The Biology of the Colonizing Ape

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ABSTRACT Hominin evolutionary history is characterized by regular dispersals, cycles of colonization, and entry into novel environments. This article considers the relationship between such colonizing capacity and hominin biology. In general, colonizing strategy favors rapid rates of reproduction and generalized rather than specialized biology. Physiological viability across diverse environments favors a high degree of phenotypic plasticity, which buffers the genome from selective pressures. Colonizing also favors the capacity to access and process information, and the ability to create and modify the environment. We propose that early hominin adaptive radiations were based upon the development of such capacities as adaptations to unstable Pliocene environments. These components came together, along with fundamental changes in morphology, behavior, and cognition in the genus Homo, who exploited them in subsequent wider dispersals. Middle Pleistocene hominins and modern humans also show development of further traits, which correspond with successful probing of, and dispersals into, stressful environments. These traits have their precursors in primate or ape biology, but have become more pronounced during hominin evolution. First, short interbirth intervals and slow childhood growth allow human females to provision several offspring simultaneously, increasing the rate of reproduction in favorable conditions. This allows rapid recovery from population crashes, or rapid population growth in new habitats. Second, despite high geographical phenotypic variability, humans have high genetic unity. This is achieved by a variety of levels of plasticity, including physiology, behavior, and technology, which reduce the need to commit to genetic adaptation. Hominin behavior may increasingly have shaped both the ecological niches occupied and the selective pressures acting back on the genome. Such selective pressures may have been exacerbated by population dynamics, predicted to both derive from, and favor, the colonizing strategy. Exposure to ecological variability is likely to have generated particular selective pressures on female biology, favoring increasing steering of offspring ontogeny by maternal phenotype. We propose that the concept of hominins as “colonizing apes” offers a novel unified model for interpreting the suite of traits characteristic of our genus. Yrbk Phys Anthropol 50:191–222, 2007.

The tendency of humans and their ancestors to disperse, migrate, and colonize new habitats and territories is well-known to academics of many disciplines. Paleontologists, archeologists, anthropologists, geographers, and historians have accumulated considerable evidence of the extent to, and the manner in, which individuals and populations have moved and interacted (Villaflor and Sokoloff, 1982; Clark, 1986; Mascie-Taylor and Lasker, 1988; Anthony, 1990; Gamble, 1993; Robinson, 1996; Diamond, 1987, 1998; Lahr and Foley, 1994, 1998; Kingdom, 2001; Shennan, 2002). The movement of individuals is one of the principal forces of evolution, along with natural selection, mutation, and genetic drift, and hence has been of major interest to population geneticists (Fix, 1999). Such dispersals may also be considered within a broader biological context (Baker, 1978; Chepko-Sade and Halpin, 1987; Dingle, 1996; Cobert et al., 2001).

Many authors emphasize two major migrations in human evolution—the dispersals of Homo erectus and anatomically modern Homo sapiens, both from Africa. These are merely the most large-scale migrations among a continuum of population movements within and between specific regions, habitats, and territories, which occurred throughout hominin evolution, commencing with the emergence of hominins and the subsequent adaptive radiation of Australopithecines. Contrasting with this evolutionary history, it is important to note that most ethnographies of contemporary or recent populations record low levels of population movement. Contemporary human populations tend to be relatively philopatric, where migration concerns only short range marital movements (Fix, 1999). Regional warfare or economic hardship within an increasingly globalized human community are important contemporary factors promoting periodic dispersals over longer distances; however, these concern movements between territories already populated. In themselves, therefore, modern population movements have limited capacity to inform about any broader tendency to colonize and its contribution to our biology.

Dispersal is one of a range of strategies whereby organisms can improve their environmental conditions, in terms of food supplies, access to mates, and the risk of predation (Fix, 1999). One challenge is that there has never been a single “real” population structure of humans. Rather, population structure and movement are just one more way in which humans adapt to the broader environment (Fix, 1999). The movement of DNA between gene pools, and the penetration of gene pools into novel environments, have therefore been consistent features of hominin evolution, although their relative influences may have fluctuated over time. Such adaptive strategies in turn are subject to constraints that limit the regional and total availability of...
resources. As predicted by Malthus (1798/1976), populations tend therefore to grow, spread, decline, or contract over time, according to the availability of resources.

Diamond (1987) noted that humans are similar to many other species in undergoing cycles of colonization, while Foley (1987) considered hominin colonization within the broader context of mammalian and geophysical trends, and suggested that successful colonization would be favored by both the retention of generalist physiological traits, and the evolution of behavioral and cultural practices aiding adaptation to novel environments. Lahr and Foley (1998) further emphasized the importance of dispersals in the recent evolutionary history of the genus Homo. The term “colonizing ape” was applied to humans by Hill and Hurtado (1996) following their detailed demographic analysis of the Ache, a foraging population from Paraguay. Gamble (1993) considered humans and their ancestors as “timewalkers” continually encountering new habitats, while Shennan (2002) reviewed the implications of population expansions and crashes for interpreting the archaeological record. These authors have all addressed the fundamental role of colonization in human evolution and history. However, despite such awareness among paleoanthropologists and archeologists that humans are and have been colonizers, it can be argued that few human biologists have appreciated the extent to which “getting there” is as relevant to our biology as “being there.”

The terms of colonization and dispersal are prevalent in the genetics, archeological, and paleoanthropological literature. In contrast, the aim of this review is to consider contemporary issues in human biology within the integrative framework of colonization, and to examine the extent to which hominins and humans fit the profile of “colonizing apes.” The second section offers a brief review of the migratory history of apes and hominins. In the third section, the broad biology of colonization is described, to provide a template against which hominin and human biology can be compared. The next section describes hominin life history and population dynamics, while the final section reviews evidence for the hypothesis that, relative to apes, humans have traits that improve the capacity to colonize.

**THE HISTORY OF DISPERSALS IN THE HOMININE LINEAGE**

Dispersals and adaptive radiations have characterized hominin evolution in its entirety (Foley, 2002). They have arisen both as habitat ranges have expanded and contracted in relation to climatic variability, and through the exploitation of novel environmental niches (Lahr and Foley, 1998). Increasing environmental fluctuation throughout the Pliocene and Pleistocene has been highlighted as a major factor in the evolution of the hominin lineage by selecting for species to be able to accommodate environmental variability and exploit a diversity of environments (Foley, 1987; Potts, 1998a). Recent literature is replete with characterizations of hominin dispersal events as Out of Africa 1 and 2 models, referring to dispersals of Homo erectus and modern Homo sapiens, respectively.

*While recent usage has favored the distinction between Homo ergaster from Africa and Homo erectus from east Asia, we will use Homo erectus (sensu lato) as a generic term to include both Asian and African variants. This simplifies the discussion and allows the focus to be placed on biological characteristics related to the capacity for dispersal within this grade of hominins, rather than taxonomic issues associated with relationships between fossils.*

Although the pattern of hominin dispersal throughout the last 1.8 million years is likely to be more complex than these characterizations would suggest. Regardless, there is little doubt that recent human populations have colonized novel environments on a scale not seen in earlier species, and that this proposition is not an artifact of fossil preservation. While these patterns of hominin dispersal would merit several reviews in themselves, the aim here is only to identify the main events and protagonists, to provide a foundation for discussion of the biological and behavioral factors, which underpin these dispersals.

**Primates and apes**

Significant movement of species between continents and ecological zones is not unknown for nonhuman primate species. Hamadryas baboons have crossed a land bridge at the Bab el Mandab strait between Africa and Arabia on a number of occasions over the past several hundred thousand years (Winney et al., 2004). While this highlights intercontinental dispersals among a primate species, environmental conditions in Arabia and East Africa would have been relatively consistent with one another, even if there were fluctuations in time. There is also evidence for dispersal events amongst apes. Although extant apes exist only within Africa and southeast Asia, where Miocene fossil apes are scarce, there is abundant fossil evidence for apes within Eurasia during the Miocene (Begun, 2002). Phylogenetic analyses of Miocene apes suggest that the common ancestor of hominins and extant African apes was Eurasian (Begun, 1997, 2000; Stewart and Disotell, 1998), which indicates a minimum of two dispersal events of Miocene apes between Africa and Eurasia. These appear to have been associated with the dispersal of other mammalian taxa including carnivores (Nargolwalla and Begun, 2005; Folinsbee and Brooks, 2007), and thus to be based upon movements within relatively consistent ecological niches, following patterns observed in other mammals, while drying conditions in sub-Saharan Africa led to extinctions (Begun et al., 2003).

**Early hominin species**

Late Miocene and early Pliocene hominin origins can be considered as the beginning of an adaptive radiation, possibly based upon the origins of bipedalism, which may have followed shortly after a Eurasian dispersal of apes into Africa (Foley, 2002). Of key importance at this time is not a dispersal event per se, but the evidence that new phenotypic traits within the emergent hominin lineage corresponded with a general trend toward more xeric conditions and ecologically diverse habitats. Climatic oscillations that occurred both on seasonal scales and within the lifespan likely defined the selective environments of hominins (Foley, 1987), but such variability may have been important across a broader temporal scale. Potts (1985a,b) proposed the term Variability Selection to refer to the selection of characteristics, which favored the ability of hominins to exploit a range of habitats across major longer term climatic fluctuations. In this model, the capacity for adaptive versatility evolves when there are large inconsistencies in selective conditions. Such a mechanism could operate on the shorter time scales proposed by Foley, which would correspond to selective pressure within the lifespan rather than across generations. From the late Miocene through the Pleistocene, environmental variability was increasing from seasonal to multimil-len-
nial time scales (Foley, 1987; Potts, 1998a). This resulted in increasing fragmentation of ecological niches, which would have emphasized local selective pressures on organisms and evolutionary novelty. In this context, ape species could either maintain a general frugivore adaptive strategy within the reducing areas of rain forest, or exploit the new and expanding savannah habitat (Foley, 1987).

Ancestral chimpanzees and gorillas appear morphologically similar to contemporary species (McBrearty and Jablonski, 2005; Sonda et al., 2007) suggesting similar adaptive niches to contemporary representatives of the species. Proposed early hominin species such as Sahelanthropus tchadensis (Brunet et al., 2002), Orrorin tugenensis (Senut et al., 2001), and Ardipithecus ramidus (White et al., 1994) are found in a range of habitats. However, fossil chimpanzee remains from the Kapurthin formation in the Rift Valley system place middle Pleistocene chimpanzees beyond their current distribution and contemporary with early Homo or Homo erectus (McBrearty and Jablonski, 2005). Although the origin of bipedalism is often interpreted as a response to increasing resource patchiness and expanding grassland in a mixed woodland savanna environment, it is difficult to determine whether individual species are associated with multiple habitat types due to the time averaging effect of many fossil assemblages. However, the data available suggest that late Miocene and early Pliocene species filled different adaptive niches within the hominin adaptive radiation, including forest, woodland, savanna, and mosaic habitats (Reed, 1997; Potts, 1998a). It is therefore likely that the foundation of hominins’ tendency to colonize can be traced to early hominins and Australopithecus, whereby populations entered new and unstable environments, which in turn imposed localized selective pressures. When previously separated populations encountered each other, each species is likely to have formed a component of the selective pressures acting on the other.

While the adaptive radiation of hominins provides the basis for the exploitation of a range of habitats in the human lineage, it is often assumed that this would be related to an increase in home range. Recent evidence for very large home range sizes (>63 km²) and the exploitation of a variety of ecological niches amongst the mosaic savanna chimpanzees at Fongoli (Pruetz and Bertolani, 2007) provides corroborative evidence that similar patterns of diverse habitat exploitation would likely have resulted in greater home ranges amongst early hominins.

**Early Homo**

The location of the origin of the genus Homo, and the taxonomy of early Homo remain controversial. Although the earliest evidence for fossils typically assigned to the genus Homo date between 2.6 and 2.4 MYA (Wood and Collard, 1999a), some now regard Homo erectus grade hominins, whose earliest appearance is about 1.89 MYA in Eastern Africa, as the first convincing member of the genus (Wood and Collard, 1999b). The predominant view of the relationship between African, Eurasian, and East Asian Homo erectus is described by the “longer chronology” Out of Africa 1 model (Antón and Swisher, 2004). This model suggests that Homo erectus evolved within Africa, and rapidly dispersed to Eurasia, by 1.7 MYA at Dmanisi, Georgia (Gabunia et al., 2000) and Indonesia, by as early as 1.8 MYA (Swisher et al., 1994).

Several assumptions central to the longer chronology Out of Africa 1 model have been challenged. The lack of both a clear ancestor of Homo erectus and diagnostic craniodental material amongst early larger bodied postcranial remains tentatively assigned to the taxa (McHenry and Coffing, 2000) remain problems. Others have suggested that Asia is a plausible alternative source of the evolution and dispersals of Homo erectus (Dennell and Roebroeks, 2005), although there is a current lack of fossil evidence to support this hypothesis. However, what is relevant to the current review is that there is unequivocal evidence for a large-scale intercontinental dispersal preceding or following the emergence of Homo erectus, regardless of its point of origin. A rapid emergence and dispersal of Homo erectus is not implausible. Other mammal species are known to have evolved rapidly in response to a novel niche, and Homo erectus may have undergone a similar process (Kingdon, 2001) in response to dramatic aridification at around 1.8 MYA (Wynn, 2003). At this time, an ecological zone of savanna and steppes stretched from Eastern and Northern Africa through the Levant and central Asia (Dennell, 2003). While early Homo erectus fossils from eastern Africa and Dmanisi were found within this environmental context, those from Indonesia and Eastern Asia were clearly associated with forest environments.

The early Pleistocene dispersal of Homo erectus was achieved using Oldowan (Mode 1) lithic technology (Antón, 2003), which has a deep chronology within Africa (Semaw et al., 2003). By 1.5 MYA, a more advanced Mode 2 Acheulean technology developed and is subsequently found associated with Homo erectus in the Middle East and Europe, but its distribution did not extend fully into Asia (Antón, 2003). As such, lithic technology appears to have played little role in the early dispersal of Homo, which suggests that other mechanisms may have been important to the evolution of the colonizing strategy.

