Guts and brains : an integrative approach to the hominin record

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Guts AND Brains

An Integrative Approach to the Hominin Record

Wil Roebroeks (ed.)

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In the early 1980s one of the contributors to this volume, Lewis R. Binford, proposed that scavenging was an important part of the subsistence behaviour of Lower and Middle Palaeolithic hominins, prior to the appearance of fully modern humans, the first species with the cognitive capacity for cooperative hunting and food sharing (Binford, 1981, 1985, 1988, 1989). This iconoclastic view was based on the reinterpretation of key archaeological sites that were previously seen as testifying to the hunting capacity of early hominins, from the earliest Palaeolithic in Africa up to and including the European Middle Palaeolithic. All through this period scavenging was the main mode of meat procurement, with a gradual increase in the importance of hunting until the appearance of modern humans. The "hunting versus scavenging" controversy raged for two decades, with recent publications for various "post-mortems" of the scavenging hypothesis (e.g. Villa et al., 2005). The debate dealt with a major issue in human evolution and provided a platform for very heated discussions (Domínguez-Rodrigo and Pickering, 2003). However, our understanding of early hominin subsistence has improved greatly, leading to new questions about the formation of the archaeological record and to new methods for discriminating between the various actors and processes that may be contributing to this record (see, for example, Villa et al., 2005).

The application of these methods to recently excavated faunal assemblages covering the 2.6 million years of the Palaeolithic record has shown that Binford was wrong (but for the right reasons): at the closing of the last millennium many researchers, using methods developed by Binford, came to the conclusion that the archaeological record did not contain reliable evidence for a scavenging mode of subsistence, at least for Neandertals (Marean, 1998; Marean and Assefa, 1999; see also Villa et al., 2005). Researchers focusing on the energetic requirements of Neandertals pointed out that these hominins would have required very high foraging returns to meet the needs of their large and active bodies (Sorensen and

Leonard, 2001). Faunal assemblages from archaeological sites were analyzed using Binford's methods. Although a few of these assemblages had been excavated decades before the hunting versus scavenging debate started (e.g. Salzgitter-Lebenstedt in Germany), most came fresh out of the ground (La Borde and Mauran in France). Theses analyses showed that Neandertals were proficient hunters of large game, an interpretation that Binford himself came to share (Van Reybrouck, 2001; Binford, this volume).

Archaeozoological studies of faunal remains uncovered at Neandertal sites have taught us that these large-brained hominins did hunt and, indeed, which species were at stake (Anwar et al., this volume; Binford, this volume), while isotope studies of Neandertal skeletal remains inform us that they were top-level carnivores (Richards, this volume). In line with the wide variety of habitats documented for Neandertals, prey species varied from reindeer in colder settings to aurochs and forest rhino in the last interglacial environments of northern Europe. A focus on prime-aged individuals has been documented at various locations. Such a specialization is unknown in other carnivores and has been interpreted as a good sign of niche separation (Stiner, 2002). In the Levant, archaeozoological studies indicate that Neandertal hunting activities may even have led to the decline of local red deer and aurochs populations (Speth, 2004).

When and where (and which) hominins started an active career in the animal food department is still very much open to debate though. The European record can be read as indicating that the hunting of large mammals occurred from the very first substantial occupation of the northern temperate latitude onwards, somewhere in the first half of the Middle Pleistocene (Roebroeks, 2001). Data from the Israelian sites of Gesher Benot Ya'aqov (0.8 Ma) and 'Ubeidiya (ca 1.4 Ma) (Gaudzinski, 2004) suggests that hominins may have hunted there, but unambiguous evidence for hunting by early Middle and Early Pleistocene hominins is thus far lacking. The recently reported data from Gona (Ethiopia) indicates that early hominins had primary access to large ungulate carcasses, either by aggressive scavenging or through hunting (Domínguez-Rodrigo et al., 2005). The Gona evidence indicates that the sudden widespread visibility of stone tools in the archaeological record might well tally with the first systematic exploitation of animal food resources. The archaeological visibility of such exploitation suggests that even as early as the Pliocene, meat procurement was far more important to the hominins who produced these stone tools, in comparison to the data recorded for wild extant chimpanzees in recent studies (Stanford, 1996, 1999; Stanford and Bunn, 2001).

The antiquity of human hunting was a prominent feature of models on the evolution of the human niche in the days of *Man the Hunter* (Lee and DeVore, 1968). The *Man the Hunter*-theory was in fact a loose set of ideas, the common theme of which was that hunting had steered much of human evolution, forming the root of the characteristics that made us special amongst our fellow primates, especially our large brains. The hunting way of life would have selected for individuals capable of learning and communicating about the many aspects of animal behaviour, and those capable of coordinating joint activities in big game hunting. Generally, hunting would have selected for increased intelligence, and our hunting past, therefore, was at the root of the encephalization process visible in the fossil record (Washburn and Lancaster, 1968). Binford's reinterpretation of some of the key archaeological sites upon which *Man the Hunter* was founded led to the demise of the hunting paradigm, even though there may have been more at stake in the demise of *Man the Hunter* than purely scientific arguments: for instance, the very marginal role ascribed to females in this view of human evolution (cf. Stanford, 1999).

The return of hunting hominins on the Middle (and possibly Lower) Palaeolithic scene does not automatically entail the resurrection of this old body of ideas. Or does it? The contributors to this volume would minimally agree that the hominin dietary shift toward the highly concentrated packets of nutrients and calories we usually refer to as "meat" may have provided us with "...a key nutritional supplement that favored the evolution of other key traits, such as cognition" (Stanford and Bunn, 2001: 4). However, just as significant progress has been made in the domain of archaeological studies of early sites, so too has the broad field of studies focusing on the various aspects of the development of the human niche advanced. Since the early days of *Man the Hunter*, anthropologists have studied in detail the foraging activities and returns of extant hunter-gatherers and compared the data to that of other primates (e.g. Kaplan et al., this volume). We have a much better idea of how diet relates to various aspects of animal (including human) behaviour and physiology (Aiello and Wheeler, 1995; Aiello, this volume), of the energetic requirements of various hominin species and of how these may have shaped specific aspects of hominin anatomy and behaviour (Leonard et al., this volume), and about male-female differences in this respect (Aiello and Key, 2002; Aiello, this volume; Mussi, this volume). Leonard et al. (this volume) show that an energetics perpective is very useful for understanding the evolution of brain size in the hominin lineage. Energetic studies have great potential for an integrative approach to the fossil and archaeological record (see the papers in this volume by Aiello, by Mussi and by Leonard et al.) and, as Anwar et al. (this volume) show, can constitute a valuable entry into the explanation of differences between the archaeological record of various hominin species. Studies of the biology of modern communities of herbivores and carnivores can help us to interpret the niches available to hominins in past communities. The conventional view that the meat of terrestrial mammals was the prime "fuel" for encephalization has been somewhat counterbalanced by workers such as Cunnane and Crawford (2003, Cunnane, 2005), who stress that fresh- and saltwater shorelines provided a uniquely rich, abundant and accessible food supply rich in brain nutrients, and argue that this was the only viable environment for brain expansion in the human lineage (see Milton, 2001; Aiello, 2006; Langdon, 2006, for a critique of this aquatic food argument).

It is therefore time to have a look at the implications of such recent studies for our interpretation of the archaeological record. An attempt at such integration was the goal of a small and informal workshop organized in November 2003 in Amsterdam, the Netherlands. The occasion was the awarding of the European Erasmus Prize to the food writer Alan Davidson. Around this event the Erasmus Foundation (Amsterdam) organized a series of meetings in which "food" and its many cultural forms and histories constituted the central topic. One of these meetings focused on the evolution of hominin diets and culture. The meeting was organized as a kind of follow-up to Leslie Aiello's (1998) call to contextualize the new archaeological data discussed above within the results of the wider range of other disciplines studying the development of the human niche. Neandertals and some earlier hominins were capable hunters of large mammals, so what? What does this entail? What, if anything, can diet tell us about the wider context of hunting, such as subsistence organization, division of labour or land use, and how this varied with different environmental settings. If modern-day hunting is indeed a knowledge-intensive strategy, as some have claimed (Kaplan et al., 2000; this volume), how do current hunter-gatherers acquire this knowledge (MacDonald, this volume)? And what does information on how extant foragers learn hunting imply about Neandertals and earlier hominins, with their primitive technologies? Others have addressed why large and energetically expensive brains were selected, and what the interaction was between ecological and social problem-solving in brain evolution (Dunbar, this volume; Kaplan et al., this volume)? And if learning was important for subsistence, and if our current extended youth was indeed selected for because of its increased learning opportunities, what information do we have on the life histories of earlier hominins, and how do these vary through time? Can we put that kind of information to use in our explanations of the archaeological record (Anwar et al., this volume)? These were some of the key questions addressed at the November 2003 Amsterdam workshop that resulted in this diverse collection of papers. It is obvious that the workshop, as well as this volume, could tackle only a small part of the issues that relate to the theme of the workshop and the title of this book. As expected, more questions were asked at the workshop than answered, but the integrative approach advocated by Leslie Aiello (1998) proved to be very fruitful in at least generating new questions and pointing out the discrepancies between the various approaches and, hence, where future research should be focused.

Most contributors to this volume have tried to link these questions to aspects of the archaeological record, but Dale Guthrie (this volume) takes us back beyond 2.6 Ma by presenting some informed speculation on the question of how small (in terms of brain and stature) hominins were able to make a living in the emerging open African environments at all, long before the first stone-flaking debris dropped to the ground. On the other end of the spectrum, archaeologists will be happy to see Lewis Binford present some of the faunal data he assembled at Combe Grenal, in the heydays of the Mousterian debate with François Bordes.

Leslie Aiello's work was central at the workshop, and though she was not able to produce a formal paper for this volume, she has allowed publication of the valuable discussion points she prepared for the Amsterdam meeting (Aiello, this volume). Her notes are in chronological order, describing why the research was carried out, what the initial questions were, and how answering these has made good connections to various social and biological events in human evolution. Aiello's summary outlines the wide-ranging implications of changes in the energy budget for foraging strategies, life history, male and female cooperation, and group size. All other papers on diet and human evolution in this volume ultimately relate to Leslie Aiello's bullet points.

The volume brings together researchers from a wide range of disciplines dealing with the evolution of the human niche in an attempt to chart where different lines of evidence lead to comparable conclusions and where discrepancies (and hence learning opportunities) exist. The book consists of a diverse collection of papers, and it is no easy a task to draw together some conclusions and pointers for it, but this has not deterred us from at least making an attempt at integrating the various approaches to the study of palaeolithic subsistence (Anwar et al., this volume). In its diversity this volume constitutes only a beginning, a rough layout of an emerging field. When this volume went to press, an important symposium on the very same "integration" issue was being organized at the Max Planck Institute for Evolutionary Anthropology at Leipzig: The Evolution of Hominid Diets: Integrating approaches to the study of Palaeolithic subsistence (Hublin & Richards, in prep). In integration lies the future of the past.

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Notes on the Implications of the Expensive Tissue Hypothesis for Human Biological and Social Evolution

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This paper starts from the research done by Peter Wheeler and myself in the mid-1990s on the energetic implications of the extraordinarily large human brain (Aiello and Wheeler, 1995; Aiello, 1997; Aiello et al., 2001). The human brain is considerably larger than expected for a primate of human body mass. Because brain tissue is very expensive in metabolic terms, this increase in size would imply an elevation in BMR (Basic Metabolic Rate) by approximately 8% over and above what would be expected for a normal primate or mammal of our body mass. However, human BMR is not elevated. The mystery is what has happened to the missing difference in BMR.

The Expensive Tissue Hypothesis and the mystery of the missing elevated BMR

1. Analysis of the body composition of humans and other primates, and particularly of the size and energetic costs of the expensive organs, demonstrated that human guts were reduced in size by precisely the amount to compensate for the energetic costs of the relatively large brain.
   A small gut can only be achieved by a relatively high-quality, easy-to-digest diet. This analysis implied that under conditions where it was important to avoid an elevated BMR, a high-quality, easy-to-digest diet was a prerequisite for brain expansion. At the time of the initial work, we argued that this was consistent with both the increased consumption of animal-derived foods and the apparent evidence in the archaeological record of increased control over animal resources. This idea has come to be known as the Expensive Tissue Hypothesis for the evolution of the human brain.

Criticisms of the Expensive Tissue Hypothesis

2. Since that time, there has been criticism of the Expensive Tissue Hypothesis on grounds of its applicability across primates (Martin, 1996), and also suggestions that meat may not have been the significant dietary change at the time of *Homo erectus* (O'Connell et al., 1999).
3. In relation to its applicability across primates, Aiello and colleagues (2001) have demonstrated that the apparent negative correlation between relative brain size and relative gut size across primates is highly dependent on the species included in the analysis and on the technique of determination of relative brain and gut sizes. They have argued that in both primates and other mammals, a lack of a significant negative correlation does not negate the importance of the relationship in humans, where there is a clear trade-off between relative brain size and relative gut size. Brain size does not make up a significant component of total body BMR in many other animals as it does in humans and therefore is not a limiting factor. However, the relationship does hold in the African freshwater fish *Gnathonemus petersii* which is characterized by both a relatively very large brain and correspondingly small stomach and intestines (Kaufman, 2003).

   The emerging field of ecophysiology also clearly demonstrates that animals as varied as snakes, birds and mammals manipulate their resting metabolic rates (RMR) through the differential size of other expensive tissues to meet varying environmental or life history challenges (Aiello et al., 2001).
4. In relation to the fact that meat may not have been the significant dietary change at the time of *Homo erectus,* Hawkes and colleagues (Hawkes et al., 1997a, 1997b, 1998; O'Connell et al., 1999) as well as Wrangham and colleagues (1999) have argued that underground storage organs – tubers – were essential.
5. When evaluating the significance of the two dietary sources, meat and tubers, it is important to keep in mind that there were at least two important factors in hominin maintenance energy requirements. The first of these was maintenance of a large brain, and the second was maintenance of a large absolute body size. In this context a diet rich in animal resources is needed to provide for the brain. It is necessary for the easy digestion that is required to have a relatively small gut and for the nutrients to support a large brain. However, a diet rich in tubers, providing rich carbohydrate sources, would be as important to support the larger hominin body mass (Milton, 1999).

Arguments in favour of a mixed diet in human evolution

6. Meat would satisfy nutritional requirements with a lower dietary bulk and would thereby allow increased reliance on plants of lower overall nutritive quality but high carbohydrate content, to provide the energy for the larger bodies (Milton, 1999; Aiello and Wells, 2002). Meat protein is easier to digest than plant protein and even with a limited amount of fat would still have been a valuable source of essential amino and fatty acids, fat-soluble vitamins and minerals (Milton, 1999). Carbohydrates also have a protein-sparing advantage over dietary supplementation with fat. In situations of calorie restriction such as might be expected during the dry season on the African savanna, a diet supplemented with carbohydrates is more efficient than one supplemented by fat in sparing limited protein from being metabolized for energy and thereby restricting the availability of the limited essential nutrients and amino acids derived from that protein (Speth and Spielmann, 1983).
7. An added advantage of including meat in the diet is the high methionine content of animal protein. This would provide an adequate supply of sulfur-containing amino acids that are necessary for the detoxification of toxic (cyanogenetic) plant foods. Milton (1999) also points out that infants need dietary protein that consists of essential amino acids for 37% of its weight (compared with 15% in adults) and that animal protein would have been a valuable component of weaning foods.
8. There would also be distinct disadvantages of a diet that is over-rich in meat. Such a diet would demand increased water intake, and this is an unlikely strategy to adopt in a hot open environment (Speth and Spielmann, 1983). Furthermore, wild African ungulates have a relatively low fat content (Speth and Spielmann, 1983; Speth, 1989), and modern African hunters and gatherers such as the San or Hadza who rely heavily on meat during the dry season also rely on cultural means to recover maximum fat from the carcasses – a strategy that would not have been available to the early hominins.
9. There is also the problem of Specific Dynamic Action (the rise in metabolism or heat production resulting from the ingestion of food), which is very high for protein. If modern people such as the Eskimos are anything to go by, where 90% of caloric needs were met by meat and fat, such a diet would elevate the RMR by 13-33% with significant implications for thermoregulation in a hot open country environment. This also means that they would have had to eat correspondingly more meat to satisfy their basic energy requirements.
10. Recent work on the thermoregulation of Neandertals has suggested that a high dietary-induced RMR may have been very important in relation to survival under the cold climatic conditions experienced by Neandertals in Europe during

Oxygen Isotope Stage 3 (Aiello and Wheeler, 2003).

11. These points suggest that a combination diet would have been the most probable diet to have arisen with the appearance of a relatively large brain and larger body sizes at the time of *Homo ergaster* approximately 2 million years ago. However, the primary point is no matter whether the diet was high in animal-based resources, relied on underground storage organs or involved considerable cultural preparation, the increased hominin body size, the relatively large brain size and the dietary change resulted in an increased reproductive burden on the females with a number of knock-on biological and social effects. A particular problem was the effect of the larger body size on the reproductive costs of the female.

The problem of a large-bodied female

12. An example comes from consideration of the effect of large body size on female reproductive costs (Aiello and Key, 2002). Daily energy expenditure (DEE) is estimated to have been almost 66% higher in a *Homo erectus* (*ergaster*) female than in an average australopithecine or paranthropine female.
13. A further effect of the increased size of *Homo ergaster* mothers and hence offspring would have been the greater energy requirements during gestation and lactation. Gestation increases DEE by 20-30% in mammals (Gittleman and Thompson, 1988) and lactation by at least 37-39% in primates (Oftedal, 1984; Aiello and Key, 2002). Aiello and Key (2002) demonstrate that the DEE for a lactating *Homo ergaster* female is about 45% higher than for a lactating australopithecine or paranthropine and almost 100% higher than a non-lactation and non-gestation, smaller-bodied hominin. The resulting high energy costs per offspring could have been considerably reduced by decreasing the interbirth interval, with the additional benefit of increasing the number of offspring per mother. A faster reproductive schedule reduces the most expensive part of reproduction, lactation, although the benefit would be countered by a smaller increase in the energy required to support dependent offspring. Interbirth intervals have been estimated to be around 4 years in gorillas, 5.5 years in wild chimpanzees and 8 years in orangutans (Galdikas and Wood, 1990), considerably longer than in most contemporary hunter-gatherer societies (Sear et al., 2000; Aiello and Key, 2002).
14. We do not know when the shorter interbirth interval was achieved in hominins, but a combination of higher accidental deaths as implied by a move to a more dangerous open environment habitat at the time of *Homo ergaster* as well as the inferred high mortality profile of early hominins suggest that it would have been advantageous early in the evolution of the genus *Homo*.

15. But in order to achieve the shorter interbirth interval, a female would accrue even higher daily energy requirements in relation to the australopithecines and paranthropines than the larger body size and higher DEEs would suggest. This is because she would be responsible for dependent weanlings while gestating or nursing a subsequent child.

Biological and social implications of dietary change and increased female reproductive costs

16. Biological Strategies. Under these conditions it would be expected that females would develop strategies to preserve energy, and children would develop strategies to reduce daily energy consumption.
    a. Slowed Growth and Development. From the point of view of the infant, slowed growth need not necessarily be attributed only to increased costs of brain growth as proposed by Foley and Lee (1991). In social species, weaned offspring may be in competition with adults for scarce food resources, and slowed growth would reduce the daily energy requirements (Janson and van Schaik, 1993). Because children remain at least partially dependent on the mother for food during the childhood and juvenile period, selection may have favoured slowed growth in human children in order to protect maternal total fitness at the expense of the fitness of individual offspring (Wells, 2003). Thus, parent-offspring and/or intra-group conflict as well as increased energy requirements for brain growth may have favoured slower growth during human childhood.
    b. Increased Female Fat. From the point of view of the females, one way to support high maintenance energy expenditure is the preservation of energy as fat in order to overcome fluctuations in food availability (Aiello and Wells, 2002).
17. Social Strategies and the Evolution of Cooperation. It would also be expected that the intergenerational transfer of resources would develop with consequent biological and social correlates.
18. Perhaps the best-known theory of intergenerational transfer of resources is the Grandmother Theory proposed by Hawkes and colleagues (Hawkes et al., 1997a, 1997b, 1998; O'Connell et al., 1999). These authors argue that post-reproductive females would increase the fitness of their daughters and thereby their own reproductive fitness through their provisioning activities and that this behaviour is at the root of selection for longevity and an extended post-reproductive lifespan. Given a low external mortality rate, longevity would be rapidly selected because those women with surviving mothers (grandmothers) would produce more offspring than those without provisioning help.

This may explain the evolution of longevity and a post-reproductive lifespan, but the main problem from the point of view of the daughters would be whether a grandmother would be available when they needed one. Analysis of the mortality profiles of the Ache and !Kung suggests that 32% of Ache daughters and 41% of !Kung daughters born to young mothers (aged ~20 years) would be without a grandmother to aid them when time came for an older woman to take up the grandmothering role (Aiello, in press). These daughters would also already be 15 years into their own reproductive period, and their own early-born children would be approaching independence and reproductive maturity without the benefit that would have accrued from grandmothering. For children born at the end of their mother's reproductive period (~40 years of age) about 70% of Ache mothers and 59% of !Kung mothers would still be alive 20 years later at the age of 60 to assume their grandmothering role. So again 30% of these late-born Ache daughters and 41% of the late-born !Kung daughters would be without grandmothers when they began their own reproductive careers.

19. Male Cooperation and Provisioning. Because not all women would have a grandmother when they needed one, it would seem logical that females would develop strategies to attract the cooperation of males. This is supported by computer simulations of the iterated Prisoner's Dilemma used to study the evolution of cooperation in groups of mixed sex (Key, 1998, 1999, 2000; Key and Aiello, 1999, 2000; Aiello, in press). These models emphasize the importance of both sexes in the cooperative support of a reproductively active female when the female reproductive costs are significantly higher than those of the male.
20. The results of the iterated Prisoner's Dilemma are consistent with the Embodied-Capital Theory that has been developed by Kaplan and colleagues (Kaplan, 1996, 1997; Kaplan et al., 2000; Kaplan and Bock, 2001) which emphasizes contributions by both males and females in a broader model to explain the evolution of human life history features, including a long lifespan and delayed age of first reproduction. The importance of intergenerational transfers has also been used specifically to explain the co-evolution of intelligence and longevity (Kaplan and Robson, 2002) and developed into a broader theory of aging by Lee (2003).
21. Other Implications of Male Cooperation. Not only are there a significant number of females without grandmothers but also males in the majority of societies are larger net producers than are the females (Kaplan et al., 2000). One would expect females to develop mechanisms to attract provisioning from other individuals, and particularly from males. These might include concealed ovulation, which would lead to extended mate guarding, and increased mating

competition between males. This is consistent with recent research suggesting that strong competition among males, and not the degree of paternity certainty, may be the important factor in relation to the evolution of monogamy (Davis, 1991; Hawkes et al., 2001). Mate guarding would seem to be incompatible with a male's role as a hunter and provisioner, but important human mate-guarding features could include sperm competition and consequent large testis size or even gossiping (Birkhead and Møller, 1992; Hawkes et al., 2001; Aiello, in press).

