hunter-gatherers, in many parts of the world change seems to have been continuous, and intensification of foraging behaviour, sometimes leading to food production, occurs relatively rapidly after colonization. Elsewhere it has been argued (Foley 1988) agriculture can be considered as an evolutionary response to demographic constraint and declining resources. The economic innovations involved, with smaller territories, larger group size, and more control over resources by both males and females, would have acted to maintain the proposed ancestral social organization consisting of polygynous family groups linked by alliances of male kin organized patrilinealy. Ironically, hunter-gatherers, as we are able to observe them today, are very different socially from these earlier manifestations, and it is probable that the eclectic and flexible foraging systems they are able to employ in the resource depleted post-Pleistocene are only possible under novel social organization, albeit one modified from the ancestral conditions.

The implication is that the human phenomena of the late Pleistocene, including such elements as the development of larger social networks, intense use of art and symbols, and the development of agriculture itself, should be seen as an integral part of the dispersal of modern humans, and that the contrast in evolutionary terms between hunter-gatherers and agriculturalists should not be overestimated. In this light, modern hunter-gatherers may represent considerable economic conservatism, but more novel social structures, while agriculturalists have radically new economic systems but more conservative social organizations. That these also give rise to new reproductive and behavioural strategies—early weaning, larger group sizes—should be seen as a significant element of the human evolutionary heritage.

EVOLUTIONARY CONDITIONS AND THE EVOLUTION OF HUMAN SOCIAL BEHAVIOUR

The EEA and the chronology of human social evolution

The previous section outlined a chronology for the evolution of human social behaviour. It should be stressed that this chronology, while based on empirical evidence, must remain tentative given the nature of the data involved. It does, however, serve a number of purposes. First, it emphazizes that neither human social behaviour, nor the capacity for 'modern' behaviour, evolved as a single package, but was the result of combining new elements with ancestral conditions over extensive periods of time. The timescale for this is over the last 35 Myr, but even within the last 1 Myr and last 100 Kyr there is considerable chronological variation. Second, the nature of social evolution is, like any evolutionary process, additive; novel components are derived from existing ones, and also become combined with more ancient ones. In the case of human social evolution, for example, the social complexity observable today has arisen from building the catarrhine patterns of kin-bonding on the already existing anthropoid propensity for sociality. This accumulation of new elements, with interactions between ancient and modern elements giving rise to new behaviours, has continued throughout human evolution. A third implication is that while there is an evolutionary heritage to human behaviour, it is not unitary. Some elements are much older than others. In the chronology described here, for example, relationships between members of the same sex have remained more stable than relationships between the different sexes. Another suggestion might be that alliance and coalition structures are more conservative than mating tactics. Figure 3 summarizes the principal phylogenetic and chronological contexts for the evolution of human social behaviour.

A fourth aspect that should be emphasized is that a closer attention paid to chronology demonstrates that human evolution is made up of multiple events, and that there is no key trigger that forces the hominid lineage in an inevitable