Current perspectives attribute the dispersing capabilities of Homo to a more complete adaptation to the savannah niche, in contrast to ancestral species that were more suited to forest margin niches. The dramatic shift toward grassland habitats offered more niches for terrestrial fauna, including both herbivores and their predators (Antón, 2003). Homo erectus may have followed a general dispersal of mammalian fauna from Africa (Turner, 1994; Antón et al., 2002). A shift to dependence upon carnivory through hunting may have helped Homo erectus capitalize on the dispersal of suitable prey species and may have been a central component of the dispersal of this species (Foley, 2002). Thus, climate change together with the generalized Homo physique and biology (see below) could have allowed the continued expansion of territory and occupation of new locations by descendant groups. Antón et al. (2002) developed a model of Homo erectus colonization in which increased diet quality and body size are shown to result in both larger estimated home range size and greater rates of dispersal, when compared to living primates and earlier hominins. They view environmental conditions, such as habitat connectivity and biomass distribution, as fundamental to driving this shift, both in terms of the direct influence of changing resource distribution on population movements, but also through changing patterns of foraging behavior, a shift to higher quality foods, and possibly technology. Increased brain size may have further contributed to the capacity to exploit such ecological changes through associated improvements in cognitive flexibility.
Dispersals out of Africa may have taken advantage of fluctuating environmental conditions, which opened a northern route of dispersal through the Levant during interglacials, allowing a migration of African fauna into Eurasia (Thernov, 1992). Conversely, if dispersals followed a southern route across the Bab al Mandab Strait, and along the coasts of Arabia and South Asia to Australia, marine resources would have been the key behavioral adaptation enabling this migration (Foley and Lahr, 1992; Lahr and Foley, 1994; Stringer, 2000). These models have importance beyond their geographic implications, as a northern dispersal may have been correlated with faunal movements, while the southern route is clearly dependent upon behavioral innovation through a shift toward marine resource exploitation. While archeological evidence to test these models is sparse, mtDNA among contemporary Asian and Australasian populations has unique derived lineages of the M, N, and R haplogroups, which coalesce between 70 and 50 KYA (Quintana-Murci et al., 1999; Macaulay et al., 2005; Thangaraj et al., 2005). The northern dispersal route was inhospitable at this time (Van Andel and Tzedakis, 1996), lending indirect support for the southern dispersal hypothesis.

Closely related to the pattern of dispersals is the issue of ancestral bottlenecks arising due to local extinctions. Genetic analyses indicate an early bottleneck in the population ancestral to all contemporary humans between 200 and 130,000 years ago, with a population size as low as around 10,000 individuals (Rogers, 1995; Rogers and Jorde, 1995; Takahata et al., 1995); however, this was followed by significant expansion of population size between 80 and 60,000 years ago (Mellars, 2006b), resulting in a degree of population subdivision prior to evidence for the primary dispersals out of Africa (Harpending et al., 1993; Rogers and Jorde, 1995).

Dispersals also spread northward through the eastern Asian continent, supported by genetic variability in southern compared to northern Chinese populations (Jin and Su, 2000). Although Paleolithic populations might also have spread eastward from the Levant area into Asia, genetic contributions from this source appear to be relatively minor (Kivisild et al., 1999). The chronology of human dispersals into the Americas remains controversial, as the traditional interpretation that all populations in the New World derived from early and/or successive migrations from northeast Asia are challenged by evidence that paleoamericans may have originated from South Asia or the Pacific rim, followed by subsequent replacement by migrations from northeast Asia (Neves et al., 1999; Gonzalez et al., 2003).

The pattern of dispersal of modern humans has clearly influenced human diversity, because of local selective environments, the history of colonization, and subsequent local isolations (Lahr, 1996; Lahr and Foley, 1998). This would increase intergroup differences, a hypothesis supported by regional variability in local assemblages in the archeological record (Phillipson, 2005; Klein, 1999), and global patterns of morphological variability (Stock et al., 2007). Overall, genetic evidence is consistent with at least two primary dispersals out of Africa (Johling et al., 2004), and a series of subsequent dispersals from these initial lineages. This produced considerable genetic diversification (Watson et al., 1997), some of which has been negated by more recent gene flow (Lahr, 1996).

These dispersals equate to substantial and continual entrance into new ecological niches, even taking into account the transitional species, intermediate between species is a challenging issue, illustrated by the difficulty of linking Homo erectus with both Homo sapiens and Neanderthals in Europe (Lahr and Foley, 1998). Most authors now recognize a transitional species, Homo heidelbergensis (Groves, 1994), which may have evolved either in Africa or Europe. Lahr and Foley (1998) recognize a further transitional species, intermediate between heidelbergensis and sapiens, Homo helmei. There is biogeographical evidence that contact between African and Eurasian biomes occurred regularly through glacial cycles, promoting a number of dispersal events in human evolution. Despite open questions about the taxonomic relationships of species, it is clear that by the middle Pleistocene (ca. 780 KYA), hominins were in temperate regions of Europe (Carbonell et al., 1995; Bermúdez de Castro et al., 1997; Manzi et al., 2001). While fossil evidence is sparse, there is lithic evidence for occupation of northern latitudes by 700 KYA (Parfitt et al., 2005).

This evidence for the colonization of Europe and northern latitudes raises important questions concerning the technological and biological characteristics associated with this dispersal. There is clear evidence for the controlled use of fire in northern Europe by 400 KYA, associated with Homo heidelbergensis (Gowlett, 2006) suggesting that such technological innovation, if not associated with the dispersal of this species (Foley, 2002), was at least necessary for the colonization of northern latitudes. It has traditionally been argued on the basis of archeological assemblages that a heavy reliance upon meat was an integral part of Neanderthal technical and physiological adaptations (Mellars, 2004), an interpretation supported by isotopic evidence (Richards et al., 2000b).

Middle Pleistocene Homo

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Anatomically modern Homo sapiens

Fossil, genetic, and archeological evidence points to a recent African origin of modern humans (Howells, 1976; Day and Stringer, 1982; Stringer and Hublin, 1984; Lahr and Foley, 1994, 1998; Lahr, 1994), with the common ancestor dating from ~150 to 200 KYA (Cann et al., 1987; Tishkoff et al., 1996; Harpending and Rogers, 2000; Ingman et al., 2000; Ke et al., 2001; Kivisild et al., 2001; Excoffier, 2002). The earliest modern human fossils from Omo Kibish, and Herto date between 200 and 120 KYA (Day, 1969; Day and Stringer, 1982, 1991; Lahr, 1996; White et al., 2003; McDougall et al., 2005). Evidence for the first dispersal of modern humans out of Africa places them in the Levant by 100–90 KYA (Bar-Yosef et al., 1986; Stringer et al., 1989; Stringer, 1992; Mercier et al., 1993; Turton et al., 1997; Holliday, 2000), although there is no strong fossil evidence for subsequent dispersals until after ~60 KYA. Modern humans colonized Europe between 46 and 41 KYA (Mellars, 2006a), while early modern human remains have been identified in Southeast Asia as early as 44 KYA at Niah Cave (Barker et al., 2002). Humans may have occupied Australia by 62 KYA (Thorne et al., 1999), but are more conservatively dated to 50 KYA at Lake Mungo (Bowler et al., 2003). These remains help to place minimum time estimates on the pattern of modern human dispersal, which may be extended in some regions if we associate microlithic technologies with anatomically modern humans (James and Petraglia, 2005).
account that populations are initially likely to have followed “corridors” of favorable geography, climate, and fauna. As humans settled in an increasing proportion of the world’s land masses, exploratory or invasive dispersals would have been accompanied or replaced by cultural diffusion of subsistence practices. Although such information transfer could have involved many aspects of technology and behavior, the most important in terms of shaping human biology and environmental interactions is the spread of agriculture. There has been considerable debate as to whether the Neolithic spread of agriculture into Europe was due to demic diffusion of Near Eastern farmers or cultural diffusion. Genetic evidence suggests that only one-fifth of contemporary mtDNA can be attributed to Neolithic farmers (Sykes, 1999), while most lineages within Europe can be traced back to Upper Paleolithic migrations from the Near East (Richards et al., 2000a). Similar patterns of genetic continuity from Paleolithic dispersals have been found in Australia (Pellekaan et al., 2006) and South Asia (Macaulay et al., 2005). While there is evidence for relatively recent large scale population movements in many areas of the world, for example the Bantu expansions in sub-Saharan Africa (Pereira et al., 2001), initial patterns of dispersal out of Africa were of fundamental importance in shaping the biological diversity found within the human species today.

**Summary**

Hominin evolution is very much a story of adaptive radiations, dispersals, colonization, and local extinctions resulting in population expansions and contractions (Lahr and Foley, 1998). Intercontinental dispersals of Miocene apes appear to have exploited similar forest niches. Increasing environmental variability across spatial and temporal scales played a key role in both extinction events and the selective landscape, which drove the adaptive radiations of early hominins (Foley, 1987; Potts, 1998b). The exploitation of varied niches appears to have been a component of the success of the dispersal of *Homo erectus* and possibly other early *Homo* species. However, behavioral, social, and technological innovations enabled the colonization of a wider range of environments and niches in the Middle and Upper Paleolithic (Lahr and Foley, 1988), augmenting the scale and success of dispersals into more diverse environments, including northern latitudes.

**THE BIOLOGY OF DISPERSAL AND COLONIZATION**

This section provides a broad summary of the biology of dispersal, against which hominins and humans can be evaluated. It is first necessary to clarify several related terms. Gamble (1993) distinguished migration (a discrete short-term movement), dispersal (a more general process still small-scale in time and space), and colonization (a process occurring on a larger temporal and geographic scale). Using these definitions, colonization is merely dispersal systematically enacted on a broader scale (Gamble, 1993). Migration is a term commonly applied to human population movements, and yet is inappropriate as a broader model: when a population expands its range on a large scale, individual organisms may move only short distances. This review uses Gamble’s terminology and focuses on colonization. However, any evaluation of the process of colonization requires understanding of the general biology of dispersal. Unlike seasonal migrations, or the movement of individuals between social groups, one-way population movements into new territories or niches predispose to unpredictable environments (Dingle, 1996). It is the greater risk inherent in dispersal as opposed to small-scale migration that underpins its effects on biological traits.

**Why disperse?**

Dispersal has been described as a process across a landscape characterized by opportunities and risks (Wiens, 2001). Relevant factors include the state of both environment and organism. Risks during dispersal may be greater than those in the old environment, while the new environment may also hold many unknowns. Dispersal should be favored when the benefits of entering and colonizing new habitats exceed the costs of migrating and adapting to the new environments (Baker, 1978). Several contexts are relevant to these costs and benefits.

Organisms can be assumed to select habitats to maximize fitness, a concept known as the ideal free distribution (Fretwell and Lucas, 1970) where individuals in different habitats would have equal average fitness. However, conspecific competition favors dispersal to exploit new resources, such that those displaced from the optimum environment may have poorer fitness (Fretwell, 1972). Conspecific competition merges into kin competition when dispersal results in relatives being aggregated in space. Even in stable habitats, avoidance of kin competition favors dispersal (Hamilton and May, 1977), and genetic studies reveal high levels of heterozygosity within primate social groups (Pusey and Packer, 1985).

Bet-hedging refers to a scenario where strategies for avoiding penalties in bad conditions are favored over strategies for maximizing fitness in good conditions (Philipi and Seger, 1989). This can be achieved either by reducing variance in fitness over generations, or by increasing phenotypic expression of a single genotype among individuals within generations (Philipi and Seger, 1989). The enforced dispersal of offspring represents parental bet-hedging, since it distributes risk across environments with different selective pressures (Den Boer, 1968; Ronce et al., 2001).

**r- and K-reproductive strategies**

Organisms’ reproductive strategies are conventionally evaluated on a continuum (May and Rubenstein, 1984). At one extreme are opportunistic r-strategists, with high rates of reproduction but short life spans. They disperse widely and do not necessarily persist in a given environment, but breed rapidly in favorable conditions. Local extinctions are common, but the “hit and run” strategy remains successful because dispersal and fast turnover rate allow rapid exploitation of new environments. Such organisms produce large numbers of offspring but invest minimally in each one (May and Rubenstein, 1984).

At the other extreme are K-strategists, which tend to occupy more stable environments with reduced mortality.
risk, allowing the benefits of increased size to be realized. However, larger organisms require relatively more resources and must compete with conspecifics, both for themselves and for their offspring. K-strategists therefore grow and reproduce more slowly, and reproductive rate is sensitive to population density. Species persist in a given area, to which they become specialized, and disperse slowly to other areas. Organisms adopting this strategy produce few offspring at a slow rate, but invest considerable parental effort in each one. In practice, few species fall at the extremes of the r–K continuum, and many can merely be placed nearer one or other ideal (May and Rubenstein, 1984). More generally, the K-concept has been criticized (Hawkes, 2006a), but the notion that organisms vary in life-cycle “pace,” and that body size is strongly associated with life-history variables, is not contested (Hawkes, 2006a).

Although humans are often portrayed as K-strategists *par excellence*, due to their long lifespans and extended periods of parental care, this perspective is not fully supported by evidence. Humans can breed more rapidly than other apes and are capable of manipulating parental investment to maximize fitness. Furthermore, overexploitation of environmental resources is increasingly considered a factor in human population dynamics.

**Who disperses?**

Dispersal tends not to be randomly distributed in a population. Even in plants, dispersal is imposed by one generation on another, such that movement takes place prior to breeding. Natal dispersal is also found in many animal species, while organisms may also move between breeding areas or social groups (Clobert, 2001). All known primates are characterized by intergroup transfer (Pusey and Packer, 1985).

In some species, dispersal is undertaken by groups of animals, which may be more successful in competing in the new environment. Examples include social carnivores (Doolan and MacDonald, 1996) and some species of primate (Pusey and Packer, 1985), and humans fit with this trend. Colonization of empty sites reduces the costs of kin competition, as does recolonization when extinctions occur due to natural events or intrapopulation competition. Given the sexual division of labor known in all contemporary human foraging societies, this pattern of colonization must itself have imposed different stresses on each sex.

**The genetics of dispersal**

Where genes are not randomly distributed, the total population may be considered as a metapopulation divided into several subpopulations. To the extent that those dispersing differ from those remaining, dispersal must influence such genetic variability. Although modern humans represent a single biological species, they cannot be considered a single interbreeding population. Rather, humans comprise “an array of locally interconnected populations (demes) whose social relations with our neighbors include an exchange of mates” (Weiss, 1988). Genes can move between populations either by the expansion of one group into the territory of another or by the exchange of mates between groups. The term demic diffusion has been used to refer to a mixture of these processes (Wijsman and Cavalli-Sforza, 1984).

Random migration promotes genetic homogeneity of populations, whereas selective migration promotes or maintains differences between populations (Mascie-Taylor and Lasker, 1988). Colonization may induce founder effects and increase genetic variability, especially through reaching “islands” of difficult access (Neel and Salzano, 1967). Likewise, differential extinction may result in genetic bottlenecks through which few variants pass. Genetic variability is further favored by any tendency for groups of kin to disperse. However, interbreeding preserves gene flow between populations and counterbalances these effects.