22. As attractive as the idea of male provisioning might be in relation to solving the problem of high female reproductive costs, there is reason to believe that preferential male provision of his own mate and offspring is NOT the norm. Although adult men in foraging societies have a considerably higher daily energy production than adult females (Kaplan et al., 2000), their partners and children frequently do not directly benefit from the male's resource acquisition (Hawkes et al., 2001). Also, there is no evidence in foraging societies studied that death or departure of the father has any significant effect on the well-being of the children (Blurton-Jones et al., 2000). How can we reconcile these results with the needs of the females?

23. Group Size as a Solution. The crucial factor that has been missing so far in the argument is group size. Where the hunting success of males is sporadic but success produces large returns, the desired group size would be one that assured a reasonably constant supply of a limiting resource. In this context, it does not matter why or how food provided by the male is distributed as long as it is distributed in the group and the size of that group is such as to insure that male-provided resources supplement those provided by the females to the degree required to support their reproductive energy requirements.

Summary

24. There are a number of basic correlates of a higher-quality diet across primates and other mammals that are shared by humans but are not specific to them. These include increased sociality (Milton, 1999), a larger home range (Leonard and Robertson, 1994, 1997), an elevated daily energy requirement (Leonard and Robertson, 1994, 1997) and slower growth in the offspring (Bogin and Smith, 1996).

25. This contribution goes beyond this and has shown that the dietary and energetic implications of the combination of a relatively large brain size and large body size in humans make the evolution of cooperation inevitable and can also be used to explain many of the physical and life history features that we recognize today as human.

26. Although we do not know when these features developed during the course of human evolution, it is probable that the evolution of a relatively larger brain size and of a large body size, and particularly large body size in females with the appearance of *Homo ergaster,* set the train in motion.

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Energetics and the Evolution of Brain Size in Early *Homo*

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Introduction

Anthropologists have increasingly begun to rely on energetic models to understand the patterns and trends in hominin evolution (e.g. Aiello and Wheeler, 1995; Leonard and Robertson, 1994, 1997; Leonard, 2002). The acquisition of food energy, its consumption, and ultimately its allocation for biological processes are all critical aspects of an organism's ecology (McNab, 2002). In addition, from the perspective of evolution, the goal for all organisms is the same – to allocate sufficient energy to reproduction to ensure their genes are passed on to future generations. Consequently, by looking at the ways in which animals go about acquiring and then allocating energy, we can better understand how natural selection produces important patterns of evolutionary change. This approach is particularly useful in studying human evolution, because it appears that many important transitions in the hominin lineage – the evolution of bipedality, the expansion of brain size and the initial colonization of northern climes – had implications for energy allocation (Leonard, 2002).

In this chapter, we use an energetic approach to gain insights into the evolution of brain size with the emergence of the genus *Homo*. We begin by looking at the energy demands associated with large brain size in modern humans relative to other primates and other mammals. We then examine the hominin fossil record to gain insights into changes in brain size, foraging strategies and dietary patterns associated with the evolution of early *Homo*. Both the comparative and fossil evidence suggest that the increased metabolic costs of larger brain sizes in the genus *Homo* were dependent upon the changes in dietary quality and alterations in body composition. Although we do not know the specific components of the diet of early *Homo*, it does appear that these hominins consumed a diet of greater energy and nutritional density than their australopithecine ancestors. In addition, it also appears that expansion of the brain size in the hominin lineage was associated with potential reductions in muscularity and/or gastrointestinal (GI) mass and increases in adiposity (body fatness).

Metabolic demands of large brain size

What is remarkable about the large human brain is its high metabolic cost. The energy requirements of brain tissue are about 29 kcal/100 grams/day, roughly 16 times that of skeletal muscle tissue (Kety, 1957; Holliday, 1986). This means that for a 70 kg adult human with a brain weight of about 1400 grams, over 400 kcal per day are allocated to brain metabolism. Yet despite the fact that humans have much larger brains than most other mammals, the total energy demands for our body – our resting energy requirements – are no greater than those of a comparably sized mammal (Kleiber, 1961; Leonard and Robertson, 1992).

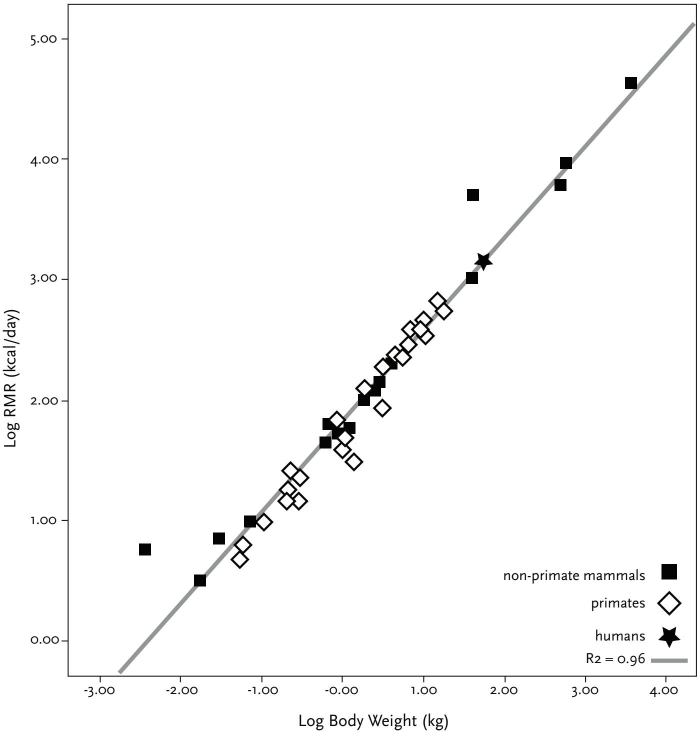

Fig. 1. Log-Log plot of resting metabolic rate (RMR; kcal/day) versus body weight (kg) for 51 species of terrestrial mammals (20 non-primate mammals, 30 primates, and humans). Humans conform to the general mammalian scaling relationship, as described by Kleiber (1961). The scaling relationship for the entire sample is: RMR = 69(Wt$^{0.755}$). Data are from Leonard et al. (2003) and Snodgrass et al. (1999).

This point is evident in Figure 1, which shows the relationship between resting metabolic rate (RMR; kcal/day) and body weight (kg) in non-primate mammals, primates, and humans. Humans conform to the general mammalian scaling relationship between RMR and body weight (the "Kleiber relationship"), in which energy demands scale to the 3/4th power of body weight (Kleiber, 1961):

$$\text{RMR (kcal/day)} = 70\text{wt}^{0.75}$$

The implication of this is that humans allocate a much larger share of their daily energy budget to brain metabolism than other species. This is evident in Figure 2, which shows the scaling relationship between brain weight (grams) and RMR for the same species noted in Figure 1.

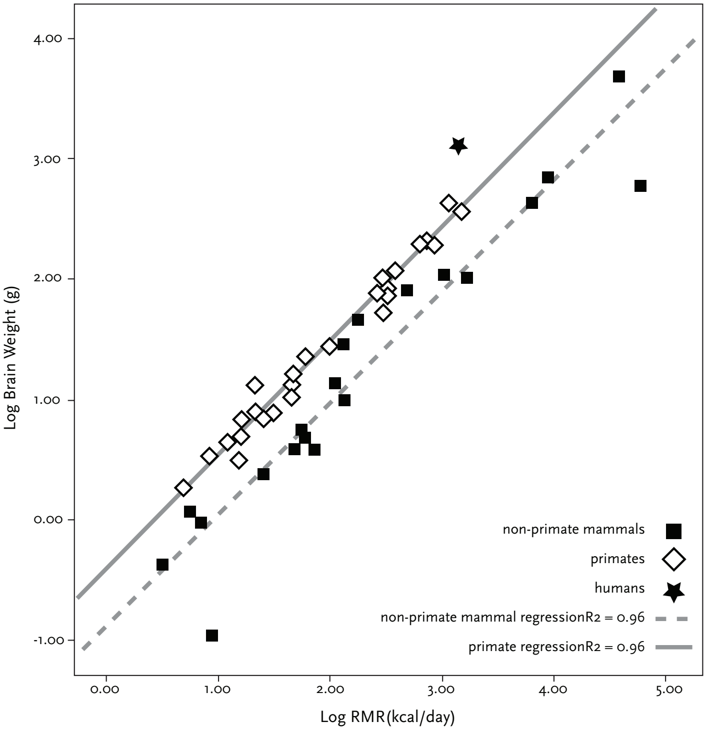

Fig. 2. Log-Log plot of brain weight (BW;g) versus RMR (kcal/day) for 51 species of terrestrial mammals. The primate regression line is systematically and significantly elevated above the non-primate mammal regression. The scaling relationships are: non-primate mammals: $BW = 0.13(RMR^{0.92})$; primates: $BW = 0.38(RMR^{0.95})$. Thus, for a given RMR, primates have brain sizes that are three times those of other mammals, and humans have brain sizes that are three times those of other primates.

We find that at a given metabolic rate, primates have systematically larger brain sizes than other mammals, and humans, in turn, have larger brain sizes than other primates. Adult humans allocate 20-25% of their RMR to brain metabolism, approximately three times that of other primates (~7-9% of RMR), and nine times that of non-primate mammals (about 3% of RMR).

Important dimensions of human nutritional biology appear to be associated with the high-energy demands of our large brains. Humans consume diets that are more dense in energy and nutrients than other primates of similar size. For example, Cordain et al. (2000) have shown that modern human foraging populations typically derive 45-65% of their dietary energy intake from animal foods. In comparison, modern great apes obtain much of their diet from low-quality plant foods. Gorillas derive over 80% of their diet from fibrous foods such as leaves and bark (Richard, 1985). Even among chimpanzees, only about 5% of their calories are derived from animal foods, including insects (Teleki, 1981; Stanford, 1996). Meat and other animal foods are more concentrated sources of calories and nutrients than most of the plant foods typically eaten by large-bodied primates. This

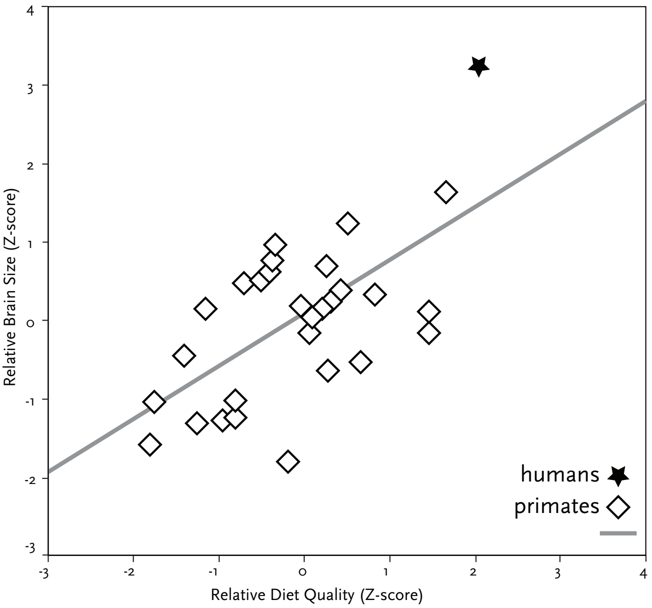

Fig. 3. Plot of relative brain size versus relative diet quality for 31 primate species (including humans). Primates with higher quality diets for their size have relatively larger brain size ($r = 0.63$; $P < 0.001$). Humans represent the positive extremes for both measures, having large brain:body size and a substantially higher quality diet than expected for their size. Adapted from Leonard et al. (2003).

higher-quality diet means that humans need to eat a smaller volume of food to get the energy and nutrients they require.

Comparative analyses of living primate species (including humans) support the link between brain size and dietary quality. Figure 3 shows relative brain size versus dietary quality (an index based on the relative proportions of leaves, fruit, and animal foods in the diet) for 31 different primate species (adapted from Leonard et al., 2003). There is a strong positive relationship ($r = 0.63$; $P < 0.001$) between the amount of energy allocated to the brain and the caloric and nutrient density of the diet. Across all primates, larger brains require higher-quality diets. Humans fall at the positive extremes for both parameters, having the largest relative brain size and the highest quality diet. This relationship implies that the evolution of larger hominin brains would have necessitated the adoption of a sufficiently high-quality diet to support the increased metabolic demands of greater encephalization.

The relative size and morphology of the human gastrointestinal (GI) tract also reflect our high-quality diet. Most large-bodied primates have expanded large intestines (colons), an adaptation to fibrous, low-quality diets (Milton, 1987). This is evident in Figure 4, which shows the relative sizes of the colon and small intestines in humans and the great apes. In all three ape species, the colon accounts for over half of the GI volume and is greatly expanded over the size of the small intestine. Humans, on the other hand, have relatively enlarged small intestines and a reduced colon.

The enlarged colons of most large-bodied primates permits fermentation of low-quality plant fibers, allowing for extraction of additional energy in the form of volatile fatty acids (Milton and Demment, 1988; Milton, 1993). In contrast, the GI morphology of humans (small colon and relatively enlarged small intestine) is more similar to a carnivore, and reflects an adaptation to an easily digested, nutrient-rich diet (Sussman, 1987; Martin, 1989).

Together, these comparative data suggest that the dramatic expansion of brain size over the course of human evolution likely would have required the consumption of a diet that was more concentrated in energy and nutrients than is typically the case for most large primates. This *does not* imply that dietary change was the driving force behind major brain expansion during human evolution. Rather, the available evidence indicates that a sufficiently high-quality diet was probably a necessary condition for supporting the metabolic demands associated with evolving larger hominin brains.

Brain evolution in early Homo

The human fossil record indicates that the first substantial burst of evolutionary change in hominin brain size occurred about 2.0 to 1.7 million years ago, associat-

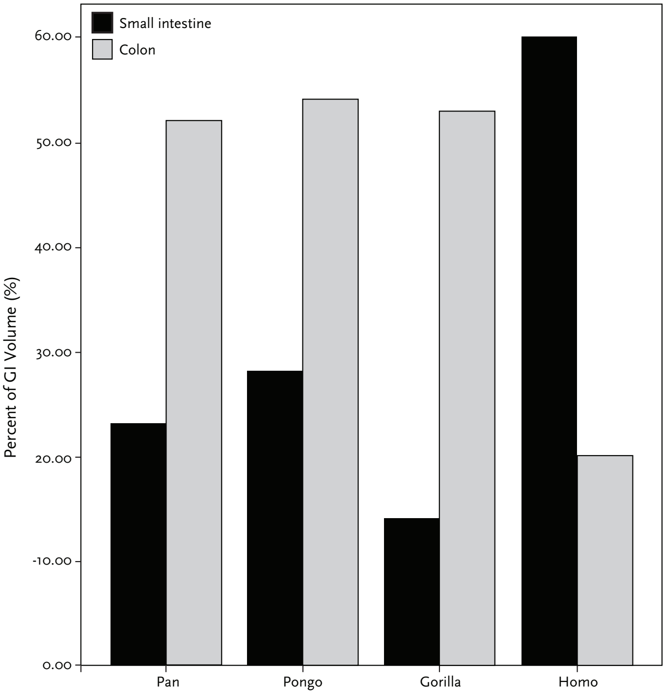

Fig. 4. Relative proportions of the small intestine and large intestine (colon) in modern humans (*Homo sapiens*) and the great apes (*Pan troglodytes, Pongo pygmaeus, Gorilla gorilla*). The colon volume of humans is markedly smaller than that of all three great apes (20% of GI volume vs. > 50% in the apes), and is indicative of adaptation to a higher-quality and more easily digested diet. Data derived from Milton (1987).

ed with the emergence and evolution of early members of the genus *Homo*. Table 1 presents data on evolutionary changes in hominin brain size (cm^3), estimated adult male and female body weights (kg) and posterior tooth area (mm^2). The australopithecines showed only modest brain size evolution from about 430 to 530 cm^3 over more than 2 million years (from about 4 to 1.5 million years ago). However, with the evolution of the genus *Homo*, there were substantial increases in encephalization, with brain sizes of over 600 cm^3 in *Homo habilis* (at 1.9 – 1.6 mya) and 800-900 cm^3 in early members of *Homo erectus* (at 1.8 – 1.5 mya). Although the relative brain size of *Homo erectus* is smaller than the average for modern humans, it is outside of the range seen among other living primate species (Leonard and Robertson, 1994).

Changes in the craniofacial and dental anatomy of *Homo erectus* suggest that these forms were consuming different foods than their australopithecine ancestors. During the evolution of the australopithecines, the total surface area of the grinding teeth (molars and premolars) increased dramatically from 460 mm^2 in *A.*

Table 1. Geological ages (millions of years ago), brain size (cm³), estimated male and female body weights (kg), and postcanine tooth surface areas (mm²) for selected fossil hominid species.

Species	Geological age (mya)	Brain size (cm³)	Body Weight Male (kg)	Body Weight Female (kg)	Postcanine tooth surface (mm²)
A. afarensis	3.9-3.0	438	45	29	460
A. africanus	3.0-2.4	452	41	30	516
A. boisei	2.3-1.4	521	49	34	756
A. robustus	1.9-1.4	530	40	32	588
Homo habilis (*sensu stricto*)	1.9-1.6	612	37	32	478
H. erectus (early)	1.8-1.5	863	66	54	377
H. erectus (late)	0.5-0.3	980	60	55	390
H. sapiens	0.4-0.0	1350	58	49	334

All data from McHenry and Coffing (2000), except for *Homo erectus*. Early *H. erectus* brain size is the average of African specimens as presented in McHenry (1994b), Indonesian specimens from Antón and Swisher (2001) and Georgian specimens from Gabunia et al. (2000, 2001). Data for late *H. erectus* are from McHenry (1994a).

afarensis to 756 mm² in *A. boisei*. In contrast, with the emergence of early *Homo* at approximately 2 million years ago, we see marked reductions in the posterior dentition. Postcanine tooth surface area is 478 mm² in *H. habilis* and 377 mm² in early *H. erectus*.

H. erectus also shows substantial reductions in craniofacial and mandibular robusticity relative to the australopithecines (Wolpoff, 1999). Yet, despite having smaller teeth and jaws, *H. erectus* was a much bigger animal than the australopithecines, being human-like in its stature, body mass and body proportions (McHenry, 1992, 1994a; Ruff and Walker, 1993; Ruff et al., 1997; McHenry and Coffing, 2000). Together these features indicate that early *Homo erectus* was consuming a richer, more calorically dense diet with less low-quality fibrous plant material. How the diet might have changed with the emergence of *H. erectus* is examined in the following section.

Dietary changes associated with brain evolution in early Homo

The marked increases in brain and body size coupled with the reductions of posterior tooth size and craniofacial robusticity all suggest that there was a shift in the composition and quality of the diet consumed by *H. erectus*. However, there remains considerable debate over what kinds of dietary changes likely occurred during this period of human evolution. The most widely held view is that the diet of early *Homo* included more animal foods (Stanford and Bunn, 2001). The environment at the Plio-Peistocene boundary (2.0 – 1.8 mya) was becoming increasingly drier, creating more arid grasslands (Vrba, 1995; Reed, 1997; Owen-Smith, 1999). These changes in the African landscape made animal foods more abundant and, thus, an increasingly attractive food resource (Behrensmeyer et al., 1997). Specifically, when we examine modern ecosystems, we find that although savanna/grasslands have much lower net primary productivity than woodlands (4050 vs. 7200 kcal/m^2/yr), the level of herbivore productivity in savannas is almost three times that of the woodlands (10.2 vs. 3.6 kcal/m^2/yr) (Leonard and Robertson, 1997). Thus, fundamental changes in the ecosystem structure during the Plio-Pleistocene transition likely resulted in a net increase in the energetic abundance of game animals in the African landscape. Such an increase would have offered an opportunity for hominins with sufficient capability to exploit the animal resources.

The archaeological record provides evidence that this occurred with *Homo erectus* – the development of the first rudimentary hunting and gathering economy in which game animals became a significant part of the diet and resources were shared within foraging groups (Potts, 1988; Harris and Capaldo, 1993; Roche et al., 1999). These changes in diet and foraging behaviour would not have turned our hominin ancestors into carnivores; however, the addition of even modest amounts of meat to the diet (10-20% of dietary energy), combined with the sharing of resources that is typical of hunter-gatherer groups, would have significantly increased the quality and stability of hominin diets.

Greater consumption of animal foods also would have provided increased levels of key fatty acids that would have been necessary for supporting the rapid brain evolution seen with the emergence of *H. erectus*. Mammalian brain growth is dependent upon sufficient amounts of two long-chain polyunsaturated fatty acids (PUFAs): docosahexaenoic acid (DHA) and arachidonic acid (AA) (Crawford et al., 1999; Cordain et al., 2001). Because the composition of all mammalian brain tissue is similar with respect to these two fatty acids, species with higher levels of encephalization have greater requirements for DHA and AA (Crawford et al., 1999). It also appears that mammals have a limited capacity to synthesize these fatty acids from dietary precursors. Consequently, dietary sources of DHA and AA were likely limiting nutrients that constrained the evolution of larger brain size in many mammalian lineages (Crawford, 1992; Crawford et al., 1999).

Cordain and colleagues (2001) have shown that the wild plant foods available on the African savanna (e.g., tubers, nuts) contain, at most, trace amounts of AA and DHA, whereas muscle tissue and organ meat of wild African ruminants provide

Table 2. Energy (kcal), fat (g), protein (g), arachidonic acid (AA) and docosahexaenoic acid (DHA) contents of African ruminant, fish and wild plant foods per 100 grams. Data derived from Cordain et al. (2001).