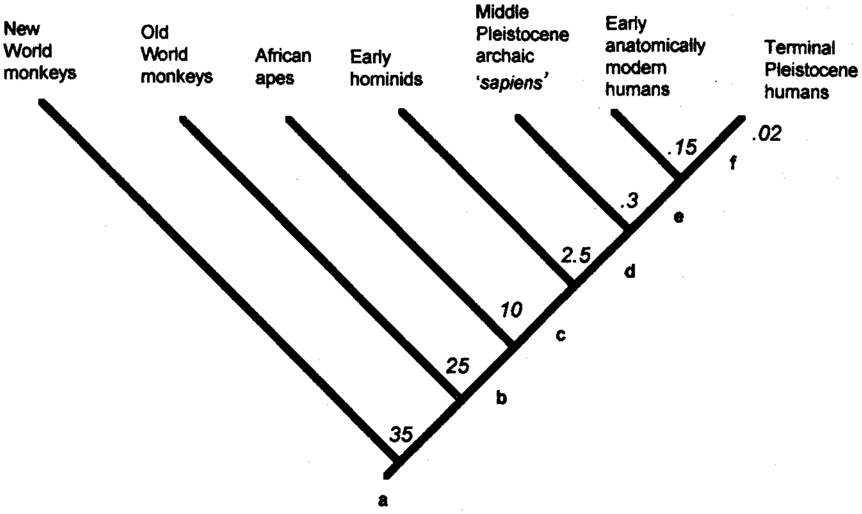

Figure 3. Cladogram showing the proposed points of evolution for key characteristics in the evolution of modern human social behaviour. Numbers indicate approximate age of branching events in millions of years. Letters indicate the evolution of the following characteristics: (a) compulsive sociality; (b) male residence patterns, small social units, and male kin-bonding; (c) increased parental effort and stronger male-female bonding; (d) modern human life history parameters and associated changes in maternal behaviour and longevity; language and more flexible use of technology may also have its origins at this point; (e) fission-fusion dispersal behaviour and inter-group competition; (f) adaptive responses to demographic crowding and resource depletion. See text for a full discussion.

direction leading to modern humans. Each event is the product of particular evolutionary, ecological and demographic interactions, the time and place of which are both significant and contingent. There is a strong and comprehensible adaptive basis for the evolution of human social behaviour, but this can only be analysed by paying attention to the context in which it has evolved.

There are a number of implications of this perspective; one of these relates to evolutionary psychology and the concept of the environment of evolutionary adaptiveness (EEA) (Symonds 1979). The EEA refers to the optimal environment to which humans are adapted. As such it is primarily taken to be the conditions that shaped human evolution. In practice the hunter-gatherer lifestyle has been assumed to be the human EEA, and by implication deviations from that lifestyle take humans into less optimal environments, and hence can lead to maladaptations, both physical and psychological. Reference to the chronological and phylogenetic context for the evolution of human behaviour shows that the EEA is by no means unitary. Different elements have different time depths, and by implication different mechanisms. In addition the social environment has evolved additively, and the various characteristics may also be treated partially at least as independent variables. Furthermore some traits may be very deeply embedded in human evolutionary history, while others are more ancient. Indeed, the phylogenetic context described here implies that many of these are shared with other primates. Finally, hunting and gathering is only one element of the human evolutionary environment, and other parts of our species' history, including denser and more settled agricultural communities, may be significant rather than just being aberrant developments.

The hominid paradox: male kin-bonding, expensive offspring and variation in life history strategy

One of the most important observations derived from the chronological and phylogenetic patterns described here is that the hominoid clade shows no tendency towards female kin-bonding. In particular, the African ape clade displays a trend towards female dispersal from their natal groups and the formation of kin-based male coalitions. On this evidence it has been argued that male kin-bonding may have been the basis for larger community structure during the course of hominoid evolution. The other major trend identified was towards the greater energetic costs of reproduction due to the larger brains. A shift towards higher quality food, especially meat, was identified as a mechanism underlying this, leading to associated reduced costs due to smaller guts. In addition, slower growth rates and delayed maturation appear to be related to the increase in brain size.

One response to high energetic costs on mothers is for females to recruit helpers. Allomothering is extensive among mammals, but Lee (1989) has shown that this occurs either under conditions of strong female dominance hierarchies, involving coercion and suppression of reproduction in some individuals, or else where females can recruit kin, especially female kin. The paradox of hominid evolution is that the context in which very expensive offspring have evolved is a social environment where females do not live in female kin-bonded groups, and therefore that their options for recruiting allomothers and helpers is limited. The major question that arises is how females have been able to cope?

Two strategies may be suggested. One is provisioning by males, and this has traditionally been seen as an important element in human evolution, the development of the pair-bond, close attachment between individual males and females, and food sharing. Leaving aside the question of the timing of such developments, the ethnographic evidence is ambiguous about the extent to which food is shared, especially between putative fathers and mothers. An alternative explanation is the evolution of more extended life history parameters.

One of the most striking things about human biology is the change in life history variables. Humans have slower growth rates, mature later, have long inter-birth intervals, and extended lifespans, although as Lee has pointed out, the difference from African apes has often been exaggerated. There is evidence that life history parameters are correlated with brain size (Harvey *et al.* 1987), with larger brains being associated with an extension of lifespan and slower and delayed rates of maturation. Smith (1989) has shown that this can be seen among primates in the context of dental development, and it also possible to see during the course of hominid evolution that as brain size increases, growth rates slow down (Smith 1993; Bromage & Dean 1985; Foley & Lee 1991; Foley 1995b).