The hominin pattern of dispersal likewise influences the capacity for genetic adaptation to occur. If adults disperse, they are adapted to the old rather than the new environment, whereas the offspring encounters the new environment from early in the life course. Such a scenario favors two types of phenotypic plasticity as an alternative mechanism for accommodating environmental stresses and stochasticity. In adults plasticity derives from behavior (altering the niche to fit physiology), whereas in the offspring plasticity derives from physiological flexibility during ontogenesis (altering physiology to fit the niche).

While plasticity appears to oppose genetic adaptation, the processes are in fact closely related.

Whether genetic variability is expressed or repressed is determined by the balance between two forces. Canalization maintains phenotypic stability in the face of environmental change, and hence maintains genetic variation (even allowing mutations to accumulate) by buffering against selection. In this way, different genotypes are constrained to produce similar phenotype regardless of environmental conditions (Flatt, 2005). In contrast, phenotypic plasticity refers to sensitivity of a single genotype to environmental variability, such that the same genes allow the possibility of different genotypes according to environmental conditions (Flatt, 2005). These processes influence each other, so that plasticity of one trait may be associated with canalization of another. Equally, a canalized trait is less plastic.

Severe environmental stresses may cause “decanalization,” resulting in the emergence of new phenotypes (Rutherford and Lindquist, 1998). This concept may be of particular importance in considering the rapid emergence of new species. In general, canalization is predicted to be favored where optimal phenotype is similar across a range of environments; in contrast if optimal phenotype differs in relation to different environments, then plasticity is predicted to be favored (De Visser et al., 2003). The relative plasticity of an organism’s biology therefore provides information about the stability of its evolutionary environment.

**Dispersal and plasticity**

Critical to plasticity is the concept that the environment acts on the organism in two ways. First, the environment influences development and hence phenotype, while second, the environment comprises the selective pressures to which the organism is the subject (Scheiner, 1993). Some factors act both as cues in development and as selective agents, but necessarily operate during different time periods. The time lag between these influences is a consequence of the inability of producing phenotypes instantaneously (Moran, 1992). In general, dispersal capacity is positively associated with plasticity, and colonizing species tend to show little local genetic differen-
tion (Levin, 1988; Bazzaz, 1996). Models suggest that the greater the environmental heterogeneity, the less accurate plastic types need be to outcompete local specialists (Sultan and Spencer, 2002). Nevertheless, plasticity becomes disadvantageous with longer time lag between initial cue and later selective pressure (Padilla and Adolph, 1996).

The benefits of plasticity comprise producing a better phenotype in any given environment (Via et al., 1995), and in the absence of costs, plasticity would allow optimal phenotype in all environments (De Witt, 1998). Penalties may include maintenance and production costs, costs of acquiring information about environmental state, costs of unstable development imposed by environmental fluctuations, and adverse impacts on related genetic traits (Relyea, 2002). Plasticity enables individuals to accommodate changes in their natal environment, but also enables low-cost adaptation to a new environment (Murren et al., 2001).

At the broadest level, the ability to migrate is itself a form of plasticity, and its success is significantly increased by complementary physiological plasticity. In general, physiological plasticity is greater during early ontogenesis, implying that the process has greatest value if the offspring encounters its new environment during early life. Older organisms with less physiological plasticity may be able to draw on behavioral options not available to young individuals, manipulating their environment to their advantage.

**Information**

Information enables organisms to evaluate their environments and adjust their development and behavior appropriately (Dall et al., 2005). As discussed above, information acquired during ontogenesis can guide physiological development. Information transmitted through behavior likewise provides a critical resource for reducing environmental uncertainty (Dall et al., 2005). In many species, behavior is organized in the form of instinct and has little capacity for modification according to the state of the environment (Plotkin, 1994). In more complex organisms, however, the processing of information allows the accommodation of environmental unpredictability (Plotkin, 1994).

The processing of information, whether through plasticity or behavior, requires gene-based capacities to extract information from the environment and incorporate them into guiding mechanisms conferring homeostasis or adaptation on the phenotype, and they are efficient at this process because they already contain some information about what requires processing or learning (Plotkin, 1994). Sophisticated information-processing requires not only access to environmental cues or signals but also the capacity to assess the possible consequences of pursuing alternative options (Dall et al., 2005).

Broadly, the information that programs behavior may be acquired by organisms in three different ways (Avital and Jablonka, 2000). Some behaviors may be innate, and relatively impervious to experience. Some behaviors may be learned through trial and error by an individual organism during its lifetime; and some behaviors may be socially acquired from conspecifics. The relative importance of these pathways is directly related to the stability of the environment. Innate behavior is valuable when the environment is relatively stable, and when there is little benefit of, or time available for, learning. Trial and error learning is favored when the experience of an individual organism is more useful than ancestral experience. Social learning is favored when an individual organism is unlikely to acquire appropriate information through its own experience and can instead benefit from the experience of conspecifics. This is particularly so when the rate of environmental change precludes sufficient time or opportunity to gain appropriate experience.

**Transgenerational plasticity and learning**

Biological mechanisms for nongenetic transgenerational heritability include hormonal and immunological programming, epigenetic inheritance, and behavior. While heritability confers a degree of stability, these mechanisms also offer increased flexibility compared to genomic transmission due to their capacity to respond faster to environmental variability.

The transgenerational transmission of phenotype via hormonal programming is well illustrated by the effect of litter placement of females on the phenotype of their offspring in gerbils (Clark et al., 1993). Immunological programming is a similar transgenerational mechanism, whereby the transmission of antibodies in breast-milk is enhanced by maternal exposure to pathogens, hence preparing the offspring for likely disease experience (Avital and Jablonka, 2000). Epigenetic inheritance refers to alterations in gene chromatin structure by mechanisms that do not involve mutation of DNA, such as methylation status. These changes can result in heritable variability in gene function without alterations to the DNA itself (Cooney et al., 2002; Waterland and Jirtle, 2003).

Behavior produces transgenerational transmission through the mechanisms of social learning and cultural evolution. Studies of mice for example illustrate how offspring learn their mother’s diet through accompanying her on foraging trips and consuming her faeces (Avital and Jablonka, 2000). Such behavioral transmission is now termed culture, which refers to socially transmitted behavior patterns or products of animal activities. Important differences between cultural and genetic transmission are first, that behaviors can only be transmitted if they are displayed (Avital and Jablonka, 2000), and second, that novel behaviors can be transmitted to future generations as soon as they emerge in any generation. These characteristics increase the flexibility and speed of cultural transmission, but at the cost of the potential loss of any adaptive information that is not used every generation.

Acquiring information socially has many advantages. Unlike material resources, information does not become depleted through sharing, though it may be copied with poor fidelity. Learnt information may also be generalizable to other contexts in the future, though it may equally constrain the organism to a specific set of conditions. However, if all information were acquired through social learning, the resulting knowledge might cease to relate to experience, and hence confer no fitness benefit (Richerson and Boyd, 2005). Other potential costs include the time and energy required (Avital and Jablonka, 2000).

Regular entry into novel environments increases the premium on the nongenetic transmission of information. Colonization mimics environmental instability, reducing the ability of organisms directly to acquire sufficient information about the environment. This is particularly the case where offspring are born into a different
environment from that in which their parents matured. The social transfer of information, whether by programming, epigenetics, or cultural transmission, facilitates rapid adaptation to new territory.

Niche construction

Niche construction refers to the way in which organisms influence, manufacture, and maintain their environment, thus manipulating the selective pressures to which they are exposed (Laland et al., 2001; Odling-Smee et al., 2003). Through such ecosystem engineering (Jones et al., 1994, 1997), organisms construct not only their own physical environment but also that of other organisms. In humans, niche construction is often a highly intentional activity, and although the details vary locally, the tendency itself is universal.

In general, larger colonizing organisms retain more generalist biology, since with increasing generation time, genetic adaptation is too slow to accommodate ecological variability. In the absence of specialized physiology, behavior takes on two functions in niche construction. First, behavior may act on the niche to make it more amenable, and hence fit it to the organism, e.g., mammalian mothers buffering external energy perturbations through lactation (Dall and Boyd, 2004). Second, through behavior organisms may converge on an optimum mode of exploiting the niche, and hence fit the organism to the niche.

Niche construction may be particularly important in hominin evolution due to the tendency of adults to disperse to new environments, a time in the life course when physiological plasticity is reduced. Although many species manipulate their niche through social or physical means, humans clearly influence their ecological environment more than other species. This is most evident in relatively recent behavior, however earlier hominins likewise constructed diverse niches using rudimentary technology and a scale of social cooperation not seen in other species.

Summary

In summary, this brief review of the biology of colonization emphasizes a number of related features, including (a) the retention of a specialist anatomy and physiology and (b) the accommodation of environmental variability and uncertainty through physiological, behavioral, and technological plasticity. As will be described in more detail in the last section of this paper, humans fit closely with this broader pattern.

LIFE HISTORY AND DEMOGRAPHY

It is life cycles rather than organisms that evolve (Bonner, 1965). Life history theory addresses the strategies pursued by organisms as they harvest energy from the environment and invest it in various vital functions (Hill and Hurtado, 1996), and is essential for understanding how a colonizing capability has emerged. The capacity of Homo to colonize and experience rapid population growth emerged from broader demographic flexibility, allowing population size and structure to accommodate ecological fluctuations.

Human demography

Relative to mammals in general, humans have large size, a long period of growth, and a long interbirth interval (Promislow and Harvey, 1990). Relative to other apes, humans likewise live longer, breed later, and develop more slowly during childhood (Hill and Hurtado, 1996; Bogin, 2001). However, the paradox is that humans breed more rapidly than contemporary ape species. Average interbirth interval is around 5 years in chimpanzees (Goodall, 1983; Nishida et al., 1990) and 7 years in orangutans (Galdikas and Wood, 1990), but around 3–4 years in foraging human populations (Howell, 1979; Blurton Jones et al., 1992) and as long as 2 in farming populations. Adult ape mortality rate appears to be an order of magnitude greater than that in foraging human populations (Goodall, 1986), though juvenile mortality is more similar between species (Table 1).

For contemporary humans therefore live for longer and breed for longer than other ape species, and yet have higher fertility rates and similar or higher offspring survival rates.

Population size in hominin evolution

Contemporary positive population growth rates are not thought to be characteristic of the majority of hominin evolution. Rather, the reproductive strategy of Homo may be considered to have evolved under a set of constraints, and to have recently been released from them by encountering new circumstances. By convention, the global population of humans is generally assumed to have shown negligible long-term growth throughout the vast majority of hominin evolution, and then to have escalated from the Neolithic, and especially rapidly from the 16th century onward. The extraordinary shift in average population growth rates is illustrated by the change in estimated doubling time from 8,000 to 9,000 years prior to the Neolithic to 40 years since 1950, such that over the last 10,000 years the human population has multiplied by a factor of ~1000 (Livi-Bacci, 1992).

Ignoring short-term fluxes, these population sizes equate to a long-term growth rate of <0.001% per year during the paleolithic (Polgar, 1972; Hassan, 1973). Average growth rate is estimated to have risen to 0.1% during the early period of food production (Carneiro and Hilde, 1966; Hassan, 1973), albeit with probable marked fluctuations over shorter time periods. The nature of exponential growth is such that even relatively low growth (1%–2% per year) induces population increases of orders of magnitude within a few centuries. For example, Hill and Hurtado (1996) calculated that at the 2.5% per year growth observed in 20th century Ache, a population of 20 individuals would increase to 3.9 × 10^{65} people in 5,000 years.

It is clear that the current distribution of humans over the majority of the Earth’s surface is itself no explanation for the characteristics of human reproductive strategy, since such a distribution could have occurred over a short period of time at very low rates of population growth. Rapid human population growth in recent millennia is therefore a product of a particular reproductive strategy in a particularly favorable environment.

Fertility rate and ecological conditions

In recent decades, anthropologists have developed a number of optimal foraging models intended to generate
and test hypotheses concerning how best to capture resources from the environment (Belovsky, 1988; Kelly, 1995; Winterhalder et al., 1998). Such models have proven useful in a variety of circumstances, but perhaps the most important conclusion is that no single model can explain the diversity of foraging behavior across a range of ecological conditions (Kelly, 1995). As illustrated by contemporary foragers, a key strategy for accommodating ecological stress is mobility. Such mobility, in response to climate trends and fluctuations in resource availability, would alter the selective pressures impacting on populations, and favor plasticity over specialization. However, even modest changes in population size and structure will influence foraging returns with any given territorial range (Kelly, 1995); hence hominin behavior may itself have contributed to such pressures and favored mobility. The relative importance of ecological stresses versus hominine behavior remains unknown for the majority of Homo evolution, but in contemporary populations some studies demonstrate population size plateauing in relation to resource availability (Attenborough, 2002).

Ecological conditions impact on fertility rate at a number of different levels. First, physiological mechanisms connect the age of menarche and the probability of conception with energy availability and flux (Slyper, 1998; Ellison, 2001). Second, lactation is well established as a critical determinant of the probability of conception (Short, 1984), with its duration explaining the majority of variability in total fertility rates between populations (Campbell and Wood, 1988). Third, these mechanisms are further influenced by a variety of social factors. Unlike other apes, humans “stack” their offspring, continuing to provision one postweaning while gestating or breast-feeding the next (Robson et al., 2006). Alloparenting has been identified as critical for this strategy, and rapid rates of reproduction typically require high levels of alloparental investment (Hrdy, 2005). Without such cooperation, the high cost of reproductions act as a constraint on female fertility. The effect of energy availability on female fertility is illustrated by differences in total fertility rate between the !Kung, Hadza, and Ache (Hrdy, 1999), and both alloparenting and technological developments impact on the interbirth interval (Hassan, 1981; Bogin, 2001; Sellen, 2006).

At some point, hominin interbirth interval appears to have decreased relative to that of apes, possibly with the emergence of Homo erectus (Aiello and Key, 2002). However, comparison of contemporary foraging, horticulturalist, and agricultural societies indicates broad similarities in fertility rates, though with a tendency for the highest rates in intensive agriculturalists (Campbell and Wood, 1988; Hewlett, 1991; Bentley et al., 1993). Substantial changes in fertility rates are thus unrealistic as the primary driver of population dynamics.

Mortality

Mortality patterns play a key role in population dynamics, by determining the likelihood of those born breeding, and the duration of adult reproductive careers. The simplest explanation for the long-term stability of hominin populations despite short interbirth intervals and long reproductive careers is that high fertility was balanced by juvenile and adult mortality. Data on juvenile mortality from a variety of primate species are illustrated in Table 1.