Food item	Energy (kcal)	Fat (g)	Protein (g)	AA (mg)	DHA (mg)
African ruminant (brain)	126	9.3	9.8	533	861
African ruminant (liver)	159	7.1	22.6	192	41
African ruminant (muscle)	113	2.1	22.7	152	10
African ruminant (fat)	745	82.3	1.0	20-180	trace
African fish	119	4.5	18.8	270	549
Wild tuber/roots	96	0.5	2.0	0	0
Mixed wild plants	129	2.8	4.1	0	0

moderate to high levels of these key fatty acids. As shown in Table 2, brain tissue is a rich source of both AA and DHA, whereas liver and muscle tissues are good sources of AA and moderate sources of DHA. Other good sources of AA and DHA are freshwater fish and shellfish (Broadhurst et al., 1998; Crawford et al., 1999; Cordain et al., 2001). Cunnane and colleagues (Cunane and Crawford, 2003; Broadhurst et al., 1998) have suggested that the major increases in hominin encephalization were associated with systematic use of aquatic or marine or lacustrine resources. However, there is little archaeological evidence for the systematic use of aquatic resources until later in human evolution (Klein, 1999).

An alternative strategy for increasing dietary quality in early *Homo* has been proposed by Wrangham and colleagues (1999, 2003). These authors argue that the controlled use of fire for cooking allowed early *Homo* to improve the nutritional density of their diet. They note that the cooking of savanna tubers and other plant foods would have served to both soften them and increase their energy/nutritional content. In their raw form, the starch in roots and tubers is not absorbed in the small intestine and is passed through the body as non-digestible carbohydrate (Tagliabue et al., 1995; Englyst and Englyst, 2005). However, when heated, the starch granules swell and are disrupted from the cell walls. This process, known as gelatinization, makes the starch much more accessible to breakdown by digestive enzymes (García-Alonso and Goñi, 2000). Thus, cooking increases the nutritional quality of tubers by making more of the carbohydrate energy available for biological processes.

Although cooking is clearly an important innovation in hominin evolution, which served to increase dietary digestibility and quality, there is very limited evidence for the controlled use of fire by hominins before 1.5 million years ago (Bellomo, 1994; Brain and Sillen, 1988; Pennisi, 1999). The more widely held view is that the use of fire and cooking did not occur until later in human evolution, at 200-250,000 years ago (Straus, 1989; Weiner et al., 1998). In addition, nutritional analyses of wild tubers used by modern foraging populations (e.g., Wehmeyer et al., 1969; Brand-Miller and Holt, 1998; Schoeninger et al., 2001) suggest that the energy content of these resources is markedly lower than that of animal foods, even after cooking (Cordain et al., 2001). Unlike animal foods, tubers are also devoid of both DHA and AA (Cordain et al., 2001; see Table 2). Consequently, there remain major questions about whether cooking and the heavy reliance on roots and tubers were important forces for promoting rapid brain evolution with the emergence of early *Homo*.

Overall, the available evidence seems to best support a mixed dietary strategy in early *Homo* that involved the consumption of larger amounts of animal foods than with the australopithecines. Ungar and colleagues (2006) have recently suggested that early *Homo* likely pursued a “flexible” and “versatile” subsistence strategy that would have allowed them to adapt to the patchy and seasonally variable distribution of food resources on the African savanna. They note that such a model is more plausible than ones proposing heavy reliance on one particular type of resource (e.g. meat or tubers). This is indeed true; however, what appears to be happening with early *Homo* – especially with *H. erectus* – is the development of a more stable and effective way of extracting resources from the environment. The increase in dietary quality and stability was likely achieved partly through changes in diet composition (Leonard and Robertson, 1994; Cordain et al., 2001) and partly through social and behavioural changes like food sharing and perhaps division of foraging tasks (Isaac, 1978; Kaplan et al., 2000). This greater nutritional stability provided a critical foundation for fueling the energy demands of larger brain sizes.

Implications of changes in body composition for brain evolution

In addition to improvements in dietary quality, the increased metabolic cost of larger brain size in human evolution also appears to have been supported by changes in body composition. Because humans allocate a substantially larger share of their daily energy budget to their brains than do other primates or other mammals, this implies that the size and metabolic demands of certain other organs/organ systems may be relatively reduced in humans compared with other species. Thus, the critical question is: which organs have been reduced or altered in their relative size over the course of human evolution to compensate for the expansion of brain size?

Analyses of human and primate body composition offer possible answers to this question. Aiello (1997; this volume) and Aiello and Wheeler (1995) have argued that the increased energy demands of the human brain were accommodated by the reduction in size of the GI tract. Since the intestines are similar to the brain in having very high energy demands (so-called "expensive tissues"), the reduction in size of the large intestines of humans, relative to other primates, is thought to provide the necessary energy "savings" required to support elevated brain metabolism. Aiello and Wheeler (1995) have shown that among a sample of 18 primate species (including humans), increased brain size was associated with reduced gut size. However, recent analyses by Snodgrass et al. (1999) have failed to demonstrate the significant differences in GI size between primates and non-primate mammals that are predicted from the "expensive tissue hypothesis". Thus, questions remain about the extent to which reductions in GI size may have accommodated the dramatic expansion of brain size during the course of human evolution. Leonard and colleagues (2003) and Kuzawa (1998) have suggested that differences in muscle and fat mass between humans and other primates may also account for the variation in budgeting of metabolic energy. Relative to other primates and other mammals, humans have lower levels of muscle mass and higher levels of body fatness (Leonard et al., 2003). The relatively high levels of body fatness (adiposity) in humans have two important metabolic implications for brain metabolism. First, because fat has lower energy requirements than muscle tissue, replacing muscle mass with fat mass results in energy "savings" that can be allocated to the brain. Additionally, fat provides a ready source of stored energy that can be drawn upon during periods of limited food availability. Consequently, the higher levels of body fat in humans may also help to support a larger brain size by providing stored energy to buffer against environmental fluctuations in nutritional resources.

Table 3. Body weight (kg), brain weight (g), percent body fat (%), resting metabolic rate (RMR; kcal/day), and percent of RMR allocated to brain metabolism (BrMet, %) for humans from birth to adulthood.)[a]

Age	Body weight (kg)	Brain weight (g)	Body fat (%)	RMR (kcal/day)	BrMet (%)
New born	3.5	475	16	161	87
3 months	5.5	650	22	300	64
18 months	11.0	1045	25	590	53
5 years	19.0	1235	15	830	44
10 years	31.0	1350	15	1160	34
Adult male	70.0	1400	11	1800	23
Adult female	50.0	1360	20	1480	27

)[a] All data are from Holliday (1986), except for percent body fat data for children 18 months and younger, which are from Dewey et al. (1993).

The importance of body fat is particularly notable in human infants, which have both high brain to body weight ratios and high levels of body fatness. Table 3 shows age-related changes in body weight (kg), brain weight (g), fatness (%), RMR (kcal/day) and percent of RMR allocated to the brain for humans from birth to adulthood. We see that in infants, brain metabolism accounts for upwards of 60% of RMR. Human infants are also considerably fatter than those of other mammalian species (Kuzawa, 1998). Body fatness in human infants is about 15-16% at birth, and continues to increase to 25-26% during the first 12 to 18 months of postnatal growth. Fatness then declines to about 15% by early childhood (Dewey et al., 1993). Thus, during early human growth and development, it appears that body fatness is highest during the periods of the greatest metabolic demand of the brain.

It is likely that fundamental changes in body composition (i.e., the relative sizes of different organ systems) during the course of hominin evolution allowed for the expansion of brain size without substantial increases in the total energy demands for the body. At present, we do not know which alterations were the most critical for accommodating brain expansion. Variation in body composition both within and between primate species is still not well understood. Among humans, our knowledge of variation in body composition is based largely on data from populations of the industrialized world. Consequently, more and better data on interspecific and ontogenetic variation in primate and human body composition are necessary to further resolve these issues.

New imaging techniques such as magnetic resonance imaging (MRI) and positron emission tomography (PET scans) offer the potential to directly explore variation in organ weight and organ-specific energy demands in living humans and primates. For example, Gallagher et al. (2006) recently used MRI technology to measure how differences in organ weights contribute to ethnic differences in RMRs among living humans. These authors demonstrated that the significant differences in RMR between their African-American and Euroamerican samples could be accounted for by differences in the summed weight of the most metabolically expensive organs (liver, heart, spleen, kidneys and brain). Similarly, Chugani (1998) has recently utilized PET scans to quantify changes in glucose utilization in the human brain from birth to adulthood. His findings suggest that the extremely high metabolic costs of brain metabolism characteristic of early human life (as outlined in Table 3) may extend further into childhood than previously realized. Together these studies highlight the potential use of new imaging techniques to improve our understanding of how interspecific variation in body composition contributes to differences in metabolic rate.

Conclusions

An energetic perspective is particularly useful for understanding the evolution of brain size in the hominin lineage. Large human brain sizes have important metabolic consequences as humans expend a relatively larger proportion of their resting energy budget on brain metabolism than other primates or non-primate mammals. The high costs of large human brains are supported, in part, by diets that are relatively rich in energy and other nutrients. Among living primates, the relative proportion of metabolic energy allocated to the brain is positively correlated with dietary quality. Humans fall at the positive end of this relationship, having both a very high-quality diet and a large brain size.

Greater encephalization also appears to have consequences for other aspects of body composition. Comparative primate data indicate that humans are "under-muscled", having relatively lower levels of skeletal muscle than other primate species of similar size. Conversely, levels of body fatness are relatively high in humans, particularly in infancy. These greater levels of body fatness and reduced levels of muscle mass allow human infants to accommodate the growth of their large brains in two important ways: (1) by having a ready supply of stored energy to "feed the brain" and (2) by reducing the total energy costs of the rest of the body.

With the emergence and evolution of the genus *Homo* between 2.0 and 1.7 mya, we find the first major pulse of brain evolution in the hominin lineage. The corresponding changes in craniofacial anatomy and postcanine tooth size, coupled with evidence from the archaeological record, suggest that these hominins were consuming a higher-quality and more stable diet that would have helped to fuel the increases in brain size.

Further research is needed to better understand the nature of the dietary changes that took place with the emergence of *Homo*. In addition, the application of new biomedical imaging techniques offers the potential to directly explore how intra- and interspecific variation in body composition may contribute to the variation in metabolic rates.

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The Evolution of Diet, Brain and Life History among Primates and Humans

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Introduction

This paper presents a theory of the brain and lifespan evolution and applies it to both the primate order, in general, and to the hominin line, in particular. To address the simultaneous effects of natural selection on the brain and on the lifespan, it extends standard life history theory (LHT) in biology, which organizes research into the evolutionary forces shaping age-schedules of fertility and mortality (Cole, 1954; Gadgil and Bossert, 1970; Partridge and Harvey, 1985). This extension, *the embodied capital theory* (Kaplan, 1997; Kaplan et al., 2000b; Kaplan and Robson, 2001b), integrates existing models with an economic analysis of capital investments and the value of life.

The chapter begins with a brief introduction to embodied capital theory, and then applies it to understanding major trends in primate evolution and the specific characteristics of humans. The evolution of brain size, intelligence and life histories in the primate order are addressed first. The evolution of the human life course is then considered, with a specific focus on the relationship between cognitive development, economic productivity, and longevity. It will be argued that the evolution of the human brain entailed a series of co-evolutionary responses in human development and aging. It concludes with a discussion of several unresolved issues raised at this workshop.

The embodied capital theory of life history evolution

According to the theory of evolution by natural selection, the evolution of life is the result of a process in which variant forms compete to harvest energy from the environment and convert that energy into replicates of those forms. Those forms that can capture more energy than others and can convert the energy they acquire more efficiently into replicates than others become more prevalent through time. This simple issue of harvesting energy and converting energy into offspring generates many complex problems that are time-dependent.

Two fundamental tradeoffs determine the action of natural selection on reproductive schedules and mortality rates. The first tradeoff is between current and future reproduction. By growing, an organism can increase its energy capture rates in the future and thus increase its future fertility. For this reason, organisms typically have a juvenile phase in which fertility is zero until they reach a size at which some allocation to reproduction increases lifetime fitness more than growth. Similarly, among organisms that engage in repeated bouts of reproduction (humans included), some energy during the reproductive phase is diverted away from reproduction and allocated to maintenance so that it can live to reproduce again. Natural selection is expected to optimize the allocation of energy to current reproduction and to future reproduction (via investments in growth and maintenance) at each point in the life course so that genetic descendents are maximized (Gadgil and Bossert, 1970). Variation across taxa and across conditions in optimal energy allocations is shaped by ecological factors, such as food supply, disease and predation rates.

A second fundamental life history tradeoff is between offspring number (quantity) and offspring fitness (quality). This tradeoff occurs because parents have limited resources to invest in offspring, and each additional offspring produced necessarily reduces the average investment per offspring. Most biological models operationalize this tradeoff as number vs. survival of offspring (Lack, 1954; Smith and Fretwell, 1974; Lloyd, 1987). However, parental investment may not only affect survival to adulthood, but also the adult productivity and fertility of offspring. This is especially true of humans. Thus, natural selection is expected to shape investment per offspring and offspring number so as to maximize offspring number times their average lifetime fitness.

The embodied capital theory generalizes existing life history theory by treating the processes of growth, development and maintenance as investments in stocks of somatic, or embodied, capital. In a physical sense, embodied capital is organized somatic tissue – muscles, digestive organs, brains, etc. In a functional sense, embodied capital includes strength, speed, immune function, skill, knowledge and other abilities. Since such stocks tend to depreciate with time, allocations to maintenance can also be seen as investments in embodied capital. Thus, the present-future reproductive trade-off can be understood in terms of optimal investments in own embodied capital vs. reproduction, and the quantity-quality trade-off can be understood in terms of investments in the embodied capital of offspring vs. their number.

The brain as embodied capital

The brain is a special form of embodied capital. Neural tissue is involved in monitoring the organism's internal and external environment, and organizing physiological and behavioural adjustments to those stimuli (Jerison, 1976). Portions (particularly the cerebral cortex) are also involved in transforming past and present experience into future performance. Cortical expansion among higher primates, along with enhanced learning abilities, reflects increased investment in transforming present experience into future performance (Armstrong and Falk, 1982; Fleagle, 1999).

The action of natural selection on neural tissue involved in learning and memory should depend on costs and benefits realized over the organism's lifetime. Three kinds of costs are likely to be of particular importance. First, there are the initial energetic costs of growing the brain. Among mammals, those costs are largely borne by the mother during pregnancy and lactation. Second, there are the energetic costs of maintaining neural tissue. Among infant humans, about 65% of all resting energetic expenditure supports maintenance and growth of the brain (Holliday, 1978). Third, certain brain capacities may actually decrease performance early in life. Specifically, the ability to learn and increased behavioural flexibility may entail reductions in "pre-programmed" behavioural routines. The incompetence with which human infants and children perform many motor tasks is an example.

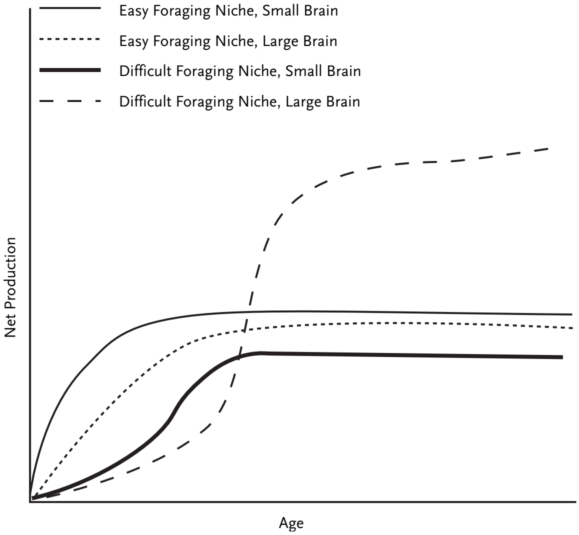

Fig. 1. Age-specific effects of brains on net production: easy and difficult foraging niches.

Some allocations to investments in brain tissue may provide immediate benefits (e.g., perceptual abilities, motor coordination). Other benefits of brain tissue are only realized as the organism ages. The acquisition of knowledge and skills has benefits that, at least in part, depend on their impact on future productivity. Figure 1 illustrates two alternative cases, using as an example the difficulty and learning-intensiveness of the organism's foraging niche. In the easy feeding niche where there is little to learn and information to process, net productivity (excess energy above and beyond maintenance costs of brain and body) reaches its asymptote early in life.

There is a relatively small impact of the brain on productivity late in life (because there has been little to learn), but there are higher costs of the brain early in life. Unless the lifespan is exceptionally long, natural selection will favour the smaller brain.

In the difficult food niche, the large-brain creature is slightly worse off than the small-brain one early in life (because the brain is costly, and learning is taking place), but much better off later in life. The effect of natural selection will depend upon the probabilities of reaching an older age. If those probabilities are sufficiently low, the small brain will be favoured, and if they are sufficiently high, the large brain will be favoured. Thus, selection on learning-based neural capital depends not only on its immediate costs and benefits, but also upon mortality schedules which affect the expected gains in the future.

Selection on mortality schedules

In standard LHT models, mortality is generally divided into two types: (1) extrinsic mortality (i.e. mortality that is imposed by the environment and is outside the organism's control, such as predation or winter) and (2) intrinsic mortality (hazards of mortality over which the organism can exert some control over the short run or which is subject to selection over longer periods). In most models of growth and development, mortality is treated as extrinsic (Kozlowski and Wiegert, 1986; Charnov, 1993) and therefore as a causal agent, not subject to selection. Models of aging and senescence (Promislow, 1991; Shanley and Kirkwood, 2000) typically focus on aging-related increases in intrinsic mortality. From this point of view, extrinsic mortality is thought to affect selection on rates of aging, with higher mortality rates favouring faster aging.

This distinction between types of mortality is problematic. Organisms can exert control over virtually all causes of mortality in the short or long run. Susceptibility to predation can be affected by vigilance, choice of foraging zones, travel patterns and anatomical adaptations, such as shells, cryptic coloration and muscles facilitating flight. Each of those behavioural and anatomical adaptations has energetic costs (lost time foraging, investments in building and maintaining tissue) that reduce energy available for growth and reproduction. Similar observations can be made regarding disease and temperature. The extrinsic mortality concept has been convenient, because it has provided a causal agent for examining other life history traits, such as age of first reproduction and rates of aging. However, this has prevented the examination of how mortality rates themselves evolve by natural selection.

Since all mortality is, to some extent, intrinsic or "endogenous", a more useful approach is to examine the functional relationship between mortality and the effort allocated to reducing it (see Figure 2). Exogenous variation can be thought of in terms of varying "assault" types and varying "assault" rates of mortality hazards. For example, warm, humid climates favour the evolution of disease organisms, and therefore the assault rate and diversity of diseases on organisms living in those climates are increased. Such exogenous variation would affect the functional relationship between actual mortality hazards such as disease and endogenous effort allocated to reduce it by mounting immunological defences. The outcome mortality rate is neither extrinsic nor intrinsic.

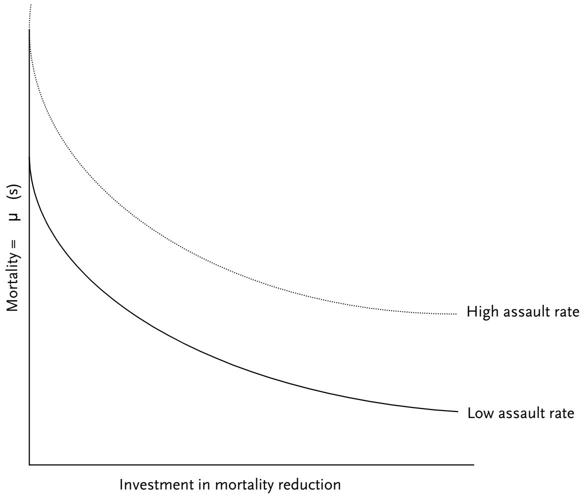

Fig. 2. Mortality rate as a function of investments.

Kaplan and Robson (2001a, 2001b) have developed formal models to analyze the simultaneous effects of natural selection on investments in both capital and reducing mortality. As a first step, it is useful to think of capital generally (interpreted as the bundle of functional abilities embodied in the soma). Organisms generally receive some energy from their parents (e.g., in the form of energy stored in eggs) to produce an initial stock of capital. Net energy acquired from the environment grows at each age as a function of the capital stock, with diminishing returns to capital (as illustrated in Figure 3).

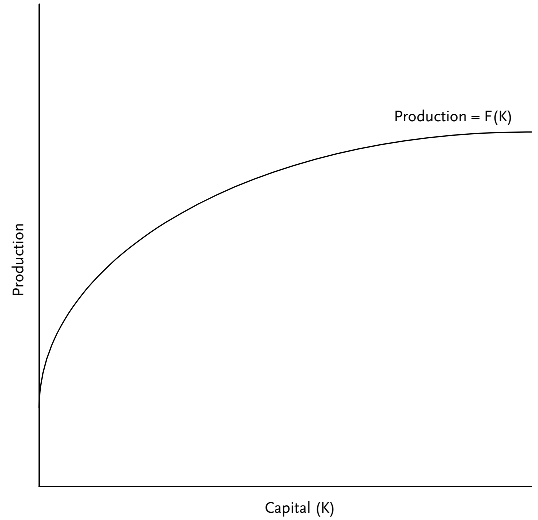

Fig. 3. Production as a function of the capital stock.

This energy can be used in three ways, which are endogenous and subject to selection. It can be reinvested in increasing the capital stock (e.g. growth of the body or brain). Some energy may also be allocated to reducing mortality (for example, in the form of increased immune function as illustrated above in Figure 2). The probability of reaching any age will be a function of mortality rates at each earlier age. Finally, energy can also be used for reproduction, which is the net excess energy available after allocations to capital investments and mortality reduction. An optimal life history programme would optimize allocations to capital investments, mortality reduction, and reproduction at each age so as to maximize total energy allocations to reproduction over the life course. This, of course, depends both on reproductive allocations and on survival.

The results of the analysis, which are presented and proven formally in Kaplan and Robson (2001a), are illustrated in Figures 4a, 4b, and 4c. During the capital investment period, the value of life (which is equal to total expected future net production) increases with age, since productivity grows with increased capital. The optimal value of investment in mortality reduction also increases, since the effect of a decrease in mortality increases as capital increases. This is illustrated in Figure 4a. At some age, a steady state is reached when capital is at its optimum level, and both capital and mortality rates remain constant.