This very marked departure from an ape life history baseline is perhaps the key to solving the paradox of human social evolution. With pressure on reproductive costs for females determined by selection for large brains, and in the absence of easily available female kin as allomothers, changes in life history in turn became the means by which the high costs of reproduction could be borne. The subsequent consequences in terms of parental behaviour, infant survivorship and demography, and social relationships in turn would have been significant, and acted as further selection for larger brains and more expensive offspring.

The interesting aspect of this link between social behaviour, in terms of the evolutionary heritage of male kin-bonded groups, and expensive offspring and the adaptive consequences for life history strategy, is that there is a further element of evolutionary heritage involved. When compared with cercopithecoids, hominoids display far more variation in body size and life history parameters. Cercopithcoids are far more conservative and homogeneous as a group in this context. Thus it could be argued that in undergoing evolutionary change in life history strategies in response to the selective pressures associated with large brains and complex sociality, the hominids were extending an evolutionary potential that had already occurred extensively within the Hominoidea.

A multiple event model for the evolution of modern humans

The central issue in palaeoanthropology over the last decade has been the origins of modern humans (Mellars & Stringer 1989; see Lewin 1993 for a review). This debate has been particularly useful in focusing research into the differences between archaic and modern humans, and avoiding simply treating other species of hominids as incipient modern humans. One element that has entered the literature as a result of this research effort has been the idea of a marked contrast between modern humans and archaic hominids, not just in terms of anatomy, but also behaviour (Binford 1989; Mellars 1996).

The success of the Recent African Origin model for *Homo sapiens*, which is linked to the notion of modern humans being something of a radical evolutionary departure, has brought with it a number of associated ideas. These ideas include the following: that there was a significant shift in biological and behavioural capacity and potential that occurred in a small population in Africa in the late middle Pleistocene; that there is a link between biological and behavioural change, and broad synchrony in these changes; that this resulted in a major adaptive shift, with descendants of the African populations (modern humans) being biologically, behaviourally, technologically and cognitively superior to archaic hominids; that this superiority led to rapid dispersals across the globe, and the displacement of non-modern populations such as the Neanderthals (Stringer & Gamble 1993); and that this dispersal is broadly associated with an Upper Palaeolithic technology and fully modern cognition and behaviour (Klein 1992); that this transformation from the archaic to modern is essentially a revolution ('the human revolution'), in which the differences between the two are discontinuous and more marked than differences between other hominid species (Mellars 1991); and that in contrast to the fully cultural behaviour of modern humans, archaic hominids lacked a number of key traits and the potential for modern behaviour. A number of different mechanisms have been proposed as the basis for the human revolution, of which language and symbolic thought (the symbolic explosion) are predominant (Mellars 1991; Knight *et al.* 1995).

The chronology presented here raises a number of serious doubts on the association of these components, principally due to the temporal spread of events (Lahr & Foley 1994). The genetically (mtDNA and Y chromosome) identified founder population in Africa probably existed in excess of 250 Kyr ago (Stoneking 1993; Dorit *et al.* 1995). The evolution of anatomically modern humans occurred between 150 and 100 Kyr, and indeed there is no clear anatomical boundary between archaic and modern; Lahr (1994) has shown that there is continual and regionally variable evolution in human cranial form over the period 100 to 10 Kyr. Behavioural change associated with the Upper Palaeo-lithic occurs no earlier than 45 Kyr, and then only in Europe and the Mediterranean. In Africa, Australia and East Asia there is no such transition, although it can be argued that the African Later Stone Age is functionally equivalent. However, by the time that the European Upper Palaeolithic was in place, the divergence of the main trajectories in human populations was already established. Events less than 50 Kyr, such as the so-called symbolic explosion in Europe, must be regionally specific, not universal or global human traits. Within Africa there are technological changes in the direction associated with the Upper Palaeolithic extending back almost to 100 Kyr, but these are ephemeral and firmly embedded in a

Middle Stone Age technology. Furthermore, dispersals occur throughout this period, such that the resulting geographical pattern is not a simple one of supplanting, but repeated demographic palimpsests with greater or lesser patterns of replacement. The result is that there is considerable genetic diversification occurring not just in early Upper Pleistocene, but in the terminal Pleistocene and Holocene.