<table>
<thead>
<tr>
<th>Species</th>
<th>Location</th>
<th>Observation period (yrs)</th>
<th>Age at 1st birth (yrs)</th>
<th>Interbirth interval (yrs)</th>
<th>Juvenile mortality (%)</th>
<th>Mortality in 1st year (%)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chacma baboon</td>
<td>Botswana</td>
<td>10</td>
<td>6.75</td>
<td>2.0</td>
<td>61</td>
<td>38</td>
<td>Cheney et al., 2004</td>
</tr>
<tr>
<td>Mountain baboon</td>
<td>South Africa</td>
<td>2</td>
<td>–</td>
<td>3.2</td>
<td>–</td>
<td>7</td>
<td>Lycett et al., 1998</td>
</tr>
<tr>
<td>Hamadryas baboon</td>
<td>Ethiopia</td>
<td>5.5</td>
<td>6.1</td>
<td>2.0</td>
<td>36 (5 yrs)</td>
<td>24</td>
<td>Sigg et al., 1982</td>
</tr>
<tr>
<td>Olive baboon</td>
<td>Kenya</td>
<td>4</td>
<td>2.1</td>
<td>48.7 (2 yrs)</td>
<td>22</td>
<td>Smuts and Nicolson, 1989</td>
<td></td>
</tr>
<tr>
<td>Orangutan</td>
<td>Sumatra</td>
<td>32</td>
<td>15.4</td>
<td>9.3</td>
<td>33 (11 yrs)</td>
<td>6.9</td>
<td>Wich et al., 2004</td>
</tr>
<tr>
<td>Mountain gorilla</td>
<td>Rwanda</td>
<td>24</td>
<td>10</td>
<td>3.9</td>
<td>34 (4 yrs)</td>
<td>26.2</td>
<td>Watts, 1991</td>
</tr>
<tr>
<td>Bonobo</td>
<td>Congo</td>
<td>20</td>
<td>15</td>
<td>4.8</td>
<td>27.3 (6 yrs)</td>
<td>4.5</td>
<td>Furuichi et al., 1998</td>
</tr>
<tr>
<td>Chimpanzee</td>
<td>Tanzania</td>
<td>15</td>
<td>14.5</td>
<td>5.5</td>
<td>38.2 (5 yrs)</td>
<td>27.3</td>
<td>Goodall, 1983, 1986</td>
</tr>
<tr>
<td>Human*</td>
<td>Foragers</td>
<td>20th century</td>
<td>19.6</td>
<td>6</td>
<td>53</td>
<td>28</td>
<td>Nishida et al., 1990</td>
</tr>
</tbody>
</table>

Juvenile mortality assessed over varying proportions of the juvenile period, noted in years (yrs).

*Sample size for human data 9 for age at first birth, 11 for interbirth interval, 20 for mortality to 15 years, and 14 for mortality in first year.
Although contemporary populations use a number of cultural methods to constrain fertility, infanticide is the only such method likely to have made a major contribution to hominin demography. Studies of foragers suggest that earlier estimates over-emphasized the level of infanticide (Kelly, 1995); however, among recent or contemporary populations, infanticide has been used at a low level to manipulate the sex ratio and to optimize birth spacing (Morales, 1987; Hewlett, 1991). It may likewise have contributed to marginally higher infant/juvenile mortality rates in the past, particularly in times of resource scarcity.

The negligible population growth prior to the current millennium described above is very much an estimation with wide confidence intervals, and an apparent linear trend may conceal significant short-term fluctuations. Until recently, archeologists emphasized a “wave of advance” model of population movement and expansion, implying the steady occupation of, or diffusion into, adjacent territory (Boserup, 1965). More recent analyses suggest that, although cultural diffusion may have operated in such fashion (Shennan, 2002), population expansion itself may have had very different dynamics. Four plausible scenarios for the evolution of human demography have been presented (Shennan, 2002). The conventional view assumes high stability, with a recent marked population increase. Other possibilities, within this same overall pattern, are constant, increasing or decreasing stochastic variability over time. The most likely scenario comprises fluctuations in global population decreasing over time in relation to the aggregate of many specific populations. Thus small discrete populations distributed in few regions across a mosaic of habitats would be subject to considerable impact of local population crashes in response to climatic stresses such as glaciations. There is therefore no reason why high population growth rates may not have occurred regularly in the past, even if long-term average growth was negligible (Boone, 2002).

**Demographic stochasticity**

Regular population fluctuations might arise for a number of reasons, including climate-induced ecological change, predation, disease, famine, and conspecific violence. Each of these might induce local extinction and therefore merits consideration.

Hominins evolved in and adapted to unstable niches. Climatic trends, inducing ecological shifts and transforming foraging returns, must inevitably have acted on demography through influencing both fertility and mortality patterns. Thus, the simplest model of demographic stochasticity would consider hominins to have occupied suitable territory when available, and to have retreated when subsistence became untenable. These pressures are still, in very broad terms, a consequence of hominin behavior, through the probing of and dispersing into such unstable environments.

In recent millennia, the movement of diseases between previously isolated populations has often exerted devastating demographic effects. For example, native South American populations were decimated in the 16th century by diseases brought in by colonizing Europeans (Livi-Bacci, 1992; Diamond, 1998). Notably, the Ache recovered their population size less than 20 years after almost half of them died (Hill and Hurtado, 1996), a phenomenon also reported in other populations (Thornton et al., 1991). This clearly illustrates the capacity of human populations to “bounce back” from significant crashes. However, the relevance of such diseases for pre-agricultural populations is probably limited, given that many modern infectious diseases followed animal domestication (Diamond, 1998).

Data from populations such as the !Kung and Ache demonstrate that predation is a significant source of mortality, but less so than homicide or disease (Hill and Hurtado, 1996). Hominins were relatively large animals and would have had few predators, particularly after developing the control of fire. Their sociality would also have discouraged predation. An intriguing possibility is that predator-prey cycles may have induced fluctuations in contexts where humans were the predator, rather than the prey. Such a hypothesis clearly depends on a major role of hunting in subsistence, and might be relevant to specific periods of human evolutionary history.

Hunting has been proposed as a convergent niche allowing colonization of new habitats without the need for physiological specialization to local vegetable foods (Foley, 2001). Furthermore, there is considerable evi-
Niche construction and population dynamics

While the above factors may have imposed stochasticity on hominin demography, we suggest that active niche construction may have made an increasingly important contribution. Characteristics aiding survival during ecological instability will overlap with those favoring the probing of new territory and novel niches. In this way, hominin strategies must increasingly have contributed to the selective pressures acting on them. Entry into novel niches, initially characterized by plentiful new resources, would allow increased population growth; however over-exploitation of these resources could lead to either renewed impetus to colonize new environments or it would bring about a population crash. Furthermore, any association between opportunistic niche appropriation and overexploitation would increase vulnerability to climatic variation.

The archeological record is replete with examples of recent populations over-exploiting local resources; this process results in a steady decrease in the quality of resources available (Shennan, 2002). The notion that nonindustrialized populations are better at maintaining the sustainability of their resource bases has been challenged (Alvard, 1995, 1998), while archeologists have also found the concept of population crashes useful in accounting for the apparent fluctuating occupation, or abandonment, of specific sites over centuries or millennia (Matson et al., 1988; Jones et al., 1999). Trade networks between populations emerged in response to differential access to key resources, and trade has been considered a recently-evolved counterbalance to local overexploitation (Shennan, 2002).

The relative importance of climatic trends versus hominin behavioral strategy as selective pressures favoring the traits that permit colonization remains unclear and is an important topic for further research. We suggest a trend of positive feedback, such that initially tentative colonizing aided by climatic variability led to more proactive colonizing. Whatever be the cause of population stochasticity, it would have favored increasing r-selection of hominin reproductive strategy.

Colonizing through agriculture

The combination of 4+ year interbirth intervals, high juvenile mortality, and population cycles is likely to have been the norm for the vast majority of hominin evolution, offering little opportunity for any systematic global population growth. Agriculture represents a new niche in hominin evolution with substantially increased productivity from a given area of land. There is considerable evidence to suggest that agriculture initially increased rather than resolved nutritional stress (Cohen and Armelagos, 1984; Larsen, 2002), and only became viable in favorable climatic conditions that appeared in the Holocene (Richerson et al., 2001). However, as it developed it appears to have stimulated fertility rate by decreasing the interbirth interval while also increasing the motivation to produce offspring, since intensive agriculture favors increased family size (Hassan, 1981). Thus, rather than stemming from systematic population growth (Boserup, 1965), agriculture appears to have both enabled it and stimulated it.

From this perspective, agriculture represents a niche ripe for colonizing in the same way that new territory can be exploited. Populations expose themselves to ecological stresses not by entering a new habitat, but by altering their subsistence strategy. Despite short-term population crashes arising from regular famines and territorial conflicts associated with access to land, the niche of food production has been associated with an extraordinary global population increase, with an estimated fivefold increase in global population by the end of the Neolithic (Hassan, 1981). According to more recent figures, swidden agriculturalists in New Guinea were observed to have a population density of 288 persons per square kilometer in 1972 (Sahlins, 1972). Although the Nile valley in upper Egypt had an estimated 0.11–0.27 persons per square kilometer in the paleolithic (Hassan, 1973), the density in 1960 was 755 persons per square kilometer (Hassan, 1981).

Figure 3 illustrates two proposed shifts in population dynamics, deriving from changes in both mortality and fertility (Deevey, 1960). The first of these shifts occurred with the origins of agriculture. A second shift occurred with the intensification and industrialization of agriculture that resulted from the industrial revolution. Rapid population increases in modernizing countries are currently sustained by the “green revolution” that, in the short term, boosts productivity.

Summary

The human capacity to colonize has emerged from assumed ancestral life history patterns through changes in the typical birth interval, in the duration of female reproductive careers, and the age-pattern of mortality. These changes are associated with an extended period of offspring growth and development, which in turn has impacted on the requirements for maternal care. Evidence from different sources implicates the emergence of the genus Homo as particularly important in this develop-
opment; however, further work is required to address this evolutionary history in greater detail and to elucidate how important human behavior itself may have been as a selective pressure favoring a generic colonizing strategy.

THE BIOLOGY OF HUMAN DISPERSAL

This section considers in greater detail the role of specific components of hominin and human biology in the capacity to colonize. Although Hill and Hurtado’s (1996) description of humans as “colonizing apes” derived from their focus on fertility rates, this section addresses many broader aspects of human anatomy, physiology, and behavior. For each trait, evidence on primates, hominins and humans is evaluated where available, (a) to test the hypothesis that hominins and humans have an enhanced colonizing capability compared to nonhuman apes, and (b) to identify likely selective pressures favoring this capability.

Speciation

Nonhuman apes have traditionally been considered to be the chimpanzee, gorilla and orangutan, and gibbons; however, recent molecular research indicates greater speciation, with two species each of chimpanzee, gorilla and orangutan (Butynski, 2001; Warren et al., 2001; Won and Hey, 2004) along with further proposed subspecies of chimpanzee and gorilla. Such speciation indicates both adaptation to local conditions and geographical isolation, and the accommodation of environmental stresses by genomic change as opposed to plasticity.

Early hominins show consistency with this pattern, with considerable evidence of environmental change as a significant factor contributing to speciation (Vrba, 1988; Foley, 1994). Pliocene environments in the African rift valley system included both forest and savanna until ~2.5 MYA; however, a drying trend produced highly variable habitats from 2.3 to 1.8 MYA, at which point there was a major shift toward grassland ecology by 1.5 MYA (Potts, 1998a). The shifting mosaic of habitats in central and eastern Africa is considered to have favored evolutionary novelty (Foley, 1987; Potts, 1998a,b) and contributed to extinctions (Foley, 1994), adaptive radiation, and speciation (Wood, 1992; Potts, 1998a; Bobe and Behrensmeyer, 2004). Successful Pliocene hominins appear to have been species, such as Australopithecus afarensis, who could successfully exploit resources across a number of biomes (Potts, 1998a; Bonnefille et al., 2004).

Selective pressures resulting from such rapid ecological change can pre-empt rapid genetic evolution in small populations, through decanalization of traits that previously resisted change (Platt, 2005). Thus, the increasing phenotypic variability observed in the late Pliocene may be seen as related to environmental instability and diversification (Potts, 1998a). This process may have been particularly important in the evolution of early Homo (2.4–2.2 MYA) and Homo erectus (2.0–1.8 MYA), as these periods are associated with faunal turnover and ecological heterogeneity (Bobe and Behrensmeyer, 2004). While Homo erectus is notoriously considered “the fossil without ancestors” (Walker and Shipman, 1996), its seemingly rapid development in response to new selective pressures might be due to the release of previously accumulated genetic variability for phenotypic expression in a new environment.

While environmental variation appears to be strongly correlated with speciation in the hominin fossil record, the increased hominin diversity that resulted may have further influenced selective environments. Homo erectus may have invoked selective pressures by probing the emerging savannah niche, since rapid evolutionary change can occur under the influence of behavioral changes (the Baldwin effect (Baldwin, 1909), now considered a component of niche construction (Odling-Smee et al., 2003)). While the relative importance of niche construction to Early Pleistocene radiations is for the time being speculative, it clearly played an important role in modern human dispersals and the colonization of higher latitudes.

At present, there is little evidence for correspondence between modern human origins and climatic fluctuations; however, the dispersal (Mellars, 2006a) of tropically adapted (Holliday, 1997) modern humans into Europe suggests that behavioral flexibility (Mellars, 2004) may have been required. While behavior will be discussed in greater detail later, the main contrast here is that the speciation of anatomically modern humans does not appear to correspond directly with their dispersal, as it did with Homo erectus. This in turn implies greater buffering of the later Homo genome by a variety of levels of plasticity.

Bipedalism

The fossil evidence increasingly indicates that bipedalism was not a characteristic exclusive to the human ancestral line, but a locomotor capacity related to a number of morphological characteristics found amongst some ground dwelling apes from at least 4.4 to as much as 7 million years ago. Early proposed hominin species Sahalanthropus tchadensis (Brunet et al., 2002), Orrorin tugenensis (Senut et al., 2001), and Ardipithecus ramidus (White et al., 1994) show changes in locomotor anatomy in the absence of significant expansion of the brain, a characteristic of subsequent Australopithecines. The location of the Sahalanthropus tchadensis discovery, 2,500 km west of the Rift Valley (Brunet et al., 2002), suggests that either (a) hominin origins may have taken place outside of the east Africa or (b) early hominins dispersed quite widely, perhaps as a consequence of bipedalism.
The diversity of bipedal species in the Pliocene suggests that bipedal locomotion helped hominin species to exploit the diversity of environments in sub-Saharan Africa that were occurring as a result of climatic fluctuations and a trend toward more xeric environments through the Pliocene (Potts, 1998a). Species adapting more successfully to variable and open savannah habitats developed more efficient bipedalism, incorporating adaptation to heat stress, and resolving the need for greater energy efficiency in occupying larger home ranges.