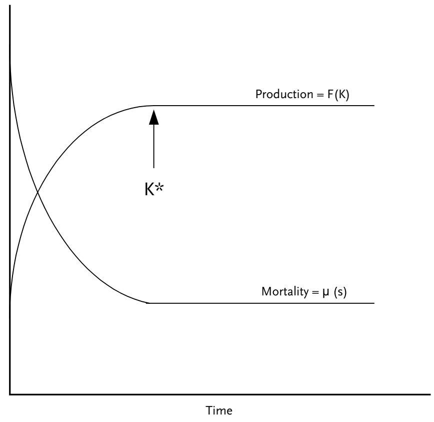

Fig. 4a. The optimal life history.

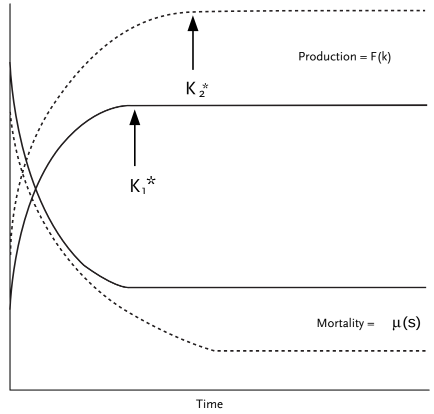

Fig. 4b. The optimal life history with a productivity shift.

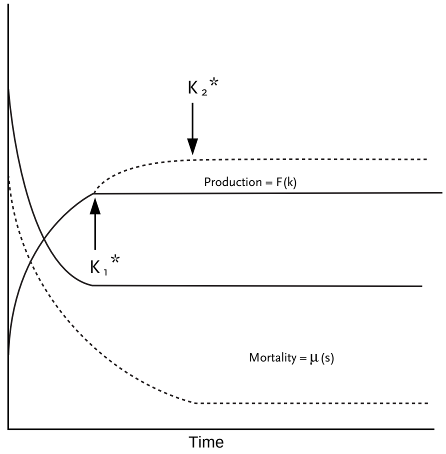

Fig. 4c. The optimal life history with a mortality shift.

Figures 4b and 4c show two important comparative results. In Figure 4b, the impact of a change in productivity is shown. Some environmental change that increases productivity (holding the marginal value of capital constant) has two reinforcing effects: it increases the optimal level of both capital investment (and hence the length of the investment period) and efforts to reduce mortality. Figure 4c shows the impact of a reduction in mortality rates, again with two effects. It increases the optimal capital stock (because it increases the expected length of life and hence the time over which it will yield returns) and produces a reinforcing increase in effort at reducing mortality, since the impact of a decrease in mortality is greater as mortality rates decrease.

Finally, the model shows that a shift in productivity from younger to older ages (for example, an increased reliance on learning that lowers juvenile energy production but increases adult production) increases the value of living to older ages and therefore optimal effort at reducing mortality. This has the effect of increasing the expected lifespan. Our theory is that brain size and longevity co-evolve for the following reasons. Ecological conditions favouring large brains also select for greater endogenous investments in staying alive. As the stock of knowledge and functional abilities embodied in the brain grow with age, so too does the value of the capital investment. This favours greater investments in health and mortality avoidance. In addition, holding the value of the brain constant, ecological conditions that lower mortality select for increased investment in brain capital for similar reasons; an increased probability of reaching older ages increases the value of investments whose rewards are realized at older ages. The next section applies this logic to the brain and lifespan evolution in the Primate order.

Brain and lifespan evolution among primates

The theoretical and empirical model

Relative to other mammalian orders, the Primate order can be characterized as slow-growing, slow-reproducing, long-lived and large-brained. The radiation of the order over time has involved a series of four directional grade shifts towards slowed life histories and increased encephalization (i.e. brain size relative to body size). Even the more “primitive” prosimian primates are relatively long-lived and delayed in reaching reproductive maturity compared to mammals of similar body size, which suggests the same of early primate ancestors. Austad and Fischer (1991, 1992) relate this evolutionary trend in the primates to the safety provided by the arboreal habitat and compare primates to birds and bats, which are also slow-developing and long-lived for their body sizes. Thus, the first major grade shift that separated the Primate order from other mammalian orders was a change to a lowered mortality rate and the subsequent evolution of slower senescence rates, leading to longer lifespans and slightly larger brains.

The second major grade shift occurred with the evolution of the anthropoids (the lineage containing monkeys, apes and humans), beginning about 35 mya. Its major defining characteristic is the reorganization of the sensory system to one dominated by binocular, colour vision as opposed to olfaction and hearing in association with hand-eye coordination. These sensory changes co-occurred with an increased emphasis on plant foods (especially hard seeds and fruits), as opposed to insects (Fleagle, 1999; Benefit, 2000). The grade shift is also seen in brain size and life history. Regressions of log brain size on log body size (Barton, 1999) as well as log maximum lifespan on body size (Allman et al., 1993) show significant differences in intercept between strepsirhine (including most prosimians) and haplorhine (including all anthropoids and a few prosimian) primates. Relative to prosimians, anthropoids also have lower metabolic rates and longer gestation times (Martin, 1996).

The evolution of monkey and ape dietary adaptations in the Miocene and Pliocene appears to be based on an early adaptation for both groups to feed on hard seeds and green fruit (Benefit, 2000). In the Late Miocene/Early Pliocene cercopithecoids, which had been semi-terrestrial, cursorial, hard seed and green fruit eaters much like modern vervet monkeys, evolved new digestive adaptations allowing the colobines to digest mature leaves. Cercopithecoids also began to compete more directly with apes in both terrestrial and arboreal habitats. Miocene apes were highly diverse and found in many habitats but were essentially agile arboreal quadrupeds. By the Late Miocene apes had fully developed their characteristic shoulder girdle morphology, allowing suspension below branches that gave special access to ripe fruits for larger bodied animals. This dietary shift to dependence on ripe fruits, based on the morphological adaptation of arm suspension, moved apes into a new grade with an emphasis on feeding higher in the food pyramid on very nutritious food packets high in energy but spatially and temporally dispersed in an arboreal habitat. This new grade reduced direct competition with monkeys, ceded open terrestrial habitat to them, and greatly reduced the number and diversity of ape species. At the same time it put a premium on acquired knowledge about the location of ripe fruits and for skills for more complex extractive foraging of embedded and protected, high-energy and fatty foods such as nuts, insects, and hard-shelled fruits.

This third major grade shift marked the evolution of the hominoid lineage (leading to apes and humans). This grade shift entailed further encephalization, as revealed by a yet greater intercept of log brain size regressed on log body size and superior performance on most tasks reflecting higher intelligence (Byrne, 1995, 1997; Parker and McKinney, 1999). The divergence of the hominin line, and particularly the evolution of the genus *Homo*, defined the fourth major grade shift.

The brain size and lifespan of modern humans are very extreme values among mammals, and even among primates. Although the record is incomplete, it appears that brain enlargement and life history shifts co-occurred. Early *Homo ergaster* shows both significant brain expansion and a lengthened developmental period (Smith, 1993), but much less so than modern humans. Neandertals display both brain sizes and dental development that are in the same range as modern humans. Modern humans have a brain size about three times that of female gorillas of similar weight, and about double the maximum lifespan.

The proposal here is that both shifts in mortality risks and in the benefits of information storage and processing due to changes in feeding niche underlie these directional changes in the primate lineage through time. However, in addition to these large-scale shifts, there exists a great deal of adaptive variation among primates. Species of all four grades continue to co-exist, often sympatrically (especially monkeys, apes and humans). Moreover, not all evolutionary change has been in the direction of larger brains and longer lives. For example, smaller-brained monkeys appear to have replaced apes in some niches at the end of the Miocene (Fleagle, 1999; Benefit, 2000). If changes in mortality risks and the learning intensiveness of the feeding niche explain the grade shifts, the same factors might also explain variation within grades.

Figure 5 illustrates the theory and the empirical model that it generates, given the available data. On the left, the two rounded boxes represent exogenous ecological

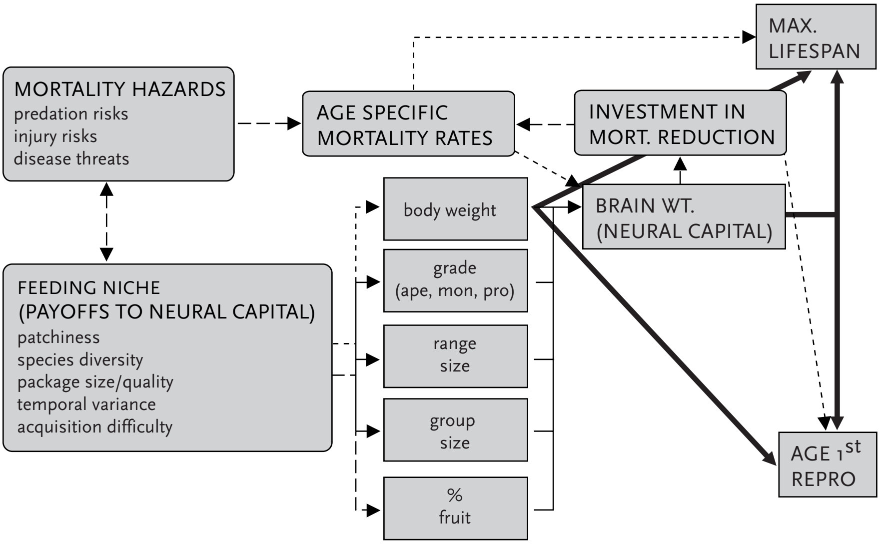

Fig. 5. A theoretical and empirical path model of primate brain evolution.

variables.[1] Some features of the feeding niche that are likely to affect the payoffs for information acquisition and processing (and hence, brain size) are listed in the lower box. Resource patchiness tends to be associated with larger home ranges and potentially greater demands on spatial memory. The number of different species consumed potentially adds to demands for spatial memory, learned motor patterns, processing of resource characteristics, and temporal associations (Jerison, 1973). Large, nutrient-dense packages (such as big, ripe fruits) tend to be patchily distributed in space and often with very short windows of availability (Clutton-Brock and Harvey, 1980; Milton, 1981, 1993). Year-to-year abundance and location of high-quality packages also appear to vary. Hence, diets with a greater relative importance of large, high-quality packages are probably associated with increased brain size through several routes: by increasing the number of species exploited, by increasing the size of the home range, and by increasing the importance of predicting the timing and location of availability. In addition, some high-quality foods, such as hard-shelled fruits, nuts, insects, and honey, must be extracted from protective casings, and their exploitation often requires learned strategies and tools.
Features of the environmental/behavioural niche of the organism that are likely to affect mortality rates and the payoffs of investments in mortality reduction are listed in the upper left box. Life in or near trees probably increases injury risk, but decreases predation risk for overall lower mortality risks. Lowered risk of mortality due to predation is expected to increase investment in combating disease and, hence, decrease disease risks as well (though these have received little attention in primate studies to date). Lower mortality rates increase the probability of reaching older ages and therefore affect the payoffs for larger brains, holding the feeding niche constant.

The co-evolution of brain size and mortality patterns is shown in the path diagram (dashed arrows depict effects of unmeasured conceptual or latent variables). Both features of the feeding niche and mortality risks affect the optimal brain size. Brain size is expected to have both direct and indirect effects on lifespan and age of first reproduction. Larger brains may confer direct survival advantages through increased physiological efficiency and through learned predator avoidance (Jerison, 1973; Armstrong, 1982; Allman et al., 1993; Hakeem et al., 1996; Rose and Mueller, 1998). In addition, since larger brains are associated with greater relative productivity at older ages, brain size is expected to be associated with investment in mortality reduction. Similarly, the energetic costs of the brain reduce energy available for growth, and learning-based feeding niches may lower productivity during the juvenile period. This would produce slower growth rates and a later age of first reproduction, holding body size constant. The greater allocations to mortality reduction (e.g. increased immune function, reduced foraging time) would also slow the growth rates.

The rectangular boxes depict measured variables for which comparative data are available, and the solid arrows depict associations that can be tested empirically. The thinner lines represent the first stage in the model, predicting brain weight. Measures of feeding niche are captured by grade (ape, monkey, vs. prosimian), range size, and percentage of fruit in the diet. We also include body and group size in this first stage. In addition to directly affecting brain size, body size is likely to be associated with dietary niche. For example, larger bodies probably favour the exploitation of larger home ranges because of their greater locomotor efficiency. Larger body masses are also associated with larger home ranges since larger animals need to work harder to get enough food (Leonard and Robertson, 2000). Furthermore, larger home ranges may also be associated with larger groups, because holding resource abundance constant, a patchy environment will tend to produce both larger home ranges and a larger number of individuals feeding at each resource patch (Wrangham, 1979). Because the social intelligence hypothesis has figured so prominently in the literature (Byrne, 1995; Barton and Dunbar, 1997; Dunbar, 1998), the path between group size and brain size is also included. In addition, if social intelligence takes time to acquire and its benefits are weighted towards older ages (as may well be the case), embodied capital theory does predict that selection on social intelligence will co-evolve with longevity and mortality rates. For example, social intelligence might allow alpha males to retain their high status to older ages, and it might confer greater benefits on females when they

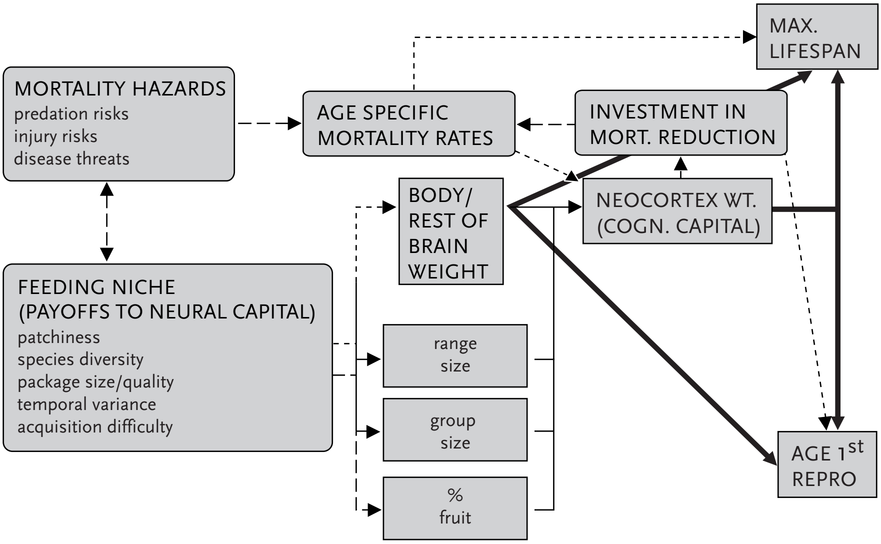

Fig. 6. A theoretical and empirical path model of neocortex evolution.

have many descendants (in the case of ranked matrilines). Such effects would also be consistent with the model. The second stage, shown with bold arrows, examines the effects of brain size and body size on age of first reproduction and maximum-recorded lifespan, respectively.

A second model will also be tested (see Figure 6). The logic of the embodied capital model suggests that the brain functions that are most involved in transforming present experience into future performance should have the greatest impact on the payoffs to living longer and allocating effort to mortality reduction. In addition, it has been argued that the association of brain size with lifespan in primates, after controlling for body size, is spurious and due to greater measurement error in body size than in brain size (Economos, 1980; Dunbar, 1998). However, Allman and colleagues (1993) have shown that brain size is a better predictor of lifespan than the size of other organs. To address these issues, the size of the neocortex will be disaggregated from the rest of the brain. The neocortex should better reflect the learning-intensiveness of the feeding niche and social system than the rest of the brain. In the second model, neocortex weight replaces brain weight, and the weight of the rest of the brain replaces body weight, as an instrument (since measurement error for neocortex and rest of brain weight, respectively, should be similar). Other people have measured the proportional ratio of neocortex to the rest of the brain (Dunbar, 1998). Rather than using a ratio that combines neocortex with the rest of the brain in one variable but is incapable of disentangling the independent effects of two different parts of the brain, we prefer placing both measures, the neocortex and the rest of the brain, in the regression analysis. Others have utilized the same approach looking at neocortex size but with a very small sample (Barton, 2000).

The primate sample

Data are available on the total adult brain weights (in grams) for 124 species, compiled from secondary sources (Harvey et al., 1987; Barton, 1999). From this sample, there are 95 species for which data are available on mean adult body weight (in grams), group size, age at first breeding for females (in months), maximum lifespan (in years), maximum home range (in hectares), and percent frugivory. Much of the data came from secondary sources (Harvey et al., 1987; Dunbar, 1992; Ross, 1992; Barton, 1996, 1999). These data differ, however, from previous analyses in a heavier reliance on primary field data for female age at first breeding, maximum home range, and percent frugivory (see details Kaplan et al., 2001). They may thus more accurately represent the selection pressures faced by wild individuals, which are assumed to be living under conditions much more representative of the context in which these features co-evolved.

Data analysis

A two-stage least squares regression analysis was performed to test the models. For the model in Figure 5, the first stage was conducted hierarchically. First, the natural logarithm of brain weight was regressed on the natural logarithms of body weight, range size, and group size, and on percentage of fruit in the diet. Then to capture other aspects of niche differentiation, grade (ape and monkey, compared to a prosimian baseline) was added as a fixed effect to determine if it significantly improved the model.

Results

The results are presented in Table 1. In the simple model without grade, body weight, range size and percentage of fruit in the diet are each positively related to brain weight, accounting for 94% of the variance. Group size was not significant. Grade significantly improved the model fit ($p<.0001$) with the model now accounting for 97% of the variance. In this model, percentage of fruit is no longer

Table 1. Two-stage model of brain size and life history.

A. Stage I, Brain Weight

	R^2=.94, N= 95				R^2=.97, N= 97			
Parameter	**B**	**Std. Error**	**t**	**Sig.**	**B**	**Std. Error**	**t**	**Sig.**
Intercept	-1.74	0.16	-11.22	0.0000	-1.74	0.16	-11.22	0.0000
Body wt.	0.68	0.03	23.01	0.0000	0.59	0.02	24.83	0.0000
Range size	0.05	0.03	1.95	0.0550	0.05	0.02	2.54	0.0130
Group size	0.07	0.04	1.64	0.1040	0.07	0.04	2.02	0.0468
Perc. fruit	0.00	0.00	2.65	0.0100	0.00	0.00	1.46	0.1484
Ape	.	.	.	0.87	0.10	8.73	0.0000	
Monkey	.	.	.	0.45	0.07	6.42	0.0000	
Prosimian	.	.	.	0.00	.	.	.	

B. Stage II

	Maximum lifespan, R^2=.52, N=80				Age of first reproduction, R^2=.74, N=79			
Parameter	**B**	**Std. Error**	**t**	**Sig.**	**B**	**Std. Error**	**t**	**Sig.**
Intercept	3.14	0.34	9.32	0.0000	2.78	0.37	7.58	0.0000
Body wt.	-0.24	0.10	-2.36	0.0208	-0.21	0.11	-1.99	0.0503
Brain wt.	0.53	0.13	4.12	0.0001	0.71	0.14	5.19	0.0000

significant, but group size is. The predicted values of log brain size from this full model are then used in the second stage of the analysis[2].

Part B of Table 1 shows the results of the second stage in which the natural logarithms of female age at first reproduction and maximum reported lifespan, respectively, were regressed on the logs of predicted brain weight and body weight. In both cases, brain weight explains most of the variance, and the effect of body weight is negative. When brain weight is not in the model, the association between body weight and both lifespan and age of first reproduction is, of course, strongly positive. It may be that after controlling for brain weight, larger bodied species eat lower quality diets (Milton, 1981, 1987, 1988, 1993; Milton and Demment, 1988; Aiello and Wheeler, 1995), which is associated with a relatively shorter lifespan and earlier age at first reproduction.

The results of decomposing brain weight into the neocortex and the rest of the brain (Figure 6) are shown in Tables 2 and 3. Using the same set of regressors as in the full model of brain size, the natural logarithms of the weights of the rest of the brain and of the neocortex (shown on the left and right sides of Table 2, respectively) are each treated as dependent variables. Body weight and grade are the only variables that significantly affect the weight of non-neocortical brain tissue, and the effect of grade is rather small. With respect to neocortex weight, however, both range size and grade have large effects. Thus, consistent with the above logic, feeding niche has a larger effect on neocortex weight than on the rest of the brain, which appears to be more a function of body weight.

In Table 3, the weight of the rest of the brain is used as an instrument for body weight in Stage 1 of the model. This model shows that neocortical weight increases more than proportionally with the rest of the brain (b = 1.1), and that both

Table 2. Neocortex and rest of brain weight.

	Rest of brain weight (brain wt-neocortex wt), R^2=.94, N=32				**Neocortex weight, R^2=.98, N=32**			
Parameter	**B**	**Std. Error**	**t**	**Sig.**	**B**	**Std. Error**	**t**	**Sig.**
Intercept	-2.03	0.30	-6.66	0.0000	-2.46	0.25	-9.68	0.0000
Body wt.	0.55	0.05	10.42	0.0000	0.57	0.04	13.02	0.0000
Range size	0.08	0.04	1.79	0.0860	0.12	0.04	3.41	0.0020
Group size	-0.05	0.07	-0.68	0.5010	0.02	0.06	0.28	0.7800
Perc. fruit	0.00	0.00	0.42	0.6810	0.00	0.00	0.77	0.4470
Ape	0.51	0.23	2.25	0.0330	0.89	0.19	4.64	0.0000
Monkey	0.27	0.16	1.73	0.0950	0.71	0.13	5.51	0.0000
Prosimian	0.00	.	.	.	0.00	.	.	.

Table 3. Two-stage model of neocortex size and life history.

Stage I				
Neocortex size, R^2=.996, N=32				
Parameter	**B**	**Std. Error**	**t**	**Sig.**
Intercept	-0.26	0.05	-5.03	0.0000
Rest of brain wt.	1.10	0.03	31.83	0.0000
Range size	0.01	0.02	0.76	0.4556
Group size	0.06	0.03	2.35	0.0270
Perc. fruit	0.00	0.00	0.88	0.3871
Ape	0.52	0.09	5.99	0.0000
Monkey	0.47	0.06	8.29	0.0000
Prosimian	0.00	.	.	.