The fact that the events associated with modern human origins are spread over more than 200 Kyr suggests that this is not a single revolutionary change. The chronology set out here implies three linked 'events'. The first of these is essentially biological and behavioural, occurring approximately around 300 Kyr, and is linked to the expansion of the brain and changes in life history strategy. It may also be associated with the development of Middle Stone Age technologies. This event probably also involves the successful dispersal of populations, most likely from an African source. Language may well have been present at this stage. The second is the evolution of anatomically modern humans, again in Africa, over a period of more than 50 Kyr. This evolution does not seem to be associated with any behavioural change, and indeed early modern humans are associated with the same Middle Stone Age technologies as Neanderthals and other archaics. However, by 100 Kyr these populations were also undergoing dispersals, not as a single expansion but as a series of multiple dispersals. The third is the regionally variable process of intensification and demographic flux that occurs after 30 Kyr, and continues through into the Holocene with the development of agriculture. It is this last phase that is associated with the rapid development of technology and the 'explosion' of symbolic life in some parts of the world.

In terms of the patterns of social evolution of concern here, this multiple event model does not imply any major transformation in the structure of human social organization in the late Pleistocene, nor necessarily in the cognitive abilities of the late Pleistocene humans. Rather any social evolution that occurred would be the transformation of the existing male kin-bonded systems in response to local demographic and ecological conditions.

CONCLUSIONS

This paper has set out to establish the evolutionary pathway to human social behaviour. I have argued that the best means of approaching this problem is to use the phylogenetic and palaeobiological context to establish a chronology of events, and that this chronology can then serve as the basis for exploring the functional and adaptive links between the various elements. In considering the available evidence it is clear that human social evolution has been the result of the addition of new traits successively. Many elements are shared with anthropoids, with other hominoids and with the African apes. The key elements identified here include the establishment of compulsive sociality among anthropoids (>35 Myr), the development of male kin-bonding in African apes (10–5 Myr), and the life history strategies evolved in response to expensive offspring in the course of the evolution of *Homo* (2–0.3 Myr).

This perspective undermines the notion that human social evolution is the result of a single trigger change, or that it is the product of highly improbable chance events. Instead I have stressed the fact that the pattern of hominid social evolution has been the consequence of specific contexts—demographic, biological, environmental and social—occurring at particular times and in particular places. The conjunction of specific ecological conditions with the phylogenetic heritage of apes and hominids has led to the evolution of the complex social behaviour, and its underlying cognitive skills, found in humans today.

Note. I thank P. C. Lee and M. M. Lahr for comments on an earlier draft of this paper.

REFERENCES

Aiello, L.C. & Dunbar, R.I.M. 1993: Neocortex size, group size and the origin of language in the hominids. *Current Anthropology* 34, 184–93.

Aiello, L.C. & Wheeler, P. 1995: The expensive tissue hypothesis. *Current Anthropology* 36, 199–222.

Binford, L.R. 1989: Isolating the transition to cultural adaptations: an organizational approach. In *The Emergence of Modern Humans: Biocultural Adaptations in the Later Pleistocene* (ed. E. Trinkaus), pp. 18–41. Cambridge: Cambridge University Press.

Bromage, T.G. & Dean, M.C. 1985: Re-evaluation of the age at death of Plio-Pleistocene fossil hominids. *Nature* 317, 525–528.

Brookes, A.S., Helgren, D.M. & Cramer, J.S. *et al.* 1995: Dating and context of three Middle Stone Age sites with bone points in the Upper Semliki Valley, Zaire. *Science* 268, 548–552.

Charles-Domique, P. 1977: *Ecology and Behaviour of Nocturnal Primates.* New York: Columbia University Press.

Clark, G.A. & Lindly, J.M. 1989: The case of continuity: observations on the biocultural transition in Europe and Western Asia. In *The Human Revolution* (ed. P. Mellars & C. Stringer), pp. 626–676. Edinburgh: Edinburgh University Press.