While a diverse range of bipedal hominins is known from the late Pliocene and early Pleistocene, there are key morphological differences in bipedal morphology between australopithecines and *Homo erectus*. *Australopithecus afarensis* has a broad thorax and pelvis, considerably smaller acetabulum, relatively robust humeri and femora (Clarke and Tobias, 1995; Kidd et al., 1996), what is perhaps most relevant is the accumulated evidence for a range of bipedal adaptations amongst Pliocene hominin species (Harcourt-Smith and Aiello, 2004). Although there are no well preserved and clearly taxonomically identified *Homo erectus* feet, the 1.85 MYA KNM-ER 813 talus appears to be quite human-like (McHenry and Coffing, 2000). The transition from a diversity of bipedal hominins with varying locomotor adaptations within the Pliocene to one remaining lineage (*Homo erectus*) in the Pleistocene suggests that this was the first to arrive at highly efficient locomotion for a biped. While the dramatically different body size and physique of *Homo erectus* has been interpreted in this context (Jungers, 1988; Wood and Collard, 1999a), the capacity for efficient endurance running may have also been a part of this morphological package (Bramble and Lieberman, 2004). Furthermore, changes in inner ear anatomy shown in fossils of *Homo erectus* imply the development of improved balance (Spoor et al., 1994).

The fossil evidence suggests that bipedalism was a generalized trait that facilitated hominin entry into diverse environments associated with increasing environmental variability. In this context, bipedalism is the foundation of the hominin adaptive radiation. It is difficult at present to link it specifically to any large scale dispersals of particular hominin species in the Pliocene. However, the emergence of the genus *Homo* clearly represents a morphological grade shift. As such, it can be seen as a fundamental component of colonizing adaptation, as it is associated with the emergence of an energetically efficient, obligate biped capable of considerable endurance and home range. It remains worth noting that associated improvements in manual dexterity are a correlate of encephalization and central to the evolution of hominin behavioral strategies, which include unparalleled niche construction.

**Size and physique**

Body size correlates with numerous physiological, energetic, behavioral, and life history traits, and represents one of the most fundamental biological characteristics of a species. Greater body size can only be realized through faster growth or the extension of the growth period, and requires either increased energy availability for the former, or a reduced risk of preadult mortality. The benefits of body size include improved thermoregulatory capacity and increased competitiveness, and greater energetic and reproductive efficiency. Larger females accommodate the energy demands of their offspring more successfully, and it is notable that sexual dimorphism decreased in *Homo erectus* due to a substantial increase in female size (Aiello and Key, 2002). However, the increase in body size and brain size is associated with compensations elsewhere. For example, human muscle mass is reduced compared to that of other ape species (Leonard et al., 2003), while trade-offs between organs has also occurred (Aiello and Wheeler, 1995).

Both stature and body mass have shown systematic change during hominin evolution. This trend emerged from a relatively modest baseline, with australopithecines considered to have been similar in size to contemporary chimpanzees but smaller than orangutans and gorillas (McHenry and Coffing, 2000). While body breadth has been relatively constant throughout hominin evolution in the tropical latitudes (Ruff, 1991), there were major changes in stature and body mass. Despite the adaptive radiation of bipedal hominins in the Pliocene, the current evidence for stature and body mass amongst these species suggests relative homogeneity, with values ranging from ~130 to 150 cm and body mass estimates from 29 to 50 kg (McHenry and Coffing, 2000). By 1.6 MYA, the most complete *Homo erectus* skeleton demonstrates a marked increase in both stature and body mass (Ruff and Walker, 1993), comparable to modern humans. There is evidence for such large bodied hominins as early as 1.95 MYA, yet these remain are of uncertain taxonomic status (Wood and Collard, 1999a; McHenry and Coffing, 2000).

The available evidence suggests there was a major shift in body size with *Homo erectus*, and possibly *Homo rudolphensis*. While there is evidence to suggest that this increase in body size led to a greater home range and capacity for dispersal in *Homo erectus* (Anton et al., 2002), the small body size of some of the remains from Dmanisi fall within the range of some modern human hunter-gatherers, and their derived morphology appears to be well adapted to long-distance locomotion (Lordkipanidze et al., 2007). The intercontinental dispersals of Miocene apes demonstrate that larger body size was not necessary for major migrations within ecological zones. The broad range of mosaic grassland environments may have also contributed to dispersals at this time (Dennell, 2003).

Contemporary humans and hominins show significant variability in size and physique, some of which corresponds with adaptations to climate (Ruff, 1994, 2002). Much of this variation has been assumed to be genetic and to reflect local physical environmental factors such as heat stress (Roberts, 1953; Katzmarzyk and Leonard, 1998). However, the effect of thermal load on growth has been proposed to commence in utero, when growth rate is more plastic (Wells and Cole, 2002). More generally, a convergence of evidence from different fields suggests that plasticity in body size can occur on intergenerational scales, in response to factors such as resource availability and patterns of mortality (Bateson et al., 2004); see Plasticity in Growth and Metabolism section below. Although it is difficult to determine whether body size variability among fossil hominins reflects a range of plasticity, this may have been an important component of hominin adaptability with particular relevance to energy requirements and environmental variability. By maintaining plasticity in size and physique, the homogeneity of more fundamental physiology and anatomical structure is preserved.
The larger body size of Homo would have offered a range of benefits in the context of colonizing, including decreased risk of predation of adults, increased home range and hence dietary range, and increased efficiency in the energetics of reproduction. These benefits aid in the exploitation of novel environments with minimal physiological specialization.

**Diet**

Hominin evolution appears to have been characterized by a series of increases in dietary quality. A complementary trend comprises decreasing physiological specialization, with dietary adaptability conferred instead by behavior and technology. The combination of these strategies has conferred on humans the capacity to access a wide variety of habitats while retaining a generalized dietary physiology.

The ecology and diet of Miocene apes was dominated by forested environments and frugivory, which have been argued to favor social and cognitive means of food procurement (Potts, 2004). Extant apes tend to eat "what there is" (mostly vegetable material) and avoid a high degree of physiological and anatomical specialization (Rodman, 2002). However, chimpanzees exhibit significant sex-differences in diet, with females consuming less animal meat than males, but greater quantities of social insects (McGrew, 1992). Recent observations of chimpanzees indicate that the use of sharpened sticks to hunt was primarily conducted by adult females, but also by juvenile males (Pruetz and Bertolani, 2007), while female bonobos share food to a greater extent than males (Hohmann and Fruth, 1996). These traits may be analogous to the sex-differences in foraging strategy among contemporary humans, indicative of sex-differential selective pressures.

Early hominin foraging likely remained broadly consistent with these strategies with the environmental shift to more fragmented forests and open habitats through the Miocene and Pliocene. Ardipithecus ramidus and subsequent australopithecines shared a dentition characterized by moderate to small incisors, large molars with relatively flat occlusal surfaces, and thick dental enamel, suggesting a dietary shift toward the hominin evolution (Teaford and Ungar, 2000). Analyses of Australopithecus dental microwear suggest the consumption of contrasting hard/soft and abrasive/nonabrasive material, consistent with a range of food seed and soft fruit eating, which has been interpreted as an adaptation to habitat diversity from gallery forest to savanna (Teaford and Ungar, 2000). This is supported by isotopic evidence for a greater consumption of C4 plants, or animals that feed upon these, in australopithecine diets (Lee-Thorp and Sponheimer, 2006).

The trend toward a generalized diet continued in Homo, with increased quality considered important for accommodating the needs of larger brains (Leonard and Robertson, 1994). A recent review of masticatory biomechanics, dental morphology, and microwear suggests that early Homo (habilis, rudolphensis) and Homo erectus were well adapted to at least periodic exploitation of a wide range of resources in different environments (Ungar et al., 2006a). While evidence for meat consumption as early as 2.6 MYA (Dominguez-Rodrigo et al., 2005) cannot be linked to a particular species, microwear evidence for an increase in food toughness makes meat consumption probable amongst Homo erectus (Ungar et al., 2006b).

Exploiting the increase in herbivore numbers that occurred at this time is a plausible strategy for meeting increased energy requirements (Antón et al., 2002). While chimpanzees hunt with relative frequency (Boesch and Boesch, 1989; Stanford, 1996), there is considerable evidence for increased consumption of meat in the genus Homo (Blumenshine et al., 1994; Bunn, 1994; Domínguez-Rodrigo, 1997; Hoberg et al., 2001; Antón and Swisher, 2004). Since the composition of meat varies less than that of plant matter between ecosystems, hunting has been proposed to allow convergence on a common niche (Foley, 2001), a phenomenon indicated by the apparent reduction in hominin speciation in the early Pleistocene with the adaptive success of Homo erectus and its occupation of an enormous geographical range. Isotopic evidence also provides further support for dietary specialization toward very high levels of meat consumption amongst the Neanderthals (Richards, 2000b; Lee-Thorp and Sponheimer, 2006), which is likely to have been a central feature of their behavioral and metabolic adaptations.

Nevertheless, hunting is not the only possible strategy for buffering dietary physiology and allowing niche homogeneity in diverse habitats. Conklin-Brittain et al. (2002) have proposed the exploitation of underground storage organs (roots, tubers, rhizomes, and corms), which savannah baboons and geladas eat during lean periods, as a key fallback food for early hominins. A diet rich in such matter has similar protein but substantially less fiber than the chimpanzee diet, and therefore could have allowed increases in energy intake (Conklin-Brittain et al., 2002). However, this strategy may have been constrained by limitations in tuber digestibility, with O'Connell et al. (2002) arguing that cooking was required for their maximal exploitation. The practice of cooking renders a wide variety of plant foods such as tubers more edible (Wrangham and Conklin-Brittain, 2003), and tubers have been proposed as a high quality alternative to meat for Homo erectus (O'Connell et al., 1999). There is limited empirical support for these interpretations at present; however, the reduction in body size dimorphism that occurred with the emergence of H. erectus (Aiello and Key, 2002) suggests increased selective pressures on female foraging activities.

Whatever the relative importance of meat versus plant products in the Homo diet, it is clear that behavioral and technological flexibility dominated over physiological specialization (Leonard and Robertson, 1994; Milton, 2002). The shift to a more versatile, generalized diet among Pliocene hominins appears to have been heightened in the early Pleistocene, and represented the most versatile approach to subsistence yet found in the primate or hominin lineages. It would allow for the exploitation of an unprecedented range of habitats, increased home range, and the potential to colonize new territories. There are clear ecological differences between the paleoenvironments at fossil bearing sites of Georgia, Java, and the East African and Levantine sites in the Rift valley system (Antón and Swisher, 2004), which demonstrate that early Pleistocene dispersals necessitated considerable dietary flexibility.

In addition to accommodating greater adult energy requirements, dietary adaptations were likely of particular importance in early life. Human development departs from the general primate pattern whereby offspring are weaned directly to the adult diet. Instead, from mid-infancy through to childhood, humans uniquely require...
specialized “supplementary” foods (Sellen, 2006), provided either by the mother or other adults. Such foods allow shortening of lactation, decreasing the interbirth interval. Aiello and Key (2002) suggested that a decrease in the duration of lactation was a fundamental component of the evolution of Homo erectus, arguing that its increased brain size would have made lactation too expensive to continue for a duration compatible with other ape species. Bogin (2001) concurs that a brief childhood phase of growth may have emerged 2 MYA, and lengthened subsequently (see below).

The “releasing” of offspring energy demand from maternal physiological constraint has been further exacerbated since the origins of agriculture. First, crop agriculture provides materials for cereal weaning foods (Hassan, 1981). Second, pastoralism has provided alternative sources of milk. In mammals in general, activity of the enzyme lactase is turned off during weaning (Avital and Jablonka, 2000). However, with animal domestication, and the availability of milk beyond infancy, it benefits the offspring to preserve activity of the lactase gene. In the minority of populations, which have practiced pastoralism over many generations, activity of the gene is maintained throughout the life course, allowing ingestion of milk at all ages (Aoki, 1986; Durham, 1990).

Accompanying behavioral trends in dietary adaptation, differences in metabolic physiology must also have occurred. The switch from a diet based on complex carbohydrates to one containing substantial quantities of meat would have required changes in insulin metabolism, to maintain appropriate blood glucose concentrations (McMichael, 2001). Such metabolic versatility again allows convergence on a common physiological phenotype in a wide variety of nutritional settings. Although such convergence initially required moderate anatomical adaptation, in the genus Homo this was achieved primarily through metabolic, behavioral, and technological adjustments. Dietary sex-differences also consolidated, indicative of selective pressures on maternal reproductive strategies.

**Growth rate**

Growth may be considered from two perspectives, the generic shape of the human growth curve and within-individual plasticity therein. This section considers only the first of these perspectives, the second being addressed in *Plasticity in Growth and Metabolism* section below.

In many species, growth rate is fairly consistent across the entire developmental period, and individuals simply grow until they reach adult size and start breeding. Many social species intersperse a slower growth period between birth and adulthood (Bekoff and Byers, 1985; Bogin, 1994), and most primates are consistent with this pattern. Contemporary ape species show such extended growth, with infant and juvenile periods. Humans display a more complex version of growth-slowing, with distinct infant, childhood, juvenile, and adolescent stages (Bogin, 2001). Humans are not unique in having growth spurts, but differ from other primates in delaying them in the growth process (Leigh, 1996). This pattern extends the total growth period, and also alters the relative rates at which different body components develop.

The human ontogenetic profile has been attributed previously to more than one underlying mechanism. Evolution occurs when ontogeny alters in timing (heterochrony) or incorporates new characters (Gould, 1977). Gould proposed human growth to have been characterized by a particular type of heterochrony, neoteny, whereby developmental rates are slowed and developmental stages found in juveniles of ancestral populations become adult features. Others including McKinney and McNamara (1991) and Vrba (1996) have argued that hypermorphosis, whereby growth phases are extended, accounts for the human growth pattern. Bogin (1999) has followed Shea (1989) in arguing that neither of these processes alone can produce human adult size and shape. Additional genetic changes are likely to have occurred, and there is evidence that these have influenced the endocrine system (Bogin, 1999).