Stage II				
Maximum lifespan, R^2=.70, N=32				
Parameter	**B**	**Std. Error**	**t**	**Sig.**
Intercept	2.66	0.11	25.21	0.0000
Rest of brain wt.	-0.20	0.24	-0.83	0.4122
Neocortex wt.	0.38	0.19	2.05	0.0506
Age of first reproduction, R^2=.79, N=32				
Intercept	2.49	0.14	17.42	0.0000
Rest of brain wt.	-0.30	0.31	-0.99	0.3304
Neocortex wt.	0.64	0.24	2.69	0.0119

grade and group size have large significant effects. In the second stage, predicted neocortical weight is positively associated with both age at first reproduction and maximum lifespan, while the rest of the brain is not significantly associated with the life history variables. This is also consistent with the model. These results should be treated with some caution, however, because the two measures of brain weight are highly collinear. In these analyses, species were treated as independent data points. We also conducted a similar set of analyses using independent phylogenetic contrasts. Here, we present results on contrasts that assume equal branch lengths (analyses using contrasts weighted by transformed branch lengths yielded similar results and are available from the authors upon request). In Stage 1 regressions, brain weight was positively predicted by body weight (t(Bailey) = 15.11, $p < .001$) and range size ($t[86] = 3.99$, $p < .001$). Neither group size nor percent fruit in the diet independently contributed to prediction, both $t < 1$, ns. In Stage 2 regressions, brain weight predicted both maximum lifespan ($t[88] = 3.33$, $p < .005$) and age at first reproduction (brain weight: $t[88] = 2.39$, $p < .02$). Body weight did not predict either of these variables in these analyses (maximum lifespan: $t[88] = -1.36$, ns; age at first reproduction: $t[88] = .24$, ns).

The evolution of **Homo**: *chimpanzees and modern humans compared*

The same principles may explain the very long lives and the very large brains characteristic of the genus *Homo* and particularly of modern *Homo sapiens*. *Homo* has existed for about 2 million years. Figure 7 shows human ancestors experienced a dramatic increase in brain size, but a much less marked increase in body size, especially during the second half of this period. Using Martin's (Martin, 1981) measure of "Encephalization Quotient (*EQ*)" (i.e., brain weight corrected allometrically for body weight, with $EQ = \dfrac{(brain\ wt)}{11.22 * (body\ wt)^{.76}}$ one is the average value for a mammal), the large increases in brain size relative to body size are shown with the bold line. *Australopithecus*, the presumed evolutionary ancestor of *Homo*, coexisted with early *Homo*. *A. boisei*, in particular, had an *EQ* of just over two, which compares to about 3.5 for early *Homo*. Lifespans of extinct species are not directly observable, of course, but indirect evidence suggests the lifespan of australopithecines was much less than that of modern humans and comparable to that of chimpanzees (Smith, 1991), with early species in the genus *Homo* having lifespans that are intermediate between chimpanzees and modern humans (Smith, 1993).

Hominins have subsisted on hunting and gathering, perhaps supplemented by scavenging, for all but the last 10,000 years of our evolutionary history. Our proposal (Kaplan, 1997; Kaplan et al., 2000b; Kaplan and Robson, 2001b) is that the hunting and gathering way of life is responsible for the evolution of these extreme values with respect to brain size and longevity. Large brains and long lives are coevolved responses to an equally extreme commitment to learning-intensive foraging strategies and a dietary shift towards high quality, nutrient-dense, and difficult-to-acquire food resources. The following logic underlies this proposal. First, high levels of knowledge, skill, coordination, and strength are required to exploit the suite of high-quality, difficult-to-acquire resources humans consume. The attainment of those abilities requires time and a significant commitment to development. This extended learning phase during which productivity is low is compensated for by higher productivity during the adult period, with an intergenerational flow of food from old to young. Since productivity increases with age, the time investment in skill acquisition and knowledge leads to selection for lowered

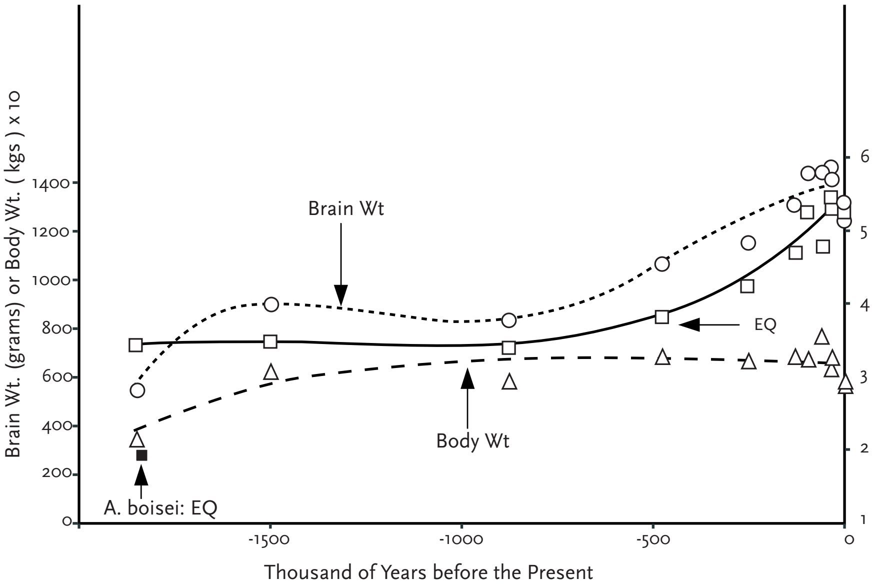

Fig. 7. Hominin brain size and body weight.

mortality rates and greater longevity, because the returns on the investments in development occur at older ages.

Second, the feeding niche specializing in large, valuable food packages, and particularly hunting, promotes cooperation between men and women and high levels of male parental investment, because it favours sex-specific specialization in embodied capital investments and generates a complementarity between male and female inputs. The economic and reproductive cooperation between men and women facilitates provisioning of juveniles, which both bankrolls their embodied capital investments and acts to lower mortality during the juvenile and early adult periods. Cooperation between males and females also allows women to allocate more time to childcare and raises nutritional status, increasing both survival and reproductive rates. Finally, large packages also appear to promote inter-familial food sharing. Food sharing assists recovery in times of illness and reduces risk of food shortfalls due to both the vagaries of foraging luck and the variance in family size due to stochastic mortality and fertility. These buffers against mortality also favour a longer juvenile period and higher investment in other mechanisms to increase lifespan.

Thus, the proposal is that the long human lifespan co-evolved with the lengthening of the juvenile period, increased brain capacities for information processing and storage, and intergenerational resource flows – all as a result of an important dietary shift. Humans are specialists in that they only consume the highest quality plant and animal resources in their local ecology and rely on creative, skill-intensive techniques to exploit them. Yet, the capacity to develop new techniques for extractive foraging and hunting allows them to exploit a wide variety of different foods and to colonize all of the earth's terrestrial and coastal ecosystems.

The best available evidence for evaluating this theory is to compare wild living chimpanzees, human's closest living relatives, with contemporary hunter-gatherers who still depend on foraging for subsistence and who have little or no access to Western medicine. Both chimpanzees and contemporary foragers have been affected by current global trends, such as war, deforestation, population movements, and other effects of modern economies. They cannot be treated as replicas of the evolutionary past. Nevertheless, the differences in the diets, survival rates, and age-profiles of productivity between chimpanzees and contemporary hunter-gatherers are striking and consistent with the theory.

Diet, survival and age profiles of productivity among chimpanzees and contemporary hunter-gatherers

Diet

There are ten foraging societies and five chimpanzee communities for which caloric production or time spent feeding were monitored systematically (Kaplan et al., 2000b). Modern foragers all differ considerably in diet from chimpanzees. Measured in calories, the major component of forager diets is vertebrate meat. This ranges from about 30% to around 80% of the diet in the sampled societies with most diets consisting of more than 50% vertebrate meat (equally weighted mean = 60%), whereas chimpanzees obtain about 2% of their food energy from hunted foods.

The next most important food category in the forager sample is extracted resources, such as roots, nuts, seeds, most invertebrate products, and difficult to extract plant parts such as palm fiber or growing shoots. They may be defined as non-mobile resources that are embedded in a protective context such as under the ground, in hard shells or bearing toxins that must be removed before they can be consumed. In the ten foraging societies sampled, extracted foods accounted for about 32% of the diet, as opposed to 3% among chimpanzees.

In contrast to hunted and extracted resources, which are difficult to acquire, collected resources form the bulk of the chimpanzee diet. Collected resources, such as fruits, leaves, flowers, and other easily accessible plant parts are simply gathered and consumed. They account for 95% of the chimpanzee diet, on average, and only 8% of the forager diet.

The data suggest that humans specialize in rare but nutrient-dense resource packages or patches (meat, roots, nuts), whereas chimpanzees specialize in ripe fruit and low nutrient density plant parts. These differences in nutrient density of foods ingested are also reflected in human and chimpanzee gut morphology and food passage time, with chimpanzees specialized for rapid processing of large quantities and low nutrient, bulky, fibrous meals (Milton, 1999).

The age profile of acquisition for collected, extracted, and hunted resources

In most environments, fruits are the easiest resources that people acquire. Daily production data among Ache foragers show that both males and females reach their peak daily fruit production by their mid to late teens. Some fruits that are simply picked from the ground are collected by two- to three-year-olds at 30% of the adult maximum rate. Ache children acquire five times as many calories per day during the fruit season as during other seasons of the year (Kaplan, 1997). Similarly, among the Hadza, teenage girls acquired 1650 calories per day during the wet season when fruits were available and only 610 calories per day during the dry season when fruits were not. If we weight the wet and dry season data equally, Hadza teenage girls acquire 53% of their calories from fruits, compared to 37% and 19% for reproductive-aged and post-reproductive women, respectively (Hawkes et al., 1989).

In contrast to fruits, the acquisition rate of extracted resources often increases through early adulthood as foragers acquire the necessary skills. Data on Hiwi women show that root acquisition rates do not asymptote until about age 35-45 (Kaplan et al., 2000b) and the rate of 10- year-old girls is only 15% of the adult maximum. Hadza women appear to obtain maximum root digging rates by early adulthood (Hawkes et al., 1989). Hiwi honey extraction rates by males peak at about age 25. Again the extraction rate of 10-year-olds is less than 10% of the adult maximum. Experiments done with Ache women and girls clearly show that young adult girls are not capable of extracting palm products at the rate obtained by older Ache women (Kaplan et al., 2000b). Ache women do not reach peak return rates until their early 20s. !Kung (Ju/'hoansi) children crack mongongo nuts at a much slower rate than adults (Blurton Jones et al., 1994), and Bock (1995) has shown that nut cracking rates among the neighbouring Hambukushu do not peak until about age 35. Finally, chimpanzee juveniles also focus on more easily acquired resources than adult chimpanzees. Difficult to extract activities such as termite and ant fishing or nut cracking are practiced less by chimpanzee juveniles than adults (Silk, 1978; Hiraiwa-Hasegawa, 1990; Boesch and Boesch, 1999).

Human hunting differs qualitatively from hunting by other animals and is the most skill-intensive foraging activity. Unlike most animals that either sit and wait to ambush prey or use stealth and pursuit techniques, human hunters use a wealth of information to make context-specific decisions, both during the search phase of hunting and then after prey are encountered. Specifically, information on ecology, seasonality, current weather, expected animal behaviour, and fresh animal signs are all integrated to form multivariate mental models of encounter probabilities that guide the search and are continually updated as conditions change (Liebenberg, 1990). Various alternative courses of action are constantly compared and referenced to spatial and temporal mental maps of resource availability (ibid.). This information is collected, memorized and processed over much larger spatial areas than chimpanzees ever cover. For example, interviews with Ache men show that fully adult men (aged 35+) had hunted in an area of nearly 12,000 km^2 of tropical forest in their lifetimes. Almost all foragers surveyed use more than 200 km^2 in a single year, and many cover more than 1,000 km^2 in a year (Kelly, 1995, Table 4.1). Male chimpanzees, on the other hand, cover only about 10 km^2 in a lifetime (Wrangham, 1975; Wrangham and Smuts, 1980).

In addition, humans employ a wide variety of techniques to capture and kill prey, using astounding creativity (Kaplan et al., 2000b). Those kill techniques are tailored to many different prey under a wide variety of conditions. For example, from 1980 to 1996 our sample of weighed prey among the Ache includes a minimum of 78 different mammal species, at least 21 species of reptiles and amphibians, probably over 150 species of birds (more than we have been able to identify) and over 14 species of fish. Finally, human hunters tend to select prey that is in prime condition from the perspective of human nutritional needs rather than prey made vulnerable by youth, old age or disease as do so many carnivorous animals (Stiner, 1991; Alvard, 1995).

The skill-intensive nature of human hunting and the long learning process involved are demonstrated dramatically by data on hunting return rates by age. Hunting return rates among the Hiwi do not peak until age 30-35 with the acquisition rate of 10-year-old and 20-year-old boys reaching only 16% and 50% of the adult maximum, respectively. The hourly return rate for Ache men peaks in the mid-30s. The return rate of 10-year-old boys is about 1% of the adult maximum, and the return rate of 20-year-old juvenile males is still only 25% of the adult maximum. Marlowe (unpublished data) obtains similar results for the Hadza. Also, boys switch from easier tasks, such as fruit collection, shallow tuber extraction and baobab processing, to honey extraction and hunting in their mid to late teens among the Hadza, Ache and Hiwi (Blurton Jones et al., 1989, 1997; Kaplan et al., 2000b). Even among chimpanzees, hunting is strictly an adult or sub-adult activity (Teleki, 1973; Stanford, 1998; Boesch and Boesch, 1999).

Survival and net food production

Figure 8 (Kaplan et al., 2000b) shows probabilities of survival and net production (i.e. food acquired minus food consumed) by age. The chimpanzee net production curve shows three distinct phases. The first phase, to about age 5, is the period of complete to partial dependence upon mother's milk and of negative net produc-

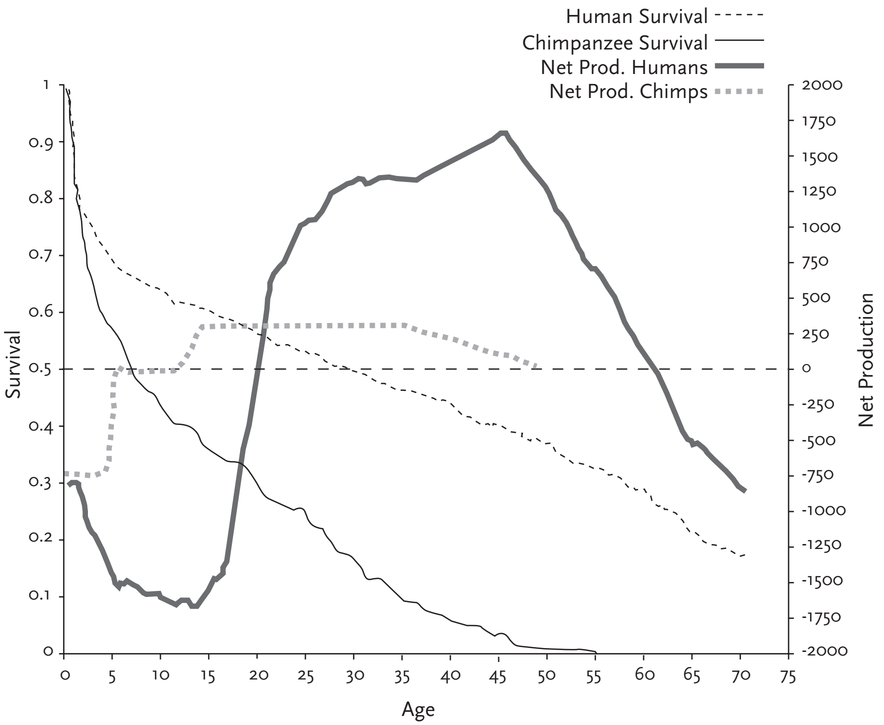

Fig. 8. Survival and net food production: human foragers and chimpanzees. On the left vertical axis is the probability of survival and on the right, is net production in calories per day. The data on chimpanzee survival are derived from averaging age-specific mortality rates from all five study sites where systematic data on births and deaths are recorded (Hill et al., 2001); data on chimpanzee food consumption and production are from Gombe (Goodall, 1986). Human survival rates are averaged from Ache (Hill and Hurtado, 1996), Hiwi (Kaplan et al., 2000a), and Hadza (Blurton Jones et al., 2002). Net production data are from the same groups (details on all sources and estimation procedures for the both human and chimpanzee production and consumption data are in Kaplan et al., 2000b.

tion. The second phase is independent juvenile growth, lasting until adulthood, during which net production is zero. The third phase is reproductive, during which females, but not males, produce a surplus of calories that they allocate to nursing.

Humans, in contrast, produce less than they consume for about 20 years. Net production becomes increasingly negative until about age 14 and then begins to climb. Net production in adult humans is much higher than in chimpanzees and peaks at a much older age, reflecting the payoff of long dependency. More precisely, human peak net production is about 1,750 calories per day, reached at about age 45. Among chimpanzee females, peak net production is only about 250 calo-

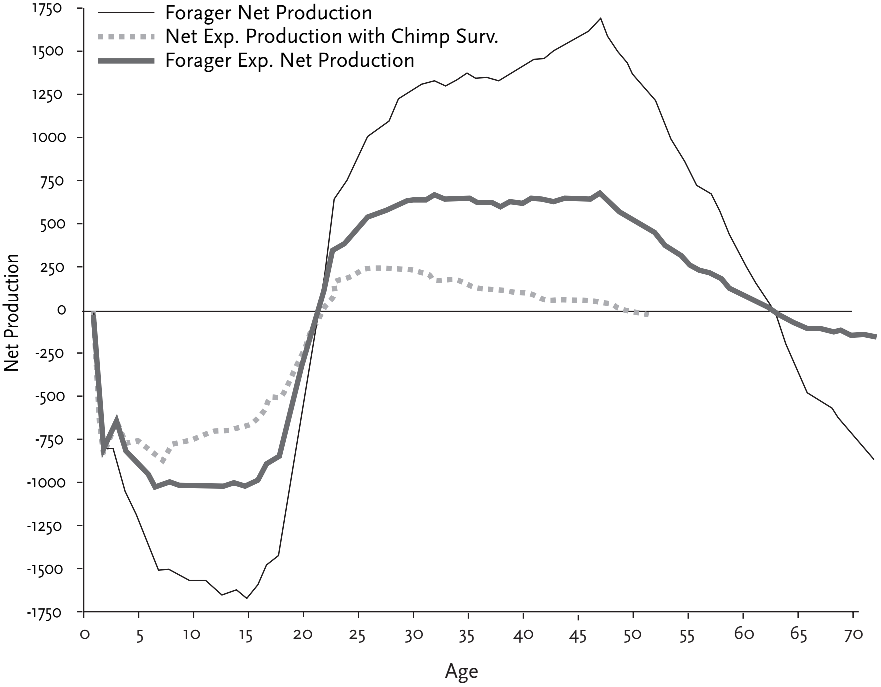

Fig. 9. Expected net production.

ries per day, and since fertility decreases with age, net productivity probably decreases throughout adulthood.

The survival curves, using the scale on the right-hand y-axis of Figure 8, reveal why the human age-profile of productivity requires a long adult lifespan. Only about 30% of chimpanzees ever born reach 20, the age when humans produce as much as they consume. Less than 5% of chimpanzees reach 45 when human net production peaks, but more than 15% of hunter-gatherers survive to age 70. By age 15, chimpanzees have consumed 43% and produced 40% of their expected lifetime calories, respectively; in contrast, humans have consumed 22% and produced only 4% of their expected lifetime calories!

The relationship between survival rates and age-profiles of production is made even clearer in Figure 9. The thin solid line plots net production by age for foragers (as in Figure 8). The bold line shows expected net production for foragers, which is net production at each age multiplied by the probability of being alive at each age. The area of the "deficit" period, prior to age 20, is about the same size as the surplus after age 20. The dashed line shows the hypothetical "contrary to fact" expected net production profile of a human forager with a chimpanzee survival function. The area of the deficit is now much larger than the area of the surplus, since very few individuals survive to the highly productive ages. This shows that the human production profile would not be viable with chimpanzee survival rates, because expected lifetime net production would be negative.

Development and cognitive function among monkeys, apes and humans

Although it has long been recognized that human intelligence is our most distinctive specialization as a species, it is now becoming increasingly clear that our larger brains and greater intellectual capacities depend upon the elongation or stretching out of development at every stage. The production of cortical neurons in mammals is limited to early foetal development and compared to monkeys and apes, human embryos spend an additional 25 days in this phase (Deacon, 1997; Parker and McKinney, 1999). The greater original proliferation of neurons in early foetal development has cascading effects in greatly extending other phases of brain development, ultimately resulting in a larger, more complex, and effective brain. For example, in monkeys, such as macaques, myelination of the brain begins prenatally and is largely complete within a few months after birth, but in humans continues to at least 12 years of age (Gibson, 1986). Dendritic development is similarly extended to age 20 or greater in humans.

The timing of cognitive development is extended in chimpanzees relative to monkeys, and in humans relative to apes (Parker and McKinney, 1999). In terms of Piagetian stages, frequently used by comparative cognitive psychologists, macaque monkeys traverse only two subperiods of cognitive development regarding physical phenomena by about six months of age and peak in their logical abilities by about three years of age; however, they fail to be able to represent objects symbolically, to classify objects hierarchically, or to recognize themselves in a mirror. Chimpanzees traverse three to four subperiods of cognitive development by about 8 years of age3. They can recognize themselves in a mirror and are much better at classification than macaques, but are not capable of constructing reversible hierarchical classes and abstract, logical reasoning. Human children traverse eight subperiods of cognitive development over 18-20 years.

It is interesting to note that even though humans take about 2.5 times as long to complete cognitive development as do chimpanzees, humans actually learn faster than chimpanzees. In most cognitive spheres, especially language, a two-year-old child has the abilities of a four-year-old chimpanzee, even with intensive training. Humans appear to have much more to learn and their brains require more environmental input to complete development. Formal abstract logical reasoning does not emerge until age 16 to 18. This is the age when productivity begins to increase dramatically among modern hunter-gatherers (see below). The ability to construct abstract scenarios and deduce logical relationships appears to allow for the growth in knowledge that results in peak productivity in the mid-30s.

Elongated development in humans is also associated with slowed aging of the brain. Macaques exhibit physiological signs of cognitive impairment, as evidenced by the appearance of Alzheimer-like neuropathology (senile plaques, neurocytoskeletal abnormalities) and cerebral atrophy by age 22-25, and chimpanzees by age 30, in contrast to humans for whom such changes are rare until age 60 (<1%) and only common (>30%) by age 80 (Finch, 2002).