Dorit, R.L., Akashi, H. & Gilbert, W. 1995: Absence of polymorphism at the ZFY locus on the human Y chromosome. *Science* 268, 1183–5.

Dunbar, R.I.M. 1988: *Primate Social Systems.* London: Croom Helm.

Dunbar, R.I.M. 1992: Neocortex size as a constraint on group size in primates. *Journal of Human Evolution* 22, 469–493.

Foley, R.A. 1987a: *Another Unique Species: Patterns in Human Evolutionary Ecology.* London: Longman.

Foley, R.A. 1987b: Hominid species & stone tools assemblages: how are they related? *Antiquity* 61, 380–392.

Foley, R.A. 1988 Hominids, humans & hunter-gatherers: an evolutionary perspective. In *Hunters and Gatherers 1: History, Evolution and Social Change* (ed. T. Ingold, D. Riches & J. Woodburn), pp. 207–221. Oxford: Berg.

Foley, R.A. 1989: The evolution of hominid social behaviour. In *Comparative Socioecology: the Behavioural Ecology of Humans and Other Mammals* (ed. V. Standen & R. Foley), pp. 474–493. Oxford: Blackwell Scientific Publications.

Foley, R.A. 1993: The influence of seasonality on hominid evolution. In *Seasonality and Human Ecology* (ed. S.J. Ulijaszek & S. Strickland), pp. 17–37. Cambridge: Cambridge University Press

Foley, R.A. 1995a: The causes and consequences of human evolution. *Journal of the Royal Anthropological Institute* 1, 67–86.

Foley, R.A. 1995b: The evolution and adaptive significance of human maternal behaviour. In *Human and Non-Human Primate Mothers: an integrated approach* (ed. C. Pryce, R.D. Martin, & D. Skuse,), pp. 27–36. Zurich: Karger.

Foley, R.A. and Lee, P.C. 1989: Finite social space, evolutionary pathways and reconstructing hominid behaviour. *Science* 243, 901–6.

Foley, R.A. & Lee, P.C. 1991: Ecology and energetics of encephalization in hominid evolution. *Philosophical Transactions of the Royal Society, London* Series B 334, 223–232.

Gamble, C. 1993: *Timewalkers*. London: Allen Lane.

Galdikas, B. 1985: Orangutan sociality at Tunjung Puting A. *Journal of Primatology* 9, 101–19.

Harvey, P.H., Martin, R.D. & Clutton-Brock, T.H. 1987: Life histories in comparative perspective. In *Primate Societies* (ed. B.B. Smuts, D.L. Cheney, R.M. Seyfarth, R.W. Wrangham & T.T. Struhsaker), pp. 181–196. Chicago: University of Chicago Press.

Hinde, R.A. 1976: Interactions, relationships and social structure. *Man* 11, 1–17.

Humphrey, N.K. 1976: The social function of intellect. In *Growing Points in Ethology* (ed. P.P.G. Bateson & R.A. Hinde), pp. 303–317. Cambridge: Cambridge University Press.

Jolly, A. 1984: *The Evolution of Primate Behaviour* (2nd Ed.). New York: MacMillan.

Kay, R. & Fleagle, J. 1994: *Anthropoid Origins*. New York: Plenum.

Keverne, E.B. 1995: Neurochemical changes accompanying the reproductive process: their significance for maternal care in primates and other mammals. In *Human and Non-Human Primate Mothers: an integrated approach* (ed. C. Pryce, R.D. Martin, & D. Skuse) pp. 69–79. Zurich: Karger.

Klein, R.G. 1992: The archaeology of modern human origins. *Evolutionary Anthropology* 1, 5–15.

Knight, C., Power, C. & Watts, I. 1995: The human symbolic revolution: a Darwinian account. *Cambridge Archaeological Journal* 5, 75–114.

Lahr, M.M. 1994: The multiregional model of modern human origins: a reassessment of its morphological basis. *Journal of Human Evolution* 26, 23–56.

Lahr, M.M. 1996: *The Evolution of Human Diversity*. Cambridge: Cambridge University Press.