Such developmental changes can be attributed to the effect of the relatively few genes controlling the rate of different developmental processes. These changes appear to be associated with the increase in brain volume. Relative to the chimpanzee, human body growth is similar whereas brain growth is markedly different. Apes in general have a rapid rate of brain growth before birth but a slow one afterward. In contrast, human brain growth is rapid both before and after birth, such that the large human brain size relative to other apes can be attributed primarily to postnatal growth patterns (Martin, 1983). This is achieved through a derived pattern of brain allometry and moderate extension of the duration of brain growth coupled with a decrease in early postnatal somatic growth (Vinicius, 2005).

The strongest contrast between humans and other apes comprises discrepancy in the significance of weaning. In apes, viable weaning requires eruption of the first permanent molar, allowing access to the adult diet (Bogin, 2006), while the offspring must also be capable of foraging. The duration of the interbirth intervals of extant apes can be related to these variables; however although the first human molar erupts at about 6 years of age, and humans at this age are still incapable of foraging for themselves, humans wean their offspring at 3–4 years in natural fertility societies (Bogin, 2006). Between the end of infancy and the beginning of juvenile growth, humans are therefore characterized by an unusual childhood period in which the slow-growing offspring is provisioned by adults but not through lactation, and not necessarily entirely by the mother. This reduces the cost of childhood growth, allowing the high costs of brain growth to be met without adverse impact on the maternal energy budget or reproductive schedule (Bogin, 2001). Hrdy (2005) has also emphasized humans as “cooperative breeders,” using investment from kin to subsidize offspring growth.

In contrast with apes, this pattern allows each human mother to “stack” several offspring at the same time (Robson et al., 2006), breast-feeding one while still provisioning several that are older. When unconstrained by juvenile mortality, the low-cost human growth pattern is particularly suitable for rapid population growth, allowing either rapid recovery from population crashes, or rapid population expansion in new habitats. While the benefits to maternal fitness are clear, this same growth pattern is also powerfully protective of offspring phenotype, with the slow growth rate protecting the offspring from severe physiological responses to ecological fluctuations.

Dental eruption and formation have been used as markers of the tempo of development among ancestral hominins (Smith, 1991; Bogin, 1999). Bogin suggests that the childhood period may have emerged around 2 MYA.
with the Homo genus, and then lengthened subsequently. Recent analyses of dental formation provide evidence that both australopithecines and early Homo more closely resemble apes (Dean et al., 2001; Moggi-Cecchi, 2001). While the modern pattern of growth was in place among anatomically modern humans by 160 KYA (Smith et al., 2007), the question of when it arose remains controversial. Studies of anterior dentition have identified evidence for both a rapid (Ramirez Rozzi and Bermudez de Castro, 2004) and slow (Guatelli-Steinberg et al., 2005) rate of dental development among Neanderthals. Recent analyses of Neanderthal molar crown and root formation support the interpretation that their development was similar to modern humans (Macchiarelli et al., 2006). While broader interpretation of these studies requires the assumption of a direct relationship among dental formation, eruption, and somatic growth, they collectively suggest that the modern human growth pattern evolved after the increase in body size with Homo erectus but prior to the large bodies and brains found among Neanderthals. If so, the unique pattern of life history developed within the time interval of the greatest encephalization of the hominin lineage (Ruff et al., 1997), indicating a close relationship between these characteristics.

Human growth patterns are consistent with general models relating growth rates to the risk of mortality, and with primate patterns of slow growth rates. Humans nevertheless stand out for the extent to which growth is slowed, and for the “stacking” of multiple offspring, increasing the independence of growth from ecological stresses.

Adiposity

Adipose tissue, unique to vertebrates, provides a means of accommodating imbalances in the intake and utilization of energy. Fat is a slow release fuel, appropriate for longer term imbalances, whereas short-term energy bursts are fueled by glycogen (Pond, 1998). In mammals, metabolic flexibility is of particular importance in meeting the energy costs of lactation, substantially higher than those of pregnancy (Clutton Brock et al., 1989; Pond, 1997). The literature contains frequent references to the role of fat in accommodating cycles of feast and famine (Prentice et al., 1992; Chakravarthy and Booth, 2004), yet this is insufficient as an explanation of the selective pressures favoring human fat stores.

The available evidence on adiposity in primates is patchy, and derives primarily from captive animals. Nevertheless, many species demonstrate a capacity to accumulate fat, indicative of its role in buffering uncertainty in energy supply (Dufour and Sauther, 2002). Reported body fat ranges include 8%–41% in lemurs (Peireira and Pond, 1995), 5%–16% in baboons (Rutenberg et al., 1987), and 19%–44% in gorillas (Zihlman and McFarland, 2000). An elegant study of orangutans in the wild demonstrated seasonal metabolism of fat stores during times of energy stress (Knut, 1998). Wheatley (1982) has estimated that such stores allow orangutans to accommodate substantially longer periods of low energy intake than crab-eating macaques, which occupy the same region but exploit a habitat with more predictable energy supply. Primates therefore fit with the general mammalian pattern of using energy stores to buffer unpredictability in energy intake; however in the wild, periodical seasonal energy stress and the need to maintain mobility for predator avoidance tend to constrain absolute body fat levels (Pond, 1997), with, e.g., 2% fat observed in wild-living baboons (Altmann et al., 1993).

As reviewed by McFarland (1997) and Dufour and Sauther (2002), primates also tend to show higher levels of body fat in females relative to males. This sex difference is likely to be most closely associated with the energy costs of reproduction, but may also be related in some species to sexual selection in relation to cues of fitness (Pond, 1997). The study of orangutans showed greater metabolism of ketones in females compared to males, with the highest rate in a female that had both a nursing infant and an accompanying older juvenile (Knott, 1998).

Humans show consistency with this general primate pattern, but appear to stand out in two respects. First, adult female humans have higher typical body fat content than any nonaquatic mammal (Dufour and Sauther, 2002; Wells, 2006a), and even in harsh conditions women tend to maintain ~20% of body weight as fat (Lawrence et al., 1987), while adult males tend likewise to have higher body fat content than other species occupying similar environments (Wells, 2006a). Second, human neonates have unusually high levels of body fat compared to the small number of species with data available (Kuzawa, 1998). The extent to which humans genuinely differ from other ape species is uncertain, because of the lack of equivalent data. However, unlike humans, observations of primate neonates suggest minimal body fat content at birth (Schultz, 1969). The life-course profile of human body composition is shown in Figure 4.

Reconstructing the emergence of adiposity in hominins is not possible on the basis of direct evidence, since soft tissue does not fossilize. An indirect approach highlights three plausible factors (Wells, 2006a), each favoring selection for energy stores.

First, energy stores are predicted to benefit both sexes in relation to stochastic variability in energy supply. Data from contemporary populations inhabiting highly seasonal environments illustrates the capacity of body fat stores to buffer regular fluctuations in energy supply. For example annual body weight fluctuations of 6 kg are typical in Gambian farmers (Prentice et al., 1992), with the majority of this variability attributable to changes in adiposity (Lawrence et al., 1987). The australopithecine exposed hominins to increasingly seasonal environments, characterized by longer dry seasons than those experienced by ancestral gorilla and chimpanzee populations (Foley, 1993). Body fat stores may have aided adaptation to such conditions, along with other strategies such as dietary adaptations.

The dispersals of Homo erectus and sapiens from Africa, exposing populations to new environments and stresses, are likely to have further increased stochasticity in energy supply. Even adjacent territories may have problematic features only evident after arrival, while dispersing over longer distances increases such risk. Many species rely on fat stores to fuel their migratory journeys (Dingle, 1996; Pond, 1998). Early hominins are unlikely to have regularly undertaken lengthy dispersals, however with increasingly opportunistic foraging such as hypothesized for Homo erectus, fat stores may have become important for buffering periods of accommodation to new territories, habitats, and dietary niches. The metabolic sensitivity of some contemporary populations has been attributed to strong selective pressures during specific recent migrations (McMichael, 2001), though this remains controversial.
Second, the enhanced adiposity in reproducing females and neonates strongly implicates the impact of the large Homo brain on reproductive energetics. The high and obligatory energy demands of brain tissue favor fat stores in the neonate to buffer uncertainty during the establishment of lactation and the onset of weaning (Kuzawa, 1998). As a proportion of body weight, the contribution of the brain is greatest at birth (Stratz, 1909), accounting for almost 90% of basal metabolic energy utilization at this time compared with only 25% in adulthood (Leonard and Robertson, 1992). Consistent with Kuzawa’s hypothesis, malnourished human neonates have been shown to metabolize fat stores efficiently (Kerr et al., 1978). Since the offspring’s fat stores must be acquired via maternal nutrition, selection is also predicted to favor fat stores in adolescent and adult females. Although incomplete, the available evidence indicates a substantially higher energy cost of the neonatal brain in humans relative to other apes. Extending the approach of Dufour and Sauther (2002), Table 2 estimates the relationship between neonatal brain weight and body composition in apes and humans. Although all species show similar ratios of neonatal brain weight to body weight, humans have substantially higher brain weight in relation to nonbrain lean body mass. These greater costs must ultimately be met by the mother. Greater female fatness may also have been shaped by sexual selection (Pond, 1997). However, such pressures are more likely to have acted on regional fat distribution, and its visibility to males, than the amount per se.

It has been proposed that the trajectory of brain growth in Homo erectus was similar to that of Homo sapiens (Leigh, 2006); however, this argument is based on reanalysis of data originally claimed to refute such similarity (Coqueugniot et al., 2004). Thus, it remains unclear when the characteristic human fatness profile evolved, and whether patterns of growth and development are similar between Homo sapiens and erectus (Bogin, 1999). Nevertheless, the fact that Homo erectus demonstrated both larger adult brain and an increased capacity to disperse, hence potentially encountering greater environmental uncertainty, favors the hypothesis of greater adiposity in both females and neonates emerging in related fashion.

The third significant factor concerns the increasing tendency of Homo to influence its niche, and hence the selective pressures acting on it. Relevant aspects of such niche construction may have included improved foraging returns and the development of supplementary foods, but also greater exposure to over-exploitation of resources. Mobility represents a key solution to energy uncertainty (Binford, 2001); however nomadic behavior may impose its own energy stress, and inevitably loses efficacy as population density rises (Kelly, 1995). Increased efficiency in energy extraction may thus paradoxically have increased the risk of population cycles, with fat stores both aiding the growth and buffering any subsequent dietary energy stress.

With the emergence of agriculture, exposure to food shortages and famine is assumed to have increased rather than decreased (Cohen, 1990; Larsen, 2002; Benyshek and Watson, 2006). The archeological record contains evidence of periodic growth interruptions among early agricultural populations (Starling and Stock,

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**TABLE 2. Estimations of brain size relative to lean mass in neonatal apes**

<table>
<thead>
<tr>
<th>Species</th>
<th>Body weight (g)</th>
<th>Brain weight (g)</th>
<th>% Adipose fat</th>
<th>Nonbrain lean weight (g)</th>
<th>Brain/nonbrain lean weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>Orangutan</td>
<td>1,728</td>
<td>170.3</td>
<td>2</td>
<td>1,526</td>
<td>0.112</td>
</tr>
<tr>
<td>Gorilla</td>
<td>2,110</td>
<td>227.0</td>
<td>2</td>
<td>1,845</td>
<td>0.123</td>
</tr>
<tr>
<td>Chimpanzee</td>
<td>1,756</td>
<td>128.0</td>
<td>2</td>
<td>1,595</td>
<td>0.080</td>
</tr>
<tr>
<td>Homo sapiens</td>
<td>3,300</td>
<td>384.0</td>
<td>16.6</td>
<td>2,432</td>
<td>0.158</td>
</tr>
</tbody>
</table>

Phenotypic plasticity is observed across a broad range of organisms (Bateson et al., 2004), and many components of human plasticity are clearly derived from a much broader baseline. In mammals, in general, the most plastic period comprises fetal life and infancy, when growth is primarily under nutritional regulation. Such plasticity allows adaptation to nutritional supply, a proxy for ecological conditions. Primate studies indicate a powerful effect of energy supply on growth rate (Janson and van Schaik, 1993; Johnson, 2002; Altmann and Alberts, 2005), and also the capacity for catch-up if short-term nutritional insufficiency is resolved (Fleagle et al., 1975; Rutenberg and Coelho, 1988), though this may be achieved at a later-longer term cost (Mcalpine and Monaghan, 2001). In contrast, prolonged nutritional insufficiency induces long-term effects on size and metabolism, and later growth is more strongly canalized (Tanner, 1963).

Primate studies also highlight the importance of maternal biology in regulating such early growth, with for example earlier weaning of offspring in good conditions (Lee et al., 1991; Bowman and Lee, 1995). To some extent, humans exhibit similar plasticity, but are also notable for distributing it across an extended growth period, and also limiting the exposure of sensitive offspring to ecological perturbations in early life.

Human growth comprises three distinct components (fetal/infant, childhood, and adolescent periods) that are to some extent additive (Karlberg, 1989). Most attention has focused on the first of these periods, emphasizing how fetal/infant growth rate varies in relation to energy supply (Wells, 2007). Associations between birth-weight and thermal environment (Wells and Cole, 2002) likewise indicate adaptation to broader climatic conditions. Childhood growth can also exhibit more minor fluctuations in relation to ecological pressures such as climatic conditions (Weitz et al., 2004). Studies of exposure to chronic low energy intake have demonstrated adaptability in metabolism, ergonomics, mechanical efficiency, and muscle structure (Waterlow, 1999), illustrating the capacity to maintain function across a range of ecological conditions. Equally, the 20th century showed a major secular trend in growth in industrialized populations (Cole, 2003), especially during the first 2 years after birth, with girls in particular reaching puberty and ceasing growth at substantially earlier ages (Garn, 1987; Karlberg, 2002). In a study of 22 small-scale nonindustrial societies, favorable conditions were associated with faster growth and earlier maturation (Walker et al., 2006). Through such plasticity, the pace of human life history can quicken when ecological constraints relax.

However, consistent with theoretical models, the same studies of small-scale societies showed that higher juvenile mortality risk was likewise associated with faster maturation (Migliano, 2005; Walker et al., 2006). These data suggest that growth rate is sensitive to different types of cues, enhancing the capacity to match life-course development to ecological conditions. Despite infant growth being the most plastic, recent studies have demonstrated the capacity for adolescent growth to continue into the third decade of life in some populations (Satharayanan et al., 1980, 1981; Little et al., 1983; Steckel, 1987), indicating the capacity for early deficits to be partially resolved through plasticity later in the life course. Some have claimed that early life plasticity represents “predictive adaptive responses” anticipating the likely environment during adulthood (Gluckman and Hanson, 2005). Others have argued instead that the human fetus adapts to information about the past rather than the future (Wells, 2003, 2007; Kuzawa, 2005). Biomedical studies demonstrate a powerful capacity for maternal physiology to buffer the fetus against external ecological perturbations during pregnancy and lactation (Wells, 2007), and maternal birth-weight predicts offspring birth-weight better than does pregnancy weight gain (Emanuel et al., 2004; Hypponen et al., 2004).