Discussion and conclusions

The analyses in this paper have applied embodied capital theory to understanding primate radiations in brain size and longevity, and the evolution of the human life course. Embodied capital theory organizes the relationships of ecology, brain size and longevity among primates, which existing debates about primate brain size evolution have failed to do. Most studies of brain evolution have ignored longevity, and focused either on the benefits or on the costs of brains, but not both. The liveliest current debate concerns whether the benefit of a large brain is to solve ecological or social problems (Clutton-Brock and Harvey, 1980; Byrne and Whiten, 1988; Allman et al., 1993; Milton, 1993; Barton and Dunbar, 1997; Dunbar, 1998). On the cost side, another debate concerns, for example, whether larger brains require smaller guts or lower metabolic rates (Foley and Lee, 1991; Aiello and Wheeler, 1995; Martin, 1996; Barton, 1999).

Studies examining the relationship between the brain and longevity fail to model simultaneous selection. One focus has been on whether the relationship between brain size and longevity is real or a statistical artifact (Economos, 1980; Foley and Lee, 1991; Allman et al., 1993; Martin, 1996; Barton, 1999). Another has been on the metabolic costs of growing large brains (Foley and Lee, 1991; Martin, 1996) and its indirect relationship to lifespan through body size. Others have focused either on the direct impacts of the brain on lifespan or on the benefits of a longer lifespan. For example, Sacher offers two proposals: (1) brains directly increase lifespan by ensuring more precise homeostasis of bodily functions and (2) brains delay maturation and lower the reproductive rate, therefore requiring an extension of the lifespan (Sacher, 1975). Other hypotheses are: (A) larger brains are beneficial to longer-lived animals because they are likelier to experience food shortages when knowledge of the habitat would facilitate survival (Allman et al., 1993); (B) larger brains decrease ecological vulnerability to environmental risks and select for increased longevity (Rose and Mueller, 1998); and (C) larger brains help maintain tissue differentiation and slow the process of entropy leading to senescence (Hofman, 1983). The embodied capital theory shows how features of ecology, including both mortality risks and information processing demands, interact in determining optimal allocations to the brain and survival.

Issues raised at this workshop and directions for future research

Several unresolved questions were discussed at the workshop. To conclude, we would like to address four of those questions, all of which are interrelated, with suggestions for future research:

1. the timing of changes in diet, brain function and longevity since the split between ape and hominid lineages;
2. the specific evolutionary processes by which diet, brain size and longevity changed over time, and the extent to which those changes occurred simultaneously;
3. sex-based specialization in economic roles, male parental investment and the relative importance of selection on females and males, respectively, in producing these macro-evolutionary trends; and
4. the relative importance of, and the relationship between, social and dietary factors in brain evolution.

Timing and measurement

With respect to the timing and tempo of evolutionary change in diet, brain and the life course, two major issues must be addressed. The first is descriptive: how can the important changes be measured, given the nature of the fossil, archaeological and molecular genetic record? The second is explanatory: what factors were responsible for the timing of the sequence of changes, and how did they vary across space? From a descriptive perspective, the documentation of changes in brain size appears the most straightforward, since the record of fossil crania is expanding and provides reasonably accurate measures of brain volume. The problem, of course, is that we are interested in brain function as well as size. It has long been recognized that changes in the internal organization of the brain may have been associated with large changes in brain function, but such changes may be largely invisible by examining fossil crania (Holloway, 1978, 1979). Our results raise another important, but perhaps more easily solved, problem. Although the sample of post-cranial fossil remains is rather sparse and unfortunately not well associated to the sample of crania, there is clear evidence of large changes in body size and muscularity over time and space in the hominid lineage (Kappelman, 1996; Ruff et al., 1997).

It is also well known, as discussed above, that it is important to take allometries between brain and body size into account when assessing changes in cognition and other neurally based capabilities. Allometry can be viewed in two ways. The first is as a simple bivariate statistical relationship, estimated from the slope of the regression of log brain weight on log body weight. The second is conceptual or causal, and here the issue is how much an increase in body size causally contributes to (or requires) an increase in brain size. The estimated slope for all nonhuman primates is close to 0.75, but within each major grade (prosimians, monkeys and apes), the slope is closer to 0.67. One might therefore view these associations as supporting one of the explanations for them, even if it is unclear which one. But the explanations for these increases are conceptual and causal, and therefore should apply to regression slopes with other variables included in the model. Our analysis shows that the estimated slope decreases to about 0.5, after controlling for life history and ecological variables. We suspect that with better measures of our predictor variables (which are probably measured with greater error than body size), the estimated slope for body size would be even lower; that is, we assume that the effects of these measurement errors would counteract the underestimation of the slope due to error in body size (Nunn and Barton, 2000). Hence, the proportional increase in brain size necessary to support an increase in body size may be much lower than either the surface area or metabolic rate theories would suggest. It is interesting to note that within-species differences in body weight due to sexual dimorphism (e.g. among gorillas and orangutans) result in very small increases in brain size, with coefficients closer to 0.20-0.25. Using standardized encephalization quotients, male gorillas are less encephalized than the average mammal, and female gorillas are exceptionally encephalized. The life history model presented here provides a reason why statistical associations between brain and body size may provide upwardly biased estimates of the proportional increase in brain size necessary to support an increase in body size. If both optimal brain size and body mass are sensitive to length of lifespan, they may coevolve positively at a greater rate than would be expected by the neural requirements of a larger body size. If standard allometric coefficients are upwardly biased, this would mean that early members of the genus *Homo* may have been more encephalized with greater cognitive capacities than current models suggest. The same could be said for Neandertals as well. It is especially important to determine whether changes in muscularity produce smaller or larger changes in brain size than do changes in mass due to increased skeletal length. Clearly, more empirical and theoretical work on brain-body size allometry is needed.

Measuring changes in diet across time and space is also problematic, but novel techniques, such as isotopic analysis of fossil bone (Sponheimer and Lee-Thorp, 1999; Richards, this volume) or bone collagen (Sponheimer and Lee-Thorpe, 1999) and analysis of dental microwear patterns (Grine, 1986) promise to provide increased precision in our ability to estimate ancient diets. We simply wish to provide some suggestions about the evaluation of evidence. The evidentiary basis of early arguments about hunting and food sharing during early hominin evolution (Isaac, 1976) has received increasing scrutiny in the last decade and a half (Binford, 1981; Schoeninger et al., 2001; Lupo and O'Connell, 2002; O'Connell et al., 2002). The role of hunting in the diets of early *Homo* has been re-evaluated, and many scholars favour a much greater role for scavenging (Bunn and Kroll, 1986; Bunn and Ezzo, 1993; Speth and Tshernov, 1998; O'Connell et al., 2000) and for female-based plant gathering (O'Connell et al., 1999; Wrangham et al., 1999). While we think that such re-evaluation is of great importance, it is also important to utilize the same high standards for evidence when evaluating the scavenging and gathering hypotheses. The lack of solid, incontrovertible evidence about hunting should not be taken to imply that scavenging or collecting must have been important, since the evidence about the quantitative importance of scavenging is equally weak, and there is virtually no evidence regarding plant product consumption. At this point, we should be agnostic about the composition of early hominin diets. In addition, much emphasis has been placed on evidence regarding the hunting of large game. Given the prey size chosen by chimpanzees, we suggest that more attention should be placed on examining assemblages in terms of small game, which may have been easier for early hominins to hunt (Stiner et al., 2000). With respect to longevity, we must be careful about using dental evidence, which may provide clearer evidence about rates of development than length of lifespan. Among primates, there are strong associations both between age of first reproduction and adult mortality rates (Charnov, 1993) and between rates of dental development and maximum lifespan in captive populations (Smith, 1991). Some new evidence suggests that early *Homo*, as represented by WT 15000, may have developed more rapidly than previously thought (Smith, 1991, 1992, 1993; Smith and Tompkins, 1995). It should be pointed out, however, that when chimpanzees are compared to modern foraging populations, the length of pre-adult development increased proportionally less than did lifespans or life expectancies at adulthood. For example, average age of first reproduction among chimpanzees has been estimated to occur at age 13 and among modern foragers at about age 18-19. This is approximately a 50% increase. However, life expectancy at adulthood for chimpanzees is about 14 additional years, whereas among humans it is just over 30 years, more than a 100% increase. Estimates of maximum lifespan also suggest such a doubling. Even though the two are highly correlated, it would be very useful to investigate factors that have independent effects on rates of development and longevity among nonhuman primates and to develop new methods for assessing longevity in the fossil record.

Neandertals may turn out to be an interesting case in point to evaluate the timing of changes in diet, brain function and longevity. Recent research suggests that Neandertals may have undergone rapid maturation on the basis of their dental growth in comparison to modern humans (Rozzi and Castro, 2004). They also appear to have been quite efficient hunters and rank as highly active, top-level carnivores (Richards et al., 2000; Sorensen and Leonard, 2001). Much more needs to be learned as to how this pattern might relate to changes in mortality risks and learning-intensiveness of their feeding niche (Anwar et al., this volume).

Timing and evolutionary mechanisms

The model we propose is silent about the timing of changes in different hominin lineages across time and space. Nevertheless, it is clear that there were progressive changes in brain size and presumably in other features of the human adaptive complex over time, at least in some lineages. Moreover, the data show that some features of the contemporary human adaptive niche absolutely require the presence of other features. The long period of juvenile low productivity (1) and costly brain growth (2) could not be supported without a long adult lifespan (3) in which both men (4) and women (5) contribute to the energetic support of juveniles. These five co-adapted traits can be thought of as an adaptive peak, *sensu* Sewall Wright (1932). One question is whether hominin evolution can be characterized by the traversing of several adaptive peaks, separated by adaptive valleys.

One view would be that long-term juvenile dependence, brain size, longevity, and increased parental investment evolved in small steps, to some extent independently within some range. In this case, the additive phenotypic effects of genes contribute to the selective environment of other genes. For example, the phenotypic effects of genes affecting brain development and function increase foraging returns for high-quality, nutrient-dense foods during adulthood. The ensuing diet and age profile of production then constitute the selective environment for genes affecting dietary physiology (e.g. the size of the large intestine) and rates of aging (e.g. accumulation of plaque and free radicals). At the same time, the phenotypic effects of those latter genes affect the selective environment for genes affecting brain tissue and brain development. This could result in a "ratcheting" process, in which both sets of genes change over time, resulting in non-random associations of brains and longevity at the species level. Such a process may take some time to unfold, but does not imply adaptive valleys.

Another view is that these traits are more tightly linked and that changes in one would not be favoured without a concurrent change in one or more of the others. This would imply that adaptive valleys would have to be traversed by some process, such as genetic drift. In this case, some population demes would by chance have founders who were extreme on one of the traits, such as brain size. This could have entailed a net fitness cost with prolonged development or parental provisioning, albeit it could only have been relatively small. Through further random events and population drift, some descendants would possess genotypes coding for higher levels on the other traits, leading to a new adaptive peak and population expansion. This piecemeal process would presumably have taken even longer, and would also imply greater divergence among hominin lineages at the same point in time.

From a mechanistic perspective, some trait associations could be due to pleiotropy (i.e., single genes influencing more than one trait) and/or linkage disequilibrium (sets of genes jointly assorting during meiosis). Research into brain aging and longevity suggests that some genes may have such pleiotropic effects. The apolipoprotein (apoE) allele system is a good example since this seems to affect neurite growth and the aging of both the brain and the cardiovascular system. (The discussion here is based on Finch and Sapolsky, 1999, which gives the original sources). Brain aging, as in the symptoms of Alzheimer's disease, is common in long-lived mammals. These signs of brain aging are delayed in humans relative to apes and in apes relative to monkeys. In humans, apoE has at least three variants (apoE 2, 3 and 4) whereas all nonhuman primates that have been studied have the same variant, most similar to human apoE 4. Interestingly, this variant is a risk factor for both Alzheimer's disease and coronary artery disease, suggesting that the apoE 2 and 3 variants may have evolved to slow down both brain and cardiovascular aging. These other variants also promote neurite growth in cultured neurons, suggesting they also stimulate greater brain development and complexity.

Pleiotropic effects of this nature could evolve by a similar ratcheting process. The sensitivity of one tissue type (e.g. neurons) to a gene product could affect selection on the sensitivity of other tissue types (e.g. vascular tissue) to that same gene product, and vice versa. To the extent that associations between brains and longevity are due to pleiotropic effects, this would generate correlations at the individual level as well as at the species level. Given the growing body of data suggesting that such individual-level associations exist among humans, pleiotropy deserves careful consideration.

A third possibility is that environmental conditions changed over time in a way that systematically changed the benefits and/or the costs of cognitive abilities. Either the changes in environmental conditions would have to have been directional, or those changes could have interacted with one of the two processes mentioned above. Some mix of environmental change and incremental change in co-adapted trait bundles is perhaps the most likely scenario. In any case, each of those possibilities deserves further theoretical and empirical attention.

Timing and the role of men

There are several other proposals that attempt to explain the evolution of human life histories, especially longevity. One model, recently proposed by Hawkes and colleagues (Hawkes et al., 1998), often referred to as the "Grandmother Hypothesis", proposes that humans have a long lifespan because of the assistance that older post-reproductive women contribute to descendant kin through the provisioning of difficult-to-acquire plant foods. Women, therefore, are selected to invest in maintaining their bodies longer than chimpanzee females. This model offers no explanation of why men live so long. In contrast to this female-centred view, Marlowe (2000) proposes that reproduction by males late in life selects for the lengthening of the human life course, with effects on females being incidental. The embodied capital theory proposes an explanation for why both men and women live long lives. Both men and women exploit high-quality, difficult-to-acquire foods (females extracting plant foods and males hunting animal foods), sacrificing early unskilled productivity for later skilled productivity at much higher rates, with a life history characterized by an extended juvenile period where growth is slow and much is learned, and a high investment in mortality reduction to reap the rewards of those investments in growth and learning.

Discrimination among these alternative proposals requires more data and a clear set of alternative predictions. Of course, it is also possible that each may be relevant for different times in the course of hominin evolutionary history. It is plausible that some of the early shifts in brain size or life history occurred primarily through shifting roles of women as they aged. One possibility is that a shift to more extractive foraging increased the benefits of three-generational resource flows among female kin. On the other hand, since some of the populations living in cold climates during the Middle and Late Pleistocene must have depended almost exclusively on meat (Hoffecker, 1999), men must have played a much larger role in the energetic support of reproduction and parental investment in those populations (Mussi, this volume). The large differences among ape mating and parental investment systems and between contemporary foraging populations and all ape species suggest that they are highly malleable and depend on the details of the food acquisition strategy and local ecology. The fact that all human peoples live in multi-male, multi-female groups with restricted sexual access mediated through some form of marriage highlights the importance of understanding the evolutionary origins of this pattern, especially since it appears to be a necessary condition to support the human life history adaptation (Rodseth and Wrangham, 2004). Uncovering its distribution over space and evolutionary time represents one of the most difficult challenges. Palaeo-molecular genetics, as it develops, may turn out to provide the best source of information on this problem.

Socio-ecology and brain evolution

As mentioned above, the liveliest current debate concerns whether the benefit of a large brain is to solve ecological or social problems (Clutton-Brock and Harvey, 1980; Byrne and Whiten, 1988; Allman et al., 1993; Milton, 1993; Barton and Dunbar, 1997; Dunbar, 1998; Dunbar, this volume). In general, proponents of the social view tend to formulate the problem in terms of *Machiavellian intelligence*, the idea that intelligence evolves to manipulate others for selfish ends in an evolutionary arms race. We wish to offer a somewhat different perspective on this debate.

There is growing environmental evidence that human populations experienced tremendous variability in climate during the Pleistocene (Potts, 1996a; Richerson and Boyd, 2000; and Binford, this volume). In fact, it has been argued that much of the selective pressure on brain size (Potts) and on the emergence of culture (Richerson and Boyd) derives from coping with high-magnitude and rapid shifts in temperature and their ecological sequelae. It is also clear that contemporary foragers also experience large fluctuations in energy gain rates over much shorter stretches of time, due to the vagaries of hunting luck. Much of this latter variability can be unsynchronized across individuals, greatly increasing the benefits of food sharing to mitigate risk and inter-temporal variation in food consumption (Kaplan and Hill, 1985; Kaplan et al., 1990; Winterhalder, 1990; Winterhalder, 1996). Moreover, as mentioned above, people also experience variation in food capture due to illness and injury, and during those periods, they are frequently subsidized by fellow members of their group (Gurven et al., 2000; Sugiyama and Chacon, 2000). Finally, contemporary human foragers can often experience great gains from cooperative pursuit of game animals (Kaplan and Hill, 1985; Bailey and Aunger, 1989; Bailey, 1990; Gurven et al., 2000; Alvard, 2001; Hill, 2002), some of which can simply not be captured by lone hunters.

Those observations may help explain some exciting new findings in experimental economics and cognitive neuroscience. Humans appear to possess a strong bias towards entering into cooperative relationships and to punish individuals who "defect" in cooperative activities. This bias has been termed strong reciprocity, (see Gintis and colleagues for a collection of papers detailing this phenomenon [Gintis et al., 2004]), that is characterized by a strong tendency to cooperate in one-shot prisoner's dilemma, ultimatum and public goods games where the dominant strategy (in the sense of the individually maximizing one) is always to defect. Moreover, people are often willing and motivated to punish non-cooperators, at a cost to themselves, even when play is completely anonymous. This tendency to cooperate and to punish breaches of fairness has been documented in a diverse array of cultures, and the phenomenon is quite robust to variations in experimental design (Henrich et al., 2004). Cognitive neuroscientists, utilizing functional Magnetic Resonance Imaging (fMRI), have now begun to document areas of the brain involved in such behaviour and in resolving moral dilemmas (Sanfey et al., 2003).

Those results appear consistent with new comparative analyses of food-sharing systems among contemporary foragers. Band-wide food sharing that is completely egalitarian is actually rather rare among modern hunter-gatherers, and appears to be restricted to small groups and to circumstances in which individual return rates from foraging are sacrificed in order to increase group return rates (Gurven, 2004; Kaplan et al., 2004). In many groups, there is evidence of significant producer control over sharing and limited scope of partners. For example, among Hiwi foragers, hunters tend to exercise control over how much and with whom they share meat, restricting those who receive shares to some 15-20% of potential recipients in large groups (Gurven et al., 2000).

Our hypothesis is that one important use of human intelligence is to take advantage of gains from cooperation and, at the same time, be selective about when and with whom to cooperate based on individual assessments of the situation and the likelihood that others will reciprocate. According to this hypothesis, humans tend to cooperate in experimental games and to punish defectors for two reasons. The tendency to cooperate on the first move allows people to experience greater gains from cooperation and to demonstrate their quality as potential cooperators in future interactions. People have a moral approach to these problems because a more Machiavellian approach, which would take advantage of all opportunities for defection in one-shot games, is outcompeted by a moral psychology when there is uncertainty about the possibility of being detected as a defector, and the costs of being labelled as a cheater have great long-term consequences. Potentially, runaway selection on the ability to detect subtle signs of a Machiavellian strategy in the context of a food acquisition strategy that depends on cooperation and sharing may have been of great importance in the evolution of social intelligence and moral reasoning.

According to this view, both social and foraging intelligence are ecologically determined, and are a function of our dietary adaptation. The pursuit of large mobile packages of food engenders both risky outcomes and great gains from cooperation. However, cooperative strategies entail risks of defections; decisions about when and with whom to cooperate, and behaviours that facilitate being selected as a cooperative partner may have played a great role in individual and family food consumption patterns. Verbal language, via gossip and coordination communication, may have played a large role in this adaptive complex (Alvard and Nolin, 2002).

With respect to timing, several alternative scenarios may be distinguished. One possibility is that the ability to engage in abstract logical reasoning evolved in response to the cognitive demands of tool-based extractive foraging and knowledge-based hunting. Those internal symbolic abilities established a cognitive infrastructural pre-adaptation for symbolically based communication. Alternatively, the gains from cooperation may have set the stage for the evolution of symbolically based communication systems that, in turn, served as a cognitive pre-adaptation for the evolution of abstract logical reasoning and its application to the food quest. A third possibility is another gradual, ratcheting co-evolutionary process, as described for the co-adaptation of life history, parental investment, and brain size. Distinguishing among such possible sequences is another difficult challenge facing human evolutionary scientists.[4]

To conclude, the human adaptation is broad and flexible in one sense, and very narrow and specialized in another sense. It is broad in the sense that as hunter-gatherers, humans have existed successfully in virtually all of the world's major habitats. This has entailed eating a very wide variety of foods, both plant and animal, and a great deal of flexibility in the contributions of different age and sex classes of individuals. The human adaptation is narrow and specialized in that it is based on extremely high investments in brain tissue and learning. In every environment, human foragers consume the largest, highest quality, and most difficult-to-acquire foods, using techniques that often take years to learn. It is this legacy that modern humans bring to the complex economies existing today, where education-based embodied capital determines income, and the economy is a complex web of specialization and cooperation between spouses, families and larger social units. We are only beginning to explore the implications of this legacy for understanding modern behaviour.

Notes

1. Although feeding niche is subject to selection, the suite of foods eaten are treated as givens in order to model how selection moulds life history traits, brain size and other features of phenotype in response to niche conditions.
2. Since brain size is endogenous, the problem of simultaneity can be addressed by using predicted brain size in this second regression. Similar results are obtained, however, when measured values are used instead of predicted values.
3. The fourth subperiod, such as conservation of quantities of liquids under container transformations, seems to require tutelage and symbolic training.
4. Similar reasoning may be applied to primate social intelligence. Co-evolutionary selection on brains and longevity due to the complexity and the navigational demands of the primate diet may have produced pre-adaptations for the evolution of social intelligence. Given that primates live long lives with enduring social relationships and given that many species of primates eat foods whose distribution generates within-group competition, there would be selection for the application of existing enhancements in memory and information processing abilities to the management of social interaction. Many animals live in social groups, but primates are notable in terms of the complexity

of their social arrangements. Perhaps, social pressures alone are not sufficient to select for markedly increased brain size, but they might select for the extension of existing abilities to social problems. This may be why apes display remarkable social intelligence, even though group size is not particularly large (Byrne, 1995; Byrne, 1997). Orangutans, for example, live in far-flung communities so are mostly solitary on a day-to-day basis, but it takes about seven years for a young orangutan to become independent of its mother (presumably because of the learning-intensive nature of the diet). If this view is correct, it also suggests that the assumption of extreme domain-specificity in intelligence may be unwarranted.