Lahr, M.M. & Foley, R.A. 1994: Multiple dispersals and the origins of modern humans. *Evolutionary Anthropology* 3, 48–60.

Lee, P.C. 1989: Family structure, communal care and female reproductive effort. In *Comparative Socioecology: the Behavioural Ecology of Humans and Other Mammals* (ed. V. Standen & R. Foley), pp. 323–340. Oxford: Blackwell Scientific Publications.

Lee, P.C. 1994: Social structure and evolution. In *Behaviour and Evolution* (ed. P.J.B. Slater & T.R. Halliday), pp. 266–303. Cambridge: Cambridge University Press.

Lee, R.B. & DeVore, I. 1968: Problems in the studies of hunters and gatherers. In *Man the Hunter* (ed. R.B. Lee & I. DeVore), pp. 3–12. Chicago: Aldine.

Leonard, W.R. & Robertson, M.L. 1992: Nutritional requirements and human evolution: a bioenergetics model. *American Journal of Human Biology* 4, 179–195.

Lewin, R. 1993: *The Origin of Modern Humans*. Washinton, DC: Smithsonian Institution.

Martin, R.D., Chivres, D.J. & MacLarnon, A. 1985: Gastrointestinal allometry in primates and other mammals. In *Size and Scaling in Primate Biology*, pp. 61–89. New York: Plenum.

McGrew, W.C. 1992: *Chimpanzee Material Culture*. Cambridge: Cambridge University Press.

McHenry, H. 1992: How big were early hominids? *Evolutionary Anthropology* 1, 15–20.

Mellars, P. 1991: Cognitive changes and the emergence of modern humans in Europe. *Cambridge Archaeological Journal* 1, 63–76.

Mellars, P.C. 1996: *The Neanderthal Legacy*. Princeton NJ: Princeton University Press.

Mellars, P. & Stringer, C. (eds) 1989: *The Human Revolution*. Edinburgh: Edinburgh University Press.

Rendall, D. & Difiore, A. 1995: The road less travelled: phylogenetic perspectives in primatology. *Evolutionary Anthropology* 4, 43–52.

Rightmire, G.P. 1981: Patterns in the evolution of *Homo erectus*. *Paleobiology* 7, 241–246.

Ruff, C. & Walker, A.C. 1993: Body size and shape. In *The Nariokotome Skeleton* (ed. A.C. Walker & R.E. Leakey), pp. 234–265. Cambridge: Harvard University Press.

Schick, K. & Toth, N. 1993: *Making Silent Stones Speak*. New York: Simon and Schuster.

Smith, B.H. 1989: Dental development as a measure of life history in primates. *Evolution* 43, 683–688.

Smith, B.H. 1993: The physiological age of WT15000. In *The Nariokotome Skeleton* (ed. A.C. Walker & R.E. Leakey), pp. 195–220. Cambridge: Harvard University Press.

Smuts,B, Seyfarth, R. & Cheney, D. *et al.* 1987: *Primate Societies*. Chicago: Chicago University Press.

Stoneking, M. 1993: DNA and recent human evolution. *Evolutionary Anthropology* 2, 60–73.

Stringer, C. & Gamble, C. 1993: *In Search of the Neanderthals*. London: Thames and Hudson.

Susman, R.L., Stern, J.T. & Jungers, W.L. 1985: Locomotor adaptations in the Hadar hominids. In *Ancestors: the Hard Evidence* (ed. E. Delson), pp. 184–192. New York: Alan Liss.

Symonds, D. 1979: *The Evolution of Human Sexuality*. Oxford: Oxford University Press.

White, F. and Wrangham, R.W. 1988: Feeding competition and patch size in the chimpanzee species *Pan paniscus* and *Pan troglodytes*. *Behaviour* 105, 148–163.

Williams, S.A. & Goodman, M. 1989: A statistical test that supports a human/chimpanzee clade based on non-coding DNA sequence data. *Molecular Biology and Evolution* 2, 338–346.

Wrangham, R.W. 1979: On the evolution of ape social systems. *Social Science Information* 18, 335–68.

Wrangham, R.W. 1980: An ecological model of female bonded primate groups. *Behaviour* 75, 262–300.