According to this perspective, phenotype of the human neonate is strongly influenced by the ecological conditions experienced by matrilineal ancestors, and the majority of adaptation to contemporary external conditions commences during infancy, when the capacity for maternal physiological buffering decreases. Such guiding of offspring by maternal phenotype has been termed “inter-generational phenotypic inertia” (Kuzawa, 2005). Its significance for a colonizing organism is profound: offspring are initially protected from the severe stresses that derive from entry into novel ecological niches and can preserve high phenotypic quality inherited from their mothers, regardless of short term ecological fluctuations during early development. However, during childhood, the offspring can adapt to more consistent ecological stresses, and in successive generations matrilineal guiding increasingly softens, as shown by migration studies (Boas, 1912; Bogin and Rios, 2003).

Overall, this mechanism means that human phenotype is slow to relinquish high quality attained over preceding generations, but at the cost that there is also a time-lag on the capacity to recover from chronic matrilineal exposure to poor conditions. This slow transgenerational response to ecological change is illustrated by long-term secular trends in human growth (Steckel, 2004, 2005), showing the depression of stature over several generations in mediaeval Europe, and a consistent recovery during the 20th century (Steckel, 2004).

The importance of maternal phenotype in guiding offspring growth rate is emphasized by a recent UK cohort...
study. Shorter, fatter mothers gave birth to daughters who grew rapidly in the first 2 years of life, but then at the same rate as the daughters of other mothers. These fast-growing infants reached puberty early, as had their own mothers, and were fatter at that time (see Fig. 5). Their earlier puberty is likely to reduce the total growth period and result in short final height, thus reproducing maternal phenotype (Ong et al., 2007). Although this association could plausibly derive from genetic transmission, it is notable that the fast growth occurred only during infancy, the period primarily under nutritional regulation. It is more likely that the fetuses of early-maturing mothers detect the large maternal energy stores, and are programmed to exploit them by growing fast during lactation. This interpretation is supported by the fact that these mothers’ sons also grew faster during infancy (Ong et al., 2007).

Human adults have an extraordinary capacity to accommodate ecological variability through behavioral, technological, and social mechanisms (see The Extended Phenotype section). These mechanisms allow them both to shape their niche, and to avoid long-term physiological adaptation. Adults entering new environments can therefore buffer a range of stresses. In contrast, the offspring has high physiological plasticity in early life, and can match physiological phenotype to prevailing conditions. However, this matching is strongly manipulated by maternal phenotype, so that the offspring adapts to the mother as well as the external environment. While some stresses are consistent (e.g., thermal load), others are unpredictable (e.g., energy supply). The combination of offspring physiological plasticity and maternal buffering optimizes overall adaptation of the offspring to novel environments. The profile of earlier hominin plasticity is difficult to reconstruct. Nevertheless, awareness of the plasticity of growth in contemporary humans may be of particular value when evaluating the fossil record (see Size and Physique section above). Overall, human plasticity accommodates the impact of ecological pressures and depresses the rate of genetic adaptation. However, more fundamental aspects of human biology (e.g., long life-span, large brain) remain strongly canalized and are therefore preserved across a great diversity of environments.

**Cognition and information processing**

After infancy, ecological accommodation is increasingly achieved via the brain rather than physiological systems. Encephalization is characteristic of modern humans, and its emergence is central to our evolutionary history. It has been argued that a general trend toward the evolution of cognitive development in the Cenozoic is the result of adaptations to increasing environmental variability (Richerson and Boyd, 2000). In this context, hominins continue a more general trend toward increased brain volume found amongst primates compared to other vertebrates, and amongst hominids compared to other primates (Begun, 2004). The relative brain volume of Australopithecines was within a continuum with contemporary ape species (McHenry and Coffing, 2006). With the evolution of the genus Homo, and in particular, Homo erectus brain size underwent significant expansion (Leonard et al., 2003) followed by general stability and further significant increases in encephalization between 600 and 150 KYA (Ruff et al., 1997). In sum, the fossil evidence suggests that, building upon the relatively large brains found amongst all apes compared to other species, significant periods of brain expansion and hence cognitive ability occurred with the hominin adaptive radiation, the origins of Homo, and throughout the evolutionary history of Homo heidelbergensis, neanderthalensis, and sapiens in the middle Pleistocene (see Fig. 6).

Increasingly, however, attention is directed to particular components of the brain rather than its total size. Recent comparisons of ape frontal lobes show them to have much greater similarity to humans than to nonape primates (Semendeferi, 1999; Semendeferi et al., 2002). Table 3 provides figures for total cranial capacity, frontal cortex as a percentage of volume of cortex of cerebral hemispheres, and relative volume and neuronal density of two specific brain regions. While non-ape primates have relatively smaller frontal cortices than apes, the table shows that apes and humans have very similar values (Semendeferi et al., 2002). More detailed cytoarchitectonic studies remain very rare; however, Semendeferi et al. (1998, 2001) have shown that the brains of all extant apes exhibit the regions known as Brodmann’s areas 10 (considered to be important in decision-making, strategy formulation, and planning) and 13 (considered relevant to emotional responses to social stimuli). Table 3 shows that humans have a relatively large area 10 (though the magnitude of the difference is modest: Holloway, 2002), but a relatively small area 13. However, complementary to these size differences is systematically lower neuronal density in both regions, a characteristic associated with greater brain connectivity (Armstrong, 1990). Relatively greater prefrontal white matter (Schoenemann et al., 2005) and relatively larger and more abundant “spindle neurons” (Allman et al., 2002) are two further traits indicative of greater connectivity between brain regions in humans. Area 10 is emerging as a particularly interesting aspect of the human brain, associated with comparing current and past experience, estimating likely pay-offs, and formul-
ing strategies, and has been proposed to be of importance in the context of food sharing (Allman et al., 2002). Comparative research on brain structure, though still at an early stage, therefore suggests that hominin cognitive capacities emerged from a sophisticated ape baseline, and that the human brain is as notable for its greater connectivity between regions, aiding the evaluation of problems, as its size.

Colonization represents a plausible stress favoring such greater brain connectivity. Figure 7 illustrates the association between major colonization expansions and stepwise increases in encephalization. Across a broad range of species, there is a clear general trend of increasing encephalization from *A. afarensis* to living humans; however, when we consider the pattern of hominin encephalization in the context of colonization and selective environments, we can see some correlations. Brain size increases amongst early bipedal hominins correspond with adaptive radiations and exploitation of a variety of niches. While further encephalization amongst early *Homo* is noted, and may be associated with the broad dispersal event characterized as Out of Africa 1, it remains relatively stable from 1.8 to 0.6 MYA (Ruff et al., 1997). The subsequent rapid increase noted by Ruff et al. in the Middle Pleistocene is associated with the first consistent hominin occupation of Northern Latitudes, which was dependent upon unprecedented cultural buffering, such as the use of fire (Gowlett, 2006). Relatively modern encephalization quotients are found in the record from circa 150 KYA, at which point modern

<table>
<thead>
<tr>
<th>Species * Period* /Group</th>
<th>Homo living worldwide</th>
<th>Homo 1-10 Ma</th>
<th>Homo 10-20 Ma</th>
<th>Homo 20-50 Ma</th>
<th>Homo 50-100 Ma</th>
<th>Homo 100-200 Ma</th>
<th>Homo 200-400 Ma</th>
<th>Homo 400-800 Ma</th>
<th>Homo 800-1200 Ma</th>
<th>Homo 1200-2000 Ma</th>
</tr>
</thead>
<tbody>
<tr>
<td>Early Homo, Homo erectus</td>
<td>colonization of northern latitudes</td>
<td>modern human behavior</td>
<td>enhanced behavioral buffering, niche construction</td>
<td></td>
<td></td>
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<tr>
<td>Middle Homo, Homo sapiens</td>
<td>colonization of northern latitudes</td>
<td>- modern human behavior</td>
<td>- enhanced behavioral buffering, niche construction</td>
<td></td>
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<tr>
<td>Late Homo, Homo sapiens</td>
<td>colonization of northern latitudes</td>
<td>- modern human behavior</td>
<td>- enhanced behavioral buffering, niche construction</td>
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</tbody>
</table>

Fig. 6. Theoretical relationship between Hominin Encephalization, adaptive radiations, and major dispersal events. The encephalization data were derived from data presented in Ruff et al. (1997) and McHenry and Coffing (2000), using Martin’s (1981) equation: $EQ = \frac{brain \ mass}{(11.22 \times body \ mass^{0.76})}$.

### TABLE 3. Comparison of selected brain characteristics across contemporary apes

<table>
<thead>
<tr>
<th></th>
<th>Orangutan</th>
<th>Gorilla</th>
<th>Chimpanzee</th>
<th>Bonobo</th>
<th>Human</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Cranial capacity (cc)</strong></td>
<td>434.4</td>
<td>534.5</td>
<td>398.5</td>
<td>1,345</td>
<td>1,435</td>
</tr>
<tr>
<td>Both sexes$^a$</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male$^b$</td>
<td>415</td>
<td>550</td>
<td>410</td>
<td>355</td>
<td>1,325</td>
</tr>
<tr>
<td>Female$^b$</td>
<td>370</td>
<td>460</td>
<td>380</td>
<td>339</td>
<td>1,435</td>
</tr>
<tr>
<td><strong>Relative frontal cortex volume (%)</strong></td>
<td>37.6</td>
<td>35.9</td>
<td>35.4</td>
<td>34.7</td>
<td>37.7</td>
</tr>
<tr>
<td>Area 10</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Relative volume (%)$^c$</td>
<td>0.45</td>
<td>0.54</td>
<td>0.57</td>
<td>0.74</td>
<td>1.22</td>
</tr>
<tr>
<td>Neuronal density per cc$^d$</td>
<td>78,182</td>
<td>47,300</td>
<td>60,468</td>
<td>55,690</td>
<td>34,014</td>
</tr>
<tr>
<td>Area 13</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Relative volume (%)$^e$</td>
<td>0.09</td>
<td>0.08</td>
<td>0.07</td>
<td>0.03</td>
<td>0.03</td>
</tr>
<tr>
<td>Neuronal density per cc$^e$</td>
<td>42,400</td>
<td>54,783</td>
<td>50,686</td>
<td>44,111</td>
<td>30,351</td>
</tr>
<tr>
<td><strong>Spindle cell volume ($\mu m^3$)</strong></td>
<td>6,648</td>
<td>5,684</td>
<td>8,796</td>
<td>7,743</td>
<td>20,822</td>
</tr>
</tbody>
</table>

$^a$ Tobias, 1971.
$^c$ Semendeferi et al., 2002.
$^d$ Semendeferi et al., 2001.
$^e$ Semendeferi et al., 1998.
$^f$ Nimchinsky et al., 1999.
human behavior was developing on spatio-temporally mosaic scales (McBrearty and Brooks, 2000). This technological and cultural evolution would become the basis for the success of modern human dispersals.

While these correlations are intriguing, brain phenotype is associated with various physiological and behavioral traits, and as such it is difficult to tease out the causes and consequences of its changes during hominin evolution. Given the expense of brain tissue, larger brains volumes could only be selected if benefits exceed costs. What factors might have conferred such benefits in hominins? Amongst the factors proposed to have favored increased cognitive capacity are technology, hunting, diet, increased home-range, and sociality. Of these, the strongest candidate is generally considered to be the last—for example, across primates in general, neocortex size is associated with social group size (Dunbar, 2003).

Humphrey (1986) argued that the primary factor favoring increased intelligence in our own genus was the benefit of predicting and manipulating the behavior of others in the social group. This argument was expanded by Byrne and Whiten (1988) in their treatise on Machiavellic intelligence. Thus “manipulating people rather than their genes or the objects they wield is what requires high intelligence” (Gamble, 1993, p 102), and the formation and maintenance of alliances has been proposed to favor a large working memory, able to process large amounts of both recent social data and prior social interactions (Byrne and Whiten, 1988). A related issue comprises the benefits of transmitting cultural information (Richerson and Boyd, 1998). However, entry into volatile niches offers a new perspective on the benefits of enhanced cognitive capacities, and recent research further implicates female reproductive behavior as a key area of importance in this context.

As noted by Popper (1982), increased cognitive capacity allows thoughts rather than the organism itself to be risked in difficult circumstances. Gamble (1993) has suggested that the acquisition and use of information about nearby habitats was critical to hominin dispersal and colonization. In many foraging populations, males only acquire proficiency in hunting during the adult years (Kaplan et al., 2000), and prior to this period they may have been unlikely or unable to provide information of sufficient value to underpin migration decisions. Furthermore, primate studies have indicated the importance of females in driving both cognitive and technological evolution (Boesch and Boesch, 1984), and female foraging strategy may have been important for determining the viability of dispersal.

Traditionally, evolutionary models have considered females as burdened with the costs of parental care. Washburn’s notion of fathers provisioning nuclear families with meat is now considered unlikely, and hunters are thought more likely to have used their skills to compete for mating opportunities (Hawkes et al., 2001). The high demands of dispersal and colonization. In many foraging populations, males only acquire proficiency in hunting during the adult years (Kaplan et al., 2000), and prior to this period they may have been unlikely or unable to provide information of sufficient value to underpin migration decisions. Furthermore, primate studies have indicated the importance of females in driving both cognitive and technological evolution (Boesch and Boesch, 1984), and female foraging strategy may have been important for determining the viability of dispersal.

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The extended phenotype

The evolution of human intelligence is clearly related to a number of other characteristics, which could be seen as exsolution adaptations, which contribute to an extended phenotype, which would contribute to colonizing ability. Foremost amongst these technology, cultural evolution, and language. While these have been discussed extensively in the literature, their relevance to colonizing will be explored briefly below.