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Why Hominins Had Big Brains

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Introduction

Human evolution is, above all, characterized by the remarkable growth in brain volume that began with *Homo habilis* some two million years ago, and then exploded with extraordinary rapidity in the later populations of *Homo erectus* as these gave way to archaic and, finally, modern humans. Very approximately, brain volume trebled over the course of this two million year period. Quite why brain volume increased so dramatically has always remained obscure. It is probably fair to say that, until relatively recently, most palaeoanthropologists simply assumed that these changes were associated with the changes that took place in tool manufacture, as this underwent its well-documented progression from Olduwan through Acheulean to Mousterian and eventually Aurignacian technologies. However, detailed comparison between the archaeological and the anatomical records subsequently demonstrated that the temporal correlation between these two sequences was poor at best (Wynn, 1988).

A common alternative assumption has probably been that brain size increased simply as a by-product of increasing body size, since the two do seem to be locked together in a close allometric relationship (Jerison, 1973). Selection is assumed to have acted on body size, and brain size is simply dragged along in its wake. However, brains are energetically much more expensive than muscle or skeletal material, mainly because the cost of replacing neurotransmitters every time a neuron fires is very high (Aiello and Wheeler, 1995). This suggests, instead, that whatever drove hominin brain expansion must have had a very significant impact on the fitness of the individuals concerned. Indeed, it can legitimately be argued that rather than brain size being a consequence of body size, larger body size might actually be a consequence of the demand for a larger brain. This follows from the fact that the energy costs of living are not a direct linear function of body mass, but rather increase only as the 0.75 power of body mass (this is known as Kleiber's Law). Since this allows savings of scale (the bigger you are, the less energy you need per kg of body weight to sustain life, and hence the more energy there is to spare for other activities such as growing a bigger brain), it means that larger animals can afford to have relatively larger brains than smaller bodied animals. The important point to notice here is that body size is acting as a developmental constraint on brain growth, not as a factor selecting for brain growth: the high cost of both growing and running brains means that we still need to provide an explanation as to why a species should want to increase its brain size above the bare minimum necessary to ensure survival and successful reproduction.

In the late 1980s, the search for plausible explanations for the factors driving brain size evolution began to focus on the social world in which primates live. Whiten and Byrne (1988) argued that it was the complex social life of primates that was broadly responsible for the fact that primates had unusually large brains for their body size compared to all other vertebrates. This view (subsequently termed "the social brain hypothesis") has gained increasing support with time, thanks mainly to the fact that when quantitative tests between competing hypotheses have been carried out they have invariably tended to support the social brain hypothesis at the expense of the alternative (largely ecological) hypotheses (Dunbar, 1992, 1998; Reader and Laland, 2002).

In this paper, I briefly review the current state of knowledge on the social brain hypothesis, and then explore some of the implications that a large social brain might have had for hominins.

The social brain hypothesis

The principal evidence in support of the social brain hypothesis is provided by the fact that a number of indices of social complexity in primates (and, now, a number of other mammalian orders as well) correlate with relative neocortex volume. These indices include the size of the social group (Dunbar, 1992), the size of grooming cliques (Kudo and Dunbar, 2001), the frequency of tactical deception (Byrne and Corp, 2004), the complexity of male mating strategies (Pawlowski et al., 1998), the amount of social play (Lewis, 2001) and the frequency of social learning (Reader and Laland, 2002).

The neocortex is taken to be the key issue here because it is neocortex volume that has grown out of all proportion to the rest of the brain during the course of primate evolution (Finlay and Darlington, 1995; Finlay et al., 2001). In other words, when we ask why primates have big brains, what we are really asking is why primates have big neocortices. While the neocortex is broadly speaking a mammalian evolutionary invention, big neocortices are a primate speciality. Mammalian neocortices rarely account for more than about 40% of total brain volume, but few primates have less than about 50% of brain volume devoted to neocortex, and this value rises to 80% in modern humans. In fact, although the neocortex is a thin sheet (in primates, just 6 cells and 7 mm deep) wrapped around the older core of the mammalian/reptilian brain, it is largely the site where most of those cognitive functions that we associate with consciousness are located; in contrast, the inner core is associated more explicitly with managing basic bodily functions. That being so, it is perhaps not too surprising that there should be a relationship between the volume of the neocortex and the various indices of sociality listed above.

The relationship between social group size and neocortex volume has been interpreted as implying that there are cognitive constraints on the number of relationships that an individual can coordinate and service effectively. While we remain uncertain how these cognitive constraints work, the issue seems to be that the relative volume of the brain places an upper limit on the size of the group that a species can maintain as a cohesive integrated social unit. Our understanding is that this is not simply a memory-for-faces issue (though memory must come into it somewhere), but rather the animal's capacity to manipulate information about other individuals' behaviour and relationships within its mental state space, and to draw inferences from these manipulations about how best to behave in the future. This, at least, is the burden of the analyses suggesting that aspects of behaviour, as opposed to just group size, correlate with neocortex volume.

In fact, more recent analyses have suggested that even better correlations are obtained if these indices of sociality are correlated with the more anterior components of the neocortex, including non-V1 cortex (the areas of the neocortex anterior to the primary visual area: Joffe and Dunbar, 1997) and the frontal lobe (Dunbar, 2003a). Increased volume in the frontal lobe (in particular) seems to be correlated with both enhanced executive function skills (e.g. problem-solving abilities: Dunbar et al., 2005) and enhanced social cognitive skills (e.g. levels of intentionality: Dunbar, 2003b). These findings add emphasis to the suggestion that it is "conscious" (or, better still, executive function) processes that are important in processing the social effects that mediate group cohesion. Since these functions are broadly associated mainly with frontal lobe elements, it may be no surprise that the predictability of the relationship between brain volume and group size improves as increasingly anterior components of the neocortex are considered.

Implications for hominin brain evolution

In a series of detailed analyses, Finlay and Darlington (Finlay and Darlington, 1995; Finlay et al., 2001) have shown that mammalian brain evolution is characterized by a series of distinct scaling relationships whereby the various components of the brain evolve in relatively discrete proportional relationships to each other. These relationships appear to reflect developmental constraints that derive from structural relationships within the brain itself. Importantly, perhaps, the scaling relationships for the neocortex are much steeper than those for any other part of the brain. Indeed, this relationship seems to apply even within the neocortex itself. The frontal lobe of the neocortex seems to have evolved at a rate that is roughly proportional to the rest of the neocortex and the brain as a whole, but the scaling factor is very much steeper even than that for the neocortex as a whole: species like humans with large total brain volume have disproportionately large frontal lobes compared to species like the smaller New World monkeys with their relatively small brains. This finding has two important implications for hominin evolution.

First, any selection to evolve more complex behaviours that are dependent on executive function necessarily mean that a larger brain has to be evolved: in very broad terms, it is not easy (though perhaps not entirely impossible: Barton and Harvey, 2000) to expand disproportionately only that component needed for the purpose in hand. The capacity to evolve brain components at the expense of others seems to be limited mainly to moderately small areas (as suggested by the findings of Barton and Harvey, 2000).

Second, notwithstanding this constraint, there do seem to be savings of scale: in other words, as overall size increases, the fact that proportional increases in some brain components are not needed (i.e. add no additional value in terms of processing efficiency) means that there is spare capacity in the system that can, in effect, be devoted to other functions that might benefit from more computing power. Joffe and Dunbar (1997), for example, showed that the neocortex anterior to V1 (the primary visual cortex) has not evolved in direct linear proportion to the expansion of V1 itself. This appears to be a consequence of the fact that the requirement for the primary visual cortex is ultimately limited by the acuity and processing capacity of the visual input system (retina and optic nerve). The capacity of the first is dictated by the densities of rods and cones, but the efficiency of the second is dictated by the diameter of the optic tract itself. Not surprisingly, perhaps, the volume of V1 across primate taxa is correlated with the volume (and hence, ultimately, the diameter) of the optic tract (Dunbar, 2003a). Since added processing capacity in the visual system does not automatically result in benefits from increased visual acuity, the benefits of assigning additional cortical material to one system have to be offset against the benefits to enlarging other systems.

In terms of hominin evolutionary history, it is not entirely obvious how an enlarged visual system might have been a greater benefit. For a tropical species – and especially those occupying relatively open habitats – light levels are rarely less than maximal, and the allocation of additional processing capacity to visual processing is unlikely to result in a significant advantage in visual acuity. This may not, of course, be true for species occupying higher latitudes, and it is conspicuous that Neandertal orbit socket volumes are significantly larger (absolutely and relative to body size) than those of both other hominins and modern tropical primates. This could reflect an adaptation to lower light levels (especially during winter) at higher latitudes. Whether or not this is so, it remains the case that, since orbit size correlates with both optic tract and V1 volumes in living primates, Neandertals would have had an absolutely and relatively larger primary visual cortex (thus perhaps explaining the Neandertal "bun").

Aside from such instances, however, the burden of the scaling relationships identified by Finlay and Darlington means that as the total brain volume increases, more neural capacity becomes available in the frontal cortex, and especially the frontal lobe. Since, as we noted in the previous section, this seems to be associated with markedly improved basic cognitive abilities, it may be that those distinctively social cognitive abilities that we associate with primates (and especially humans) are the outcome of the scale at which more basic executive function processes like causal reasoning, causal chaining and analogical reasoning can be executed (Barrett et al., 2003) and that these in turn are explicitly dependent on the amount of computational power that can be brought to bear on them (as reflected in the number, and hence volume, of core cortical neuronal masses). The availability of additional capacity in the frontal lobe may thus lead to an accelerating scale of abilities in these more sophisticated domains.

Implications for hominin social evolution

If there are explicit relationships between brain component volumes and explicit cognitive skills, then it is possible to use these relationships to say something about the broad sweep of evolving cognitive abilities of hominins. I have attempted to do this in two particular respects. One is based on the relationship between neocortex volume and social group size, and the other on the relationship between frontal lobe volume and social cognitive skills. I will explore each briefly in turn.

The finding of a general relationship between relative neocortex volume and social group size in primates (Dunbar, 1992) that extends to modern humans (Dunbar, 1993) has raised the possibility that such a relationship can be applied to fossil hominin populations. While such relationships are inevitably subject to considerable error variance (and particularly given that error variances are compounded multiplicatively when interpolating through a series of regression equations: see also Steele, 1996), nonetheless the broad pattern of change can tell us a great deal about the sequence of developments that might have occurred. Where we can anchor these kinds of relationships either side of the hominins (in this case, in the values for the great apes and modern humans) we are in much less danger of wild extrapolation beyond the data.

Aiello and Dunbar (1993) used this approach to explore the likely group sizes of hominins. Since there are simple linear relationships between cranial volume, brain volume and neocortex volume, it is possible to estimate neocortex volume with some degree of accuracy from cranial casts. By interpolating these values into the equation relating relative neocortex volume to social group size in primates, it is possible to estimate social group size for any given fossil hominin population.

It is important to bear two points in mind here. One is the fact that there are very clear grade shifts in the basic relationships, not only between primates and other mammalian species (see for example, Dunbar and Bever, 1998) but also among the primates themselves (Dunbar, 1998). Strictly speaking, since the apes (hominoids) fall on a separate grade to the monkeys, it is the hominoid regression equation that we should use for extrapolations to hominins. The key point here is that apes seem to require more neocortex volume to support a given group size than monkeys do, presumably because the cognitive and behavioural processes they use in cohering their social groups are more complex in some way. I interpret this as implying that ape social relationships are in some way more complex than those of monkeys, or at least require more computational power (perhaps, for example, because they involve deeper levels of mindreading). Because Aiello and Dunbar (1993) used the generic primate regression equation, which is shallower than that for the hominoids alone, this will have resulted in a tendency to overestimate the values for social group size in the mid-range values of neocortex volume (mainly those corresponding to earlier hominins).

The second point concerns the nature of the social groups in question. It is important to appreciate that the regression equation between neocortex volume and group size in primates refers to a specific kind of social grouping. On the basis of what we know about the equivalent group size in humans, my assumption is that this group is the number of individuals whose relationships are known explicitly. I sometimes refer to this as the "cognitive group size" on the grounds that it is not necessarily about the number of individuals who happen to be together at one time and place, but rather about the knowledge that animals have about each other. This is not the same as the total number of faces to which one can put names (which is often very much larger).

This definition would, of course, apply well enough to the kind of group that is typical of most species of monkeys – that is, spatio-temporally coherent groups whose members remain together most of the time, and who therefore know each other well from close daily observation and interaction. However, we have more difficulty with those species (mainly apes, including humans) who live in fission-fusion social systems where a clear distinction is usually made between parties (the animals together in one place at any one time) and the community (the set of individuals who occupy a common range and out of whose membership the more obviously observable parties are made up). The brain-size/group-size relationship points very clearly to the community as the appropriate equivalent of the baboon or macaque troop.

The fact that great ape societies in general are characteristically dispersed (or fission-fusion) social systems may make them sufficiently cognitively demanding to require the additional computational power that explains the grade shift between monkeys and apes (Dunbar, 2003b; Barrett et al., 2003). One likely explanation is that when trying to decide how they should behave, individuals living in such a social system have to be able to factor virtual individuals who are not physically present into the mental state space representing the individuals who are physically present.

Since dispersed social systems are characteristic of all the hominoids, we must assume that they would also have been typical of all hominin taxa that occupied the taxonomic space between the last common ape/human ancestor and modern humans. Thus, in terms of hominin evolution, it is the extended community that we are predicting from the regression equation relating neocortex volume to group size. With brain size expansion following an exponential pattern across the course of hominin evolution, it is not especially surprising (or, for that matter, interesting) that predicted group (i.e. community) sizes should do so too. Rather, the significant issue here is how this translates into group sizes at different stages. In general terms, group sizes among the australopithecines are broadly in line with that seen in chimpanzees, begins to increase gradually through the early *Homo* taxa, but only really starts to take off in a serious way in the later stages of *Homo erectus*. By the time we reach archaic humans (*Homo heidelbergensis*), group sizes are very large relative to those of the great apes.

Group size and social cohesion

Individuals live in social groups because doing so provides benefits. Among primates in general, the principal benefit seems to be communal defence against predators (Dunbar, 1988). However, this is less clear in the case of chimpanzees where party size seems to be the equivalent grouping level that subserves the anti-predation function. Quite what function chimpanzee communities serve is not clear, although one obvious suggestion is that they are essentially sets of individuals (principally male brotherhoods) that cooperate in the defence of a territory (mainly for access to females). It is important to appreciate that the specific *function* for which groups exist has no relevance for the cognitive constraint on group size (i.e. the social brain hypothesis itself). Rather, the argument is that there is simply a cognitive limit on the size of groups that can be maintained at a particular level of social coherence, and any such grouping could in principle be used for any purpose for which a group of that particular size (or, alternatively, coherence) is appropriate. In effect, this means that if any particular function requires a certain level of social integration (or bonding), then brain size will constrain those groups to a certain size.

It seems likely that during the course of later hominin evolution, the principal selection benefit of sociality may have shifted into the creation and maintenance of trading networks within which support and/or access to monopolized resources can be exchanged reciprocally (Dunbar, 1996). The latter suggestion derives from two observations. One is that the groupings in contemporary hunter-gatherer societies that seem to correspond to the size predicted by human neocortex volume is the clan or regional grouping, which can often be identified as a grouping that "owns" access to specific keystone resources (for example, dry season waterholes) in a given geographical area (Dunbar, 1993). Second, there is some suggestion that larger scale groupings may be specifically involved in trading networks. Nettle (1999), for example, showed that the size of a given language community (the number of speakers of a given language and/or the geographical area over which a particular language is spoken) increases with latitude (and hence seasonality and the declining length of the growing season): this relationship was interpreted in terms of the need to have larger, more extensive trading or exchange networks in ecologically more risky habitats.

It seems likely that the shift to this second benefit (i.e. relationships of reciprocal exchange, as reflected in trading and exchange networks) coincides with the dramatic increase in group size estimates late in hominin evolutionary history. The fact that the chimpanzee lineage had already enabled additional functions besides predation risk to be included in the structure of grouping levels presumably facilitated the switch of one particular grouping level to a new function, while retaining the anti-predation function of foraging parties (in one interpretation, bands in conventional hunter-gatherer societies).

Sociality, however, does not come without its costs. Living in groups creates tensions and frustrations simply by virtue of the fact that individuals are forced together in a relatively confined space where they must inevitably get in each other's way. In addition, as group size increases, individuals are forced to forage further afield in order to meet their daily nutrient requirements, thereby imposing real ecological costs measured in terms of travel time and the additional food intake required to fuel the extra travel. Increased group size may also result in a significant increase in the opportunity for harassment and aggression that may add further centrifugal forces that tend to drive animals in groups apart. All else being equal, these kinds of dispersive forces would eventually lead to the collapse of groups as social phenomena if they remained unchecked. The social brain hypothesis assumes that large brains have been selected for specifically to provide the cognitive basis for maintaining social cohesiveness through time.

However, in one sense, there is a price to pay for increased social skills, as they can be used for exploitative as well as cohesive functions. Because all primate social groups are communal solutions to the problems of successful survival and reproduction, they are, in effect, implicit social contracts. Their stability through time depends on individuals being willing to trade-off short-term losses that arise from the need to forgo their immediate personal demands in the interests of greater long-term benefits to be derived through cooperation. The temptation to renege on social contracts of this kind is both inevitable and widespread: it is a consequence of the fact that the temptation to cheat is a simple function of the magnitude of the immediate gains to be made through pursuing short-term interests. The persistence of social groups is the outcome of the fine balance between these opposing forces.

However, exploiting one's fellow group members in these contexts is freeriding (taking the benefits of sociality without paying all the costs) and rapidly becomes very disruptive and ultimately leads to the collapse of the social contract, and thus to the dispersal of the group. Enquist and Leimar (1992) have modelled the conditions under which freeriding prospers as a strategy and have shown that freeriders' ability to invade (and thus take over) a community depends on its size and dispersion. Freeriders are difficult to control in large dispersed communities because, under these conditions, it is relatively easy for them to find new naïve individuals to exploit. Both of these conditions are, of course, especially characteristic of the later stages of hominin evolution.

Cognitive strategies for enhancing social bonding

The problem of managing and controlling freeriders is sufficiently serious that some major mechanisms need to be in place, otherwise it would not be possible to evolve large social groups that have any kind of temporal stability. While there are a number of behavioural, psychological and even psycho-pharmacological mechanisms that seem to be designed to contribute to this (see discussions in Dunbar, 1999, 2004a, b; Cox et al., 1999), what I want to concentrate on here is the explicitly cognitive question of what role our large brains might have played. One reason for doing so is that there remains a puzzling gulf between the size (and hence cost) of our species' large brain and any requirement for so much processing capacity in terms of actual everyday social interaction.

To put it more explicitly, while there is a clear relationship between social group size and neocortex volume across the primates (including modern humans), it is not entirely obvious what all the processing capacity made possible by large neocortex size is actually being used for. This comes especially into focus when we recognize that there seems to be a relationship between frontal lobe volume (and it is the frontal lobe volume that has increased out of *all* proportion in humans) and achieving levels of intentionality (the ability to mind-read reflexively through a series of individuals' mental states). While monkeys generically seem to be stuck at first-order intentionality (equivalent to statements like "I *believe* that something is the case") (Tomasello and Call, 1997) and chimpanzees can just about manage second-order ("I *believe* that you *think* that something is the case") (O'Connell and Dunbar, 2003), normal adult humans seem to be able to cope with about five orders ("I *believe* that you *think* that I *wonder* whether you *suppose* that I *believe* that something is the case") (Kinderman et al., 1998). Five orders of intentionality seems to be grossly unnecessary for successful everyday functioning, even in the modestly complex societies of modern humans. How often, one wonders, does everyday social life extend beyond third-order intentionality?

Given that achievable intentionality seems to be dependent on the volume of the frontal lobe of the neocortex (possibly simply because a proportional level of "conscious" computing power is needed) and that adding significant additional brain volume is very costly, one has to ask why so much additional computing power is necessary. The commonly voiced suggestion that these are simply by-products of having a large brain is just not sufficient: brains are far too expensive for evolution to produce something that is not really necessary but happens to provide us with a curious (though otherwise wholly unnecessary) cognitive capacity.

Having pondered this problem at some length, I have been able to come up with only one serious suggestion. We need fifth-order capacities to manage the world of the imagination, and this explicitly relates to two different yet related phenomena – religion and story-telling. Both, it seems, are extremely demanding cognitively. Both effectively require fifth-order intentionality in at least some (but not necessarily all) individuals.

Consider, for example, the cognitive demands on a story-teller composing a story. To make a story socially interesting, it must have at least three characters. So Shakespeare, to take an arbitrary example, had to *intend* that his audience *believed* that Iago *wanted* Othello to *suppose* that Desdemona *intended* [to run off with someone else]. Although the audience could get by quite nicely with just four levels of intentionality on this, Shakespeare, as the story-teller, had to rise one level beyond them. Of course, he could have composed the story without reference to his audience – and no doubt many story-tellers do – but if he did ignore their take on the events in the story, he would be less well placed to ensure that he does not overtax his audience's ability to manage and integrate the mental states of his characters. A good writer has to be able to factor his audience's perspective into the story.

Something similar seems to be needed for religion. If we see religion as a mechanism for ensuring (or even enforcing) the communality of the social group (as I have argued elsewhere: Dunbar, 2003b, 2004b), then it is easy to see that religion as a *communal* activity is cognitively very demanding. Contrast the following two statements:

1. "I *intend* that you *believe* that God *wants* us to *act with righteous intent*"
2. "I *intend* that you *believe* that God *understands* that I *want* him to be *willing* to intervene…"

The first has four orders of intentionality and provides an adequate description of what I would call *social* religion – a statement sufficient to allow the exchange of a view about a supernatural world. But that does not, it seems to me, provide sufficient social force to allow us to use religion as a mechanism to enforce adherence to the communal will. When you insist that statement (1) is true, I can take it or leave it as I feel inclined: it is an argument that I can accept as true *or* false, and still continue with my daily activities without giving it a second thought. You have no way of compelling me to believe it or adhere to its claims.