Technology. Technological developments are often considered to be a central component of human evolution, and certainly from the emergence of Homo, stone tools are associated with all populations in the fossil record. It remains more difficult to identify patterns of tool use amongst australopithcines and other Pliocene hominins. Those studying chimpanzees have noted that many simple tools are made of vegetable material and would not have survived the process of fossilization. Despite this, we know that there is considerable variation in chimpanzee material culture (McGrew, 1992, 2004), much of which is based upon degradable organic material (McGrew, 1992; Whiten et al., 1999). New discoveries continue to illuminate the ways in which chimpanzees use organic materials as tools, including the first documented use of spears (Pruetz and Bertolani, 2007). Despite the frequency of use of organic tools among chimpanzees, their use of stone anvils and percussive technology to crack nuts has been documented not only among living
chimpanzees, but has also produced an archeological record with some antiquity (Mercader et al., 2002, 2007). Of particular interest are chimpanzee sex-differences in tool use. While the use of tools in hunting by males is negligible, a sophisticated toolkit has been observed applied to the gathering of social insects (McGrew, 1992) and vertebrates (Pruetz and Bertolani, 2007). This has led to increasing interest in the hypothesis that the origins of hominin tool use may be most closely associated with female gathering (McGrew, 1981; Zihlman, 1981; Tanner, 1987). Compared to humans, chimpanzees are notable for their lack of use of containers to transport food items, and their tendency to consume foods where acquired (McGrew, 1992). Collectively, the ape evidence highlights the importance of tool use in the gathering of vegetable, invertebrate, and occasionally mammalian foods by females, and again highlights selective pressures acting disproportionately on females.

Technology clearly plays a key role in opening up novel niches. Since rudimentary technology contributes to a wide variety of subsistence activities among chimpanzees, aiding in the capture of animals, access to plant resources, the transport of materials, and the processing of foods, it is reasonable to predict it would have played a similar role in early hominins. Interpretations have often been based upon perceived associations between major evolutionary transitions and material culture (Leakey et al., 1964; Klein, 1999); however, evidence for stone tools as early as 2.6 MYA (Semaw et al., 1997; Semaw et al., 2003), which were used to butcher animals (Domínguez-Rodrigo et al., 2005), leaves the question of the association between Oldowan tools and hominin species open. Disparity between the dates of the earliest Homo erectus fossils (Antón, 2003) and the first Acheulean tools (Asfaw et al., 1992), and the chronology of dispersals characterized as Out of Africa 1 (Gabunia et al., 2000), further highlights this issue.

Despite the disparities noted above, technology may have been important in some aspects of the adaptive radiation of Pliocene hominins in response to environmental instability (Potts, 1998a) and the dispersal of Homo erectus (Morwood et al., 1998), and has clearly played an important role in subsequent population movements. Stone tool technologies developed throughout the Oldowan and Acheulean (between 2.5 and 0.3 MYA), and raw material transport distances were low; however, both the rate of technological change and transport distances increased considerably by the Middle Stone Age (Ambrose, 2001). More recent developments, including the production of clothing and shelter and the invention of watercraft, would have been essential technological components of the dispersal of modern humans. Although the package of technological components that we consider to relate to “modern human behavior” developed over a considerable time in Africa (Lahr and Foley, 1998; McBrearty and Brooks, 2000), much of this technological package was in place by the time of the first permanent dispersal of anatomically modern humans out of Africa (Lahr and Foley, 1998; Underhill et al., 2001; Stringer, 2002). While the benefits of technology require no elaboration here, we emphasize the capacity for modern technological flexibility to facilitate entry into and exploitation of a wide variety of niches while preserving a common physiology and anatomy. Technology appears particularly important in colonizing higher latitudes (Torrence, 1983), indicating its capacity to mediate more extreme environmental conditions. Consistent with that hypothesis, chimpanzees exploit tools to a greater extent in harsher environments (McGrew, 1992).

In addition to its obvious practical implications, technology also represents an important component of the biology of human migration for its capacity to store information extrasomatically (Pfaffenberger, 1992). As material artefacts are created, they encapsulate in themselves information about their design and often their utility. Artefacts overcome a major limitation of morphological adaptation, namely that they can be discarded when not wanted (Petraglia et al., 2005). Thus the capacity to make technology when required is as important as the technology itself. This benefit comes at the cost that such knowledge may be lost if both the articles, and those who know how to produce them, fail to be replaced over time.

**Cultural evolution.** Recent evaluations highlight the great ape clade as the source of a novel cultural repertoire from which subsequent hominin evolution drew (van Schaik et al., 2003; Whiten et al., 2003; McGrew, 1992, 2004). The role of culture in chimpanzee biology has been clarified by a detailed evaluation of local group practices and variability in their within-group transmissions (Whiten et al., 1999). Ethnographic studies have demonstrated both the emergence of local traditions, and conformity bias maintaining their integrity over time (Whiten et al., 2005). Such learned behavior has been shown to be adaptive, including exploiting alternative resources during seasons of poor fruit availability, and swallowing leaves to treat nematode infections (Whiten, 2006). However, unlike in humans, there is very little evidence of direct teaching among apes (McGrew, 1992; Whiten, 1999).

Contemporary human populations illustrate extraordinary cultural variability, in which social learning is complemented by individual learning, ensuring that acquired information has ecological validity (Richerson and Boyd, 2005). Providing this validity is preserved, culture becomes increasingly adaptive when learning is difficult and the environment is unpredictable. Under these conditions, it is beneficial to accumulate the culturally acquired knowledge of many others, providing a store of information impossible for any individual to acquire alone (Richerson and Boyd, 2000; Wells, 2006b). Compared to genetic inheritance, the speed of cultural transmission combined with a broad pool of potential information confers markedly higher phenotypic plasticity. There are two potential mechanisms through which cultural evolution can influence human adaptation to new environments. One is as a simple buffering system, through which environmental stresses are mediated through cultural mechanisms that passively confer advantages to survivorship and reproduction, thus ensuring genetic survival (Dawkins, 1976). A more active relationship between culture and evolution is proposed by models of niche construction (Laland et al., 2001; Odling-Smee et al., 2003) and gene-culture coevolution (Durham, 1990), in which culture directly changes the selective environment of the species and thus in part determines the trajectory of evolution within the species.

There is substantial evidence that cultural transmission is encouraged by psychological mechanisms predisposing individuals to favor information from more memorable or common sources, or those considered prestigious (Richerson and Boyd, 2005). These traits allow not only adaptation but also systematic maladaptation; hence,
culture tends to be most adaptive when it incorporates accurate emulation and teaching. However, rapid cultural adaptation may favor mechanisms protecting in-group members from receiving information from other groups. This scenario may account for the emergence of strong group identities among human populations, particularly at their boundaries (Richerson and Boyd, 2005), and some apparently maladaptive behaviors may be directed toward such group identity rather than fitness per se. The concept of bet-hedging may also merit greater attention in this context: when prior experience offers a poor guide to novel problems, behavioral diversity within and between groups may represent a viable longer-term survival strategy.

The question of how cultural evolution relates to human evolution is challenging to address (Foley and Lahr, 2003). Cumulative cultural change is a necessary component of human survival in a variety of stressful environments, although it is difficult to identify in the early archeological record (Henrich and McElreath, 2005). While cultural transmission is clearly a part of the adaptive phenotype of great apes, at present it cannot be firmly linked to the ability to colonize specific habitats, and certainly not to the extent found within modern humans. The cognitive differences between other species and humans may relate to the combination of ontogenetic factors such as the ability to infer the thoughts of other individuals (theory of mind) and an understanding of other individuals as intentional agents (Tomasello and Rakoczy, 2003). While there is evidence that chimpanzees possess aspects of a theory of mind (Hare et al., 2001), the extension from individual to collective intentionality may underpin human culture and cognition (Tomasello and Rakoczy, 2003). Our understanding of this change remains speculative, although the cognitive capacity for collective intentionality must have been greatly enhanced by language, and thus can only confidently be said to have been in place within Homo sapiens (see Communication and Language section below).

Cognitive developments can be seen as a major component of dispersals within our species and may have corresponded with the early occupation of higher latitudes (Parfitt et al., 2005); however, cultural diversity shows significant associations with ecological parameters such as temperature and rainfall in contemporary human populations (Collard and Foley, 2002). There is also evidence of increasing cultural differentiation in more productive regions, suggesting that such differentiation is constrained in harsher environments due to the greater need for interaction between populations (Nettle, 1998), and constraints of resource availability. Equally, more productive environments may favor niche construction and associated cultural differentiation, leading to greater diversity (Collard and Foley, 2002). Cultural evolution can therefore be considered to have played a key role in the behavioral adaptations that have been central to colonizing within our species, while relieving selective pressures on anatomy and physiology.

Communication and language. Language is a defining feature of our species and has attracted considerable attention from evolutionary biologists. While human language appears to have evolved in parallel with other forms of communication such as calls and gestures, it was likely preceded by the capacity for some form of symbolic thought and representation (Deacon, 1997).

However, the development of vocal language must be considered as a separate process, linked with anatomical and neurobiological changes. Patterns of basioccipital flexion (Lieberman et al., 1992), hyoid (Arensburg et al., 1989), and hypoglossal canal morphology (Kay et al., 1998) provide controversial evidence for language amongst Neanderthals and possibly Homo heidelbergensis, but not early Homo or australopithecines. However, the discovery of the normal human variant of the FOXP2 gene, which differs between humans and other mammalian species and corresponds with fine motor control of the mouth, appears to have arisen between 50 and 200 KYA (Enard et al., 2002). Thus, the full symbolizing capabilities of modern humans appear to have had a relatively recent emergence, perhaps linked with this genetic change (Fisher, 2005). This time period coincides with the mosaic pattern of origins of modern human behavior (McBrearty and Brooks, 2000) and suggests that a complete linguistic and cultural package facilitated the expansion of modern humans across the globe.

The symbolism afforded by the origins of language is an inherently social process and would have conferred the ability of individuals to share a “virtual common mind” (Deacon, 1997). It also would have been a necessary precursor for the rapid technological evolution found within our species by enhancing the transmission of information between individuals and minimizing trial and error. Symbolism may therefore have been of particular value in the most recent disposals of Homo sapiens, where sea crossings and expansion into previously unhabited and ecologically stressful niches required a greater degree of planning and evaluation. Likewise language may have offered significant benefits to social groups as they consolidated niches, competed for regional resources and emphasized local cultural identity. In contrast, the morphological and genetic evidence suggests that earlier dispersals of Homo erectus must have been achieved with much simpler forms of communication, perhaps providing one of the mechanisms restricting dispersal of this species within tropical regions.

Summary

In this section, we have reviewed evidence concerning the characteristics of hominin and human biology that facilitate the capacity to enter new territory, habitats, and ecological niches. Comparisons between humans and apes demonstrate a markedly greater degree of plasticity and behavioral flexibility, and support the hypothesis that at many levels, humans have the biology of a “colonizing ape.” Plio-pleistocene adaptive radiations appear to have been contingent upon the morphological and technological ability to exploit a diverse range of habitats, leading to the dispersal events resulting in a distribution of Homo erectus from southern Africa to South-East Asia, within a band of tropical latitudes. The colonization of the broad range of habitats, including periglacial environments, was most accessible with a complete package of human body size, cognition, culture, physiology, and plasticity. Despite this, there remain open questions about whether these characteristics only came together within modern humans, or arose in a mosaic fashion amongst Pleistocene hominins, thus enabling the occupation of northern Europe by Homo heidelbergensis and Neanderthalensis. It is important to note the potential feedback and selective environments that may have resulted from colonizing. These may be important in...
driving much of the directional change in the hominin phenotypes, in particular regarding the Homo brain.

CONCLUSIONS

Although all organisms have the potential to reproduce in geometric ratio (Malthus, 1798/1976), such potential is balanced in practice by mortality and constraints on resources. These balancing factors shape each organism’s biology and reproductive strategy. When organisms inhabit stochastic environments, and experience regular demographic cycles, natural selection will favor traits that promote the potential for rapid population growth, allowing the capacity to bounce back. Such traits comprise not only reproductive strategy, but many other components of biology. In this paper, we considered how life cycles [identified by Bonner (1965) as the primary target of selection] may be considered as a form of risk management, and evolve by varying a set of life history strategies. The story of hominin evolution over the last 6 million years represents the adaptation of life cycles to increasingly stochastic environments, favoring greater plasticity in many aspects of phenotype. We highlight a number of related issues, and argue that such plasticity has played a key role in the emergence of the genus Homo as a colonizing ape.

First, we suggest that the radiation of Australopithecines into more variable niches initiated the exposure of early hominins to selective pressures favoring the capacity to accommodate fluctuating ecological conditions. These capacities then played a key role in the emergence of the genus Homo. Plasticity both protects genetic variation and also releases it under strong environmental stresses. The rapid shift in phenotype that characterizes Homo relative to australopithecines may, we argue, be considered the product of such a decanalizing release. Phenotypic plasticity subsequently remained preserved in Homo and was fundamental to its successful dispersal across diverse habitats.

Second, the high level of plasticity relative to other apes allows humans to opt out of genetic adaptation. We are an animal that above all refuses to commit to specific long-term strategies. Adults use a combination of behavior and technology to alter their environments to suit their anatomy and physiology. Offspring show greater cognitive development, allowing the fit between their physiology and ecological conditions during the ontogenetic process, but adapt to parental experience rather than the environment directly. Human biology therefore displays an extraordinary capacity for behavior and technology to homogenize diverse habitats and construct a narrower range of ecological niches, further accommodated by metabolic plasticity, thus buffering selective pressures on the human genome.

Third, we suggest that the tendency to probe new territories, habitats, and niches has generated, through positive feedback, sustained selective pressures favoring traits that accommodate environmental variability. Increasingly, Homo colonized niches rather than territory, but also homogenized these niches to fit anatomy and physiology. Bursts of colonizing success may have promoted selection for the very traits that predispose to such niche-probing. When during Homo evolution this began to induce positive feedback selection remains open to debate, but we suggest that the notion of the genus Homo as increasingly contributing to its own selective pressures through niche-probing and dispersal would explain continued genetic change over 2 million years, demonstrated in particular by the systematic expansion and increasing sophistication of the Homo brain. This issue merits further investigation, through both the paleoanthropological record and simulation models.

Fourth, we emphasize the powerful impact of selective pressures on females in particular. Research in both humans and primates increasingly highlights the importance of female reproductive strategy for the evolution of cognitive capacities, and recent studies break with tradition, suggesting that females rather than males may also have driven key aspects of technological evolution. Understanding the challenges of buffering vulnerable offspring from the stresses of stochastic environments and new habitats, despite maintaining fast rates of reproduction, is relevant not only to our conception of hominin evolution, but also to the sensitivity of contemporary health to social and metabolic perturbations (Kuzawa, 2005; Wells, 2007).

Human reproductive strategy is notable for its capacity for rapid bursts in population growth. Today, humans are applying their colonizing reproductive strategy to the highly productive niche of modern agriculture. This latest population boom is exerting its own selective pressures on human biology, and as noted by Shennan (2002), further population crashes are not unlikely.

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