But the second statement does provide the basis for enforcing the communal will. It involves five orders of intentionality, and it has its moral force precisely because of that fifth level. That fifth level explicitly provides a stick with which to beat recalcitrant backsliders. More importantly, it provides a stick of a particularly powerful kind. I can lean on you and assert that you have to do what I (and the other members of the community) ask, but whether you agree to do so or not depends ultimately on whether you feel that I have the power (and, ultimately, that means the *physical* power) to compel you. You may feel that you and your allies are powerful enough to ignore what I say. But if, in addition, I assert that the supernatural might take a view on your behaviour, it adds a level of compulsion that is hard to counter.

This is so for two reasons. First, the supernatural (almost by definition) has powers that greatly exceed anything that I and my earthly allies could possibly muster. Only an alliance with some other supernatural power would be strong enough to counter its force. Second, refusing to do as you ask under these circumstances carries with it a very serious risk. If we accept that there is another world to which we all proceed on departing the present one, the threat of eternal hellfire and damnation (or rebirth in a lower form, or whatever future consequences one cares to consider) carries with it much more serious consequences than the use of any amount of physical force in the here and now could possibly ever achieve. And the problem is that I have no way of checking whether or not you are right in your claims. I can ignore you (and risk some terrible consequences) or I can be cautious and accept what you say on trust. The cost of getting it wrong is on such a huge scale that it simply isn't worth taking the risk. I suspect humans tend to be risk-averse in these circumstances.

In effect, resort to religion provides a very powerful stick to use in enforcing social conformity (and hence the war against freeriders). But that can only work if we can aspire to fifth-order intentionality. Fourth-order simply won't do the trick. Since this seems to be about the only phenomenon that is sufficiently demanding cognitively to require fifth-order intentionality, I am led into hazarding the suggestion that underpinning religion is why humans eventually evolved such large brains. Religion presumably gained selective benefit because it allowed later hominins (presumably humans or near-humans by then) to manage and coordinate group cohesiveness (and hence group action) in a more effective way than would otherwise have been possible, and that this (and only this?) made possible the continuing evolution of ever-larger group sizes during the later stages of our evolutionary history.

Interestingly, story-telling seems to play a particularly important part in religion throughout the world. Origin stories, or stories that set out why the particular people in question are special, form a core part of almost all religious systems. Story-telling at the purely narrative level could have a relatively ancient history, since probably no more than third-order intentionality is required. But story-telling of a more sophisticated kind – that involving the interactions of several different individuals (God, Adam *and* Eve, not to mention the Serpent) in addition to the audience and the story-teller – must require the capacity to run to proportionally more levels of intentionality (sixth-order for the composer of the original Garden of Eden story). I would suggest that story-telling and religion went hand-in-hand.

I should emphasize here that this argument does not imply group selection in the conventional biological sense. Rather, groups are selected for because they provide individuals with mechanisms for maximizing their individual fitnesses. Groups will exist only so long as, on average, the benefits they provide their individual members are greater than those they would gain by living alone (or in smaller groups).

One final point is worth raising here: did the Neandertals have religion? In terms of brain volume alone, they ought to have had as large a frontal lobe as modern humans – in which case, of course, they should have been able to exhibit all the many signals of the world of the imagination that modern humans did. That they apparently did not might lead us to ask whether their neocortices were distributed differently to those of modern humans. One might suppose that the Neandertal "bun" implies a disproportionate quantity of neocortex allocated to vision, since the primary visual area (region V1) occupies the back of the brain. Similarly, the relatively flattened frontal part to the cranium might be taken to imply a relatively smaller frontal lobe. At present, we have no satisfactory way of determining just how large the different lobes of the Neandertal brain might have been. But we can ask how small their frontal lobe needed to be to prevent them from being able to aspire to fifth-order intentionality (and, hence, religion and story-telling) and why they might not have opted to invest so heavily in these regions of the brain. I don't pretend to have any answers, but it seems to me that the ideas sketched out above at least point us in the direction of questions we can ask. Having a question in mind can often allow us to identify the kinds of evidence we need to answer them.

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Ecological Hypotheses for Human Brain Evolution: Evidence for Skill and Learning Processes in the Ethnographic Literature on Hunting

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Evolutionary hypotheses

Ecological hypotheses for primate brain evolution focus on the difficulty of tracking variable food resources, particularly across larger home ranges, and the learning requirements and tool use involved in extracting food from a protective matrix (Clutton-Brock and Harvey, 1980; Gibson, 1986; Harvey and Krebs, 1990; Milton, 2000). Species that focus on large, high-quality items of food may have to deal with several of these problems (Kaplan et al., 2000; Milton, 2000). In addition, large body size can increase the demands of such a dietary niche, as individuals need to get more food and travel further (Milton, 2000). These factors are seen as calling for an increasing reliance on cognitive skills, particularly learning and memory, as well as behavioural plasticity, in order to respond to novel environmental conditions. Milton (2000) suggests that human foragers can be viewed as part of a continuum of foraging complexity, with the implication that similar selective pressures could have applied in human evolution. The results of attempts to test this for primates have been equivocal (Deaner et al., 2000; Dunbar, 2003). Reader and Laland (2002) have shown that instances of tool use, innovation and social learning, most of which occurred in foraging contexts, correlate with measures of brain size, and this result could support ecological hypotheses. In addition, Kaplan et al. (2000, this volume) suggest that the skills required to increase dietary quality were a driving force in the evolution of a larger human brain. They argue that high levels of knowledge, skill, coordination and strength are required to exploit the high-quality resources that make up the human diet, and highlight hunting and fishing and gathering underground storage organs as skill- and learning-intensive ways of foraging.

A number of models stress the role of increasing environmental variability in human evolution, including the evolution of larger brains (Potts, 1998; Boyd and Richerson, 2000). Both authors suggest that the chief benefit of larger brains is in allowing flexible responses to change, while Boyd and Richerson (2000) stress the role of social learning or culture in cutting some of the costs of adjustment. These authors also differ in the rates of change that they deem important, the latter highlighting rates relevant to individual life history and the former, longer-term fluctuations. Individuals might experience increasing rates of variation due to external changes in ecological or social contexts or because a change in behaviour such as a dietary shift and occupation of a large home range increases the variability to which they are exposed. Interestingly, Binford (1983) argues that some contemporary hunter-gatherers maintain knowledge of a larger area as insurance in case of seasonal or yearly resource variability. This suggests that a dietary shift combined with increasing rates of environmental fluctuation might select for modes of foraging employing more information. Attempts to test the relationship between environmental variability and brain size and other measurements of cognitive ability have produced negative results for the primates (Reader and MacDonald, 2003); however, clever bird species are more successful in colonizing new areas and less likely to cope with seasonal climate change by migrating (Sol and Lefebvre, 2000; Lefebvre et al., 2004).

Kaplan et al. (2000) also suggest that life history parameters may co-evolve with brain size because of the importance of learning for complex behaviour, and highlight the benefits of learning complex foraging skills. Because learning a complex foraging skill results in increased productivity later in life, the benefits of a longer juvenile period in which to learn depend on the length of the lifespan. In this model, a switch to a diet based on learning- and skill-intensive foraging will increase both time spent in development and investment in behaviour that reduces the risk of mortality. Other scholars who have attempted to apply life history theory to human evolution differ as to the importance of learning adult social and subsistence skills in the longer human juvenile period. Charnov (1993) has developed a model in which other life history parameters, including age at reproductive maturity, are determined by adult mortality. The extended human lifespan can be explained in terms of the benefits to fitness of grandparents in caring for their grandchildren (O'Connell et al., 1999). Based on this model, O'Connell et al. have argued that the extension of the juvenile period is a function of the extension of lifespan, and that therefore it has nothing to do with learning. Blurton-Jones and Marlowe (2002) comment that human learning is often very rapid when it involves processes such as language, imitation and instruction. If these processes are important in learning foraging skills, a long learning period would be less necessary. Finally, Bock (2002) points out that there are periods when certain experience-based skills can be acquired most effectively, based on the individual's strength or height. This observation is compatible with the model of Kaplan et al. (2000), but also predicts the evolution of critical periods for learning certain skills.

While some authors focus on the demands of foraging, others argue that living in complex social groups selected for greater intelligence in primates and humans (Dunbar, 2003). Chimpanzees, the brainiest non-human primates, live complex social lives, use tools frequently in the wild, have regionally distinct traditions, and hunt colobus monkeys. Social learning, innovation and tool use frequencies correlate with each other and with brain size in primates (Reader and Laland, 2002). Reader and Laland (2002) suggest that social and ecological hypotheses should not necessarily be considered as alternatives: the ability to generate solutions by innovation or by learning a useful response from someone else could be advantageous in the same circumstances. By contrast, Dunbar (2003) suggests that environmental changes will lead to selection for specifically social cognitive abilities, as primates solve ecological problems together. Another possibility is that socio-ecological demands might often evolve in tandem. For example, species that forage for high-quality resources also tend to have fission-fusion social organization. This could be more complex because in these contexts primates use different forms of long-distance communication, and because maintaining social relations may be more demanding in terms of memory and cognitive representation of individuals who are absent (Milton, 2000; Barrett et al., 2003). This interaction is also relevant to hypotheses based on environmental variability: Boyd and Richerson (2000) argue that social or cultural learning would cut some of the costs of using a larger brain to adjust to changes in the environment.

The role of social solutions is particularly clear in human foraging strategies. Cooperative acquisition, sharing food and information, and educating young people are all key elements of foraging as practised by contemporary hunter-gatherers. Social interaction and communication are likely to influence human foraging strategies and efficiency in many ways. Buckley and Steele (2002) suggest that language could increase cooperative foraging efficiency, particularly where this involves monitoring resource conditions across dispersed patches on large spatial scales. Interestingly, Widlok (1997) has described how the orientation skills of Hai||om people are based on a combination of individual experience and "topographic gossip" about journeys and destinations. Finally, language allows people to negotiate about food sharing, and the classification of relationships may help to stabilize cooperation (Buckley and Steele, 2002). It is possible that social and ecological factors interacted in the evolution of larger human brains and linguistic skill. Kaplan et al. (this volume) suggest that human ecological and social intelligence evolved in the context of a distinctive foraging strategy, with strong benefits to cooperation selecting for greater social intelligence and subsequently language skills. Consistent with this, a number of models suggest that language evolved in the social context of extended provisioning networks (Cavalli-Sforza and Feldman, 1983; Knight, 1996; Power and Watts, 1996; Deacon, 1997; Nowak and Plotkin, 1999; Livingstone and Fyfe, 2000). More theory development is required to explore the different scenarios for the interaction between social solutions and foraging strategies that could be proposed.

Current hypotheses about human evolution link cognition, social behaviour, and life history to diet and foraging skill. In the "hunting hypothesis", hunting was seen as the catalyst for changes in social behaviour and cognition (Washburn and Lancaster, 1968). Hunting was associated with the use of tools, cooperation and a division of labour but also by extension with learning and language. The recurrence of the hunting hypothesis has been attributed to underlying Western cultural traditions (Cartmill, 1993). While current models of human evolution and dietary shifts share themes with the hunting hypothesis, they use an evolutionary framework that produces testable predictions.

Predictions

The different ecological hypotheses discussed above make a range of predictions for the historical trajectory represented by the fossil and archaeological record, for cross-species comparisons, mathematical models, and adaptive behaviour in primates and contemporary hunter-gatherers. Here, I will discuss predictions for human behaviour compared to other primates, human behaviour in the past and the historical trajectory of changes.

If we extend ecological hypotheses about primate brain evolution to humans, we would expect to find that humans exploit larger home ranges, experience high levels of spatial or temporal variability in resources within their home ranges, have a wider dietary breadth or more selective diet, and/or practise more extractive foraging than their close primate relatives. Humans' ability to cope with these environmental challenges should rely heavily on knowledge and learned skills (Kaplan et al., 2000) make a number of additional predictions regarding the characteristics of foraging for humans and closely related primate species. The difficulty of acquisition should explain the age profile of production for humans and closely related primates. Human foraging success should be based on skills or knowledge that are difficult to learn – for instance, in hunting, knowledge of prey behaviour is more important than marksmanship as a determinant of foraging success (Kaplan et al., 2000).

Based on the former hypotheses, we would expect to find evidence for correlations between increases in brain size, dietary shifts and increases in home range size in the fossil and archaeological record. According to Kaplan et al.'s (2000) hypothesis, the first major increases in brain size in the hominin line should also be accompanied by extensions of the juvenile period, increased longevity, as well as increased complexity of learned foraging strategies. Boyd and Richerson (2000) and Potts (1998) predict increases in brain size to accompany increases in environmental fluctuations. The former hypothesis would also predict evidence of changes in cultural learning processes, which might be evident in the archaeological record. Potts (1998) specifies that hominin species should persist in regions with evidence for environmental change.

More theory development is required to explore the different scenarios for the interaction between social solutions and foraging strategies that could be proposed. Investigating current processes can help us to develop hypotheses about how natural selection might have acted on the costs and benefits of alternative courses of action in the past. Some questions that might be interesting include: how does communication influence people's foraging ability, for instance to monitor resources across their home range? How does it influence their efficiency in specializing in certain resources? How do people negotiate food sharing? And what is the role of teaching in acquiring subsistence skills?

Testing dietary hypotheses

The evidence of foraging behaviour in contemporary human groups is suitable for testing evolutionary hypotheses in a number of ways. First, contemporary hunter-gatherers provide the most relevant data available on a range of traits for comparison of human behaviour with that of other species with the aim of identifying derived traits (Marlowe, 2005). Second, contemporary hunter-gatherers have been used as an analogy for Pleistocene foragers. While a direct analogy is untenable, we can study relationships, for instance between social organization, habitat and technology, so that their effects can be accounted for when modeling hominin behavioural evolution (Marlowe, 2005). Data from contemporary hunter-gatherers is useful in conjunction with archaeological data for reconstructing the historical trajectory of changes in behaviour. Finally, data from contemporary groups can tell us about the costs and benefits of alternative courses of action, and this can be used as a source of inference as to how selection would have acted on these costs and benefits in different conditions in the past. In this case, data from contemporary groups can be used to build evolutionary models, or to suggest how comparable situations would have shaped responses in the past.

One possible issue is the relevance of contemporary hunter-gatherer foraging strategies to human evolution. A range of technological innovations, from early bone and stone tools to relatively recent iron-working, has had major repercussions on foraging strategies (Marlowe, 2005). For instance, projectile weapons would have greatly increased efficiency and also made it possible for solitary hunters to bring down large game. On the other hand, while we have little idea what the biomass of ancient environments would have been, there is some reason to suppose that a dense human population has reduced modern ungulate biomass in a range of areas and habitats. This suggests that encounter rates would have been higher for hunters in the distant past, making locating prey easier. In addition, if current hunter-gatherers occupy relatively marginal land, this could have influenced return rates and foraging strategies. However, Marlowe (2005) points out that contemporary hunter-gatherers and farmers occupy areas that are similar in terms of net primary productivity. If this is the case, the key issues are the effects of technology in increasing return rates, and the possible confounding trend associated with reduced biomass. Differences in encounter or return rates might make evidence from contemporary hunter-gatherers on adult productivity and perhaps hunting strategies less relevant to past conditions. Finally, the complexity of current technology and strategies of foraging, as well as the range of species exploited, can be seen as a part of foraging intensification (Stiner, 2002: 25-26). Kuhn and Stiner (1998) describe directional shifts in small-game use from the early Upper Palaeolithic of Europe onwards. This suggests that various aspects of foraging complexity are likely to have increased with time. However, Kuhn and Stiner (2001) also suggest that some characteristics of contemporary hunter-gatherers are evident in the Upper Palaeolithic of Europe, including greater technological investment in response to unpredictable food supplies, and evidence for exchange. Hunter-gatherers in the Upper Palaeolithic may have used a smaller range of tools and exploited less low-ranked resources than contemporary groups.

Evidence for changes in brain size and life history comes from the fossil record, interpreted with the aid of studies of contemporary primates and humans. Raw material transfer data has the potential to tell us about mobility patterns and home range size in the past, but interpreting this is complex (Gamble and Steele, 1999). Evidence for changes in diet, foraging strategies and foraging skill comes from the archaeological record, and involves a range of data and varied methods of analysis. Interpreting such data in terms of the learning and skill requirements of foraging may require complementary data from contemporary hunter-gatherers: for instance the strategies associated with certain tools or prey species. We also need data on life history parameters in different hominin species to complement reconstructions of brain growth relative to body mass (Kappelman, 1996).

Kaplan et al. (2000) suggest a number of ways of testing the argument that foraging success is based on skill and knowledge: for instance, that hunting returns should be better predicted by knowledge than marksmanship, and that naïve individuals should catch up with tests of marksmanship faster than those involving encountering animals. While Kaplan and colleagues (2000) use detailed quantitative data from a few well-documented groups to test their hypotheses, the ethnographic record gives less well-controlled data on a large sample of historic and contemporary hunter-gatherers. The ethnographic literature often records the technology, strategies, food types and the size of range used by particular groups of people. These factors can easily be compared cross-culturally, allowing us to see the effects of large-scale environmental variation on the foraging niche. Ethnographic studies also describe people's environmental knowledge (ranging from general comments on the breadth of knowledge to attempts to document the content of ecological knowledge of a particular group). In addition, many studies describing a particular hunting strategy or episode comment on the knowledge applied in that context. The ethnographic literature can provide descriptions of the role of social factors in foraging, and the ways in which food or foraging strategies are used to achieve social ends. Ethnographic accounts also describe communication: what people talk about, to whom, when, and how often. They can potentially answer some questions about the role of communication and learning in contemporary foraging strategies. I aim to assess the relevance of this alternative dataset, and also present some preliminary results of such an analysis. I focus on hunting as a possibly learning-intensive foraging skill. An alternative suggestion is that it is the package of foraging behaviours and exploitation of multiple habitats that makes the human foraging niche complex.

A number of authors describe quantitative tests of the role of learning in changing foraging return rates with age using data from contemporary hunter-gatherers. Among the Ache, hunting ability increases with age and reaches a peak surprisingly late in life, after peaks in strength (Walker et al., 2002). For the Hadza, there are increases in return rates for digging tubers, and also in success at target archery, with age and strength (Blurton-Jones and Marlowe, 2002; Walker et al., 2002). However, important subsistence skills (digging tubers, climbing baobab trees and target archery) did not show significant variation with practice time (Blurton-Jones and Marlowe, 2002). This raises an important query about the interpretation of trends in return rates with age – are they based on learning, growth, or motivation? Bird and Bliege Bird (2003) argue that optimal foraging models explain differences between children's and adult's foraging patterns, implying that learning is unnecessary as an explanation. The authors suggest that differences in Martu children's and adult's foraging strategies are based on the constraints of walking speed, rather than differences in skill, although this does not explain why older children continue to use different strategies. The ethnographic literature on hunting by contemporary or historic human groups provides an alternative source of information on the processes by which humans learn to hunt, and fills in a number of gaps in the evidence. A cross-cultural approach makes it possible to examine how the processes of learning hunting skills vary between groups, and whether these vary with different environmental or social conditions. It would be interesting to find out how growth, strength and work influence the costs and benefits of gaining hunting experience (Bock, 2002). Although learning processes have been highlighted as a significant factor, none of the studies described above document these. Interaction with other people is likely to be important in learning to hunt: this is another area in which social solutions may be important in foraging.

Cross-cultural comparison of contemporary human hunting strategies

Human hunting is unique in employing weapons and other technology. Hunters use a range of weapons, including rocks, sticks or just hands, to capture and dispatch prey (Hill and Hawkes, 1983: 165; Puri, 1997: 309). The primary hunting weapons are bow and arrow, atlatl spearthrower, blowgun, and gun. These weapons possess characteristics that make them particularly useful in different environmental situations (Churchill, 1993; Puri, 1997: 286). The important properties of hunting weapons include effective range, accuracy, velocity, penetration, and impact (Yost and Kelley, 1983: 194; Churchill, 1993; Binford, this volume). The range of a weapon will influence how close a hunter has to get to an animal before shooting: if the hunter needs to get quite close, this may require more knowledge of animal behaviour, or techniques for disadvantaging the animal (Churchill, 1993; Binford, this volume). By using a weapon that kills rapidly, the hunter will avoid the need to track a wounded animal for long distances. According to Kelly (1995: 95), most bows and arrows and spears do not kill large animals quickly. Poisons may be applied to hunting weapons (Lee, 1979: 209; Puri, 1997: 286); this makes a kill more likely, but not immediate. Kill statistics for large game by colonial hunters suggest that a very high level of hunting success is associated with the use of a gun (Struthers, 1991). Other technology used in modern human hunting includes devices such as lures, whistles, traps, hunting blinds and game surrounds. These may be used to attract an animal, to get closer to it at a place with attractive resources, and to prevent it from getting away (Torrence, 2001).

The assemblage of hunting weapons varies from place to place: in addition, certain weapons may contain more components or parts. Hunting with the main Ju/'hoansi weapon (a bow and arrow) requires use of a range of items including the bow, iron-tipped arrows, arrow poison, arrow poison kit, and bark quiver (Lee, 1979: 209-210). The number of weapons and average number of components of each weapon used by hunter-gatherer groups increase with latitude (Torrence, 1983, 2001: 76). Tended and untended facilities are both more important among high-latitude groups (Holliday, 1998; Torrence, 2001: 80), who also tend to have more technology associated with transport, such as canoes, snowshoes, or snowmobiles (Gusinde, 1931, 1937, 1974; Gubser, 1965; Nelson, 1973; Tanner, 1979). This latitudinal trend in the number and complexity of weapons and number of facilities is interpreted in terms of an increased need to manage risk in environments where the costs of failure are particularly high, because there is low availability of food and few alternative resources (Torrence, 2001: 79). In addition, tended facilities are most useful where resources are aggregated, while untended facilities have the advantage of reducing search time.

Cooperative hunting is widespread (Nelson, 1969: 209, 287-289; Nelson, 1973: 88, 105, 107-108; Lee, 1979: 211; Tanner, 1979: 51; Silberbauer, 1981: 209; Hill and Hawkes, 1983: 147; Ichikawa, 1983; Yost and Kelley, 1983: 205; Rai, 1990: 48; Puri, 1997: 310). A large proportion of hunts by the Inujjuamiut involve cooperation between two or more hunters (Smith, 1991; Kelly, 1995: 219), while 47% of Waorani hunts involve more than one individual (Yost and Kelley, 1983). Cooperative hunts vary greatly in the number of people involved and the way in which they are organized. In both carnivores and humans, group hunting is likely to be useful when capturing large game, or breaking through herd defences. However, studies of hunting group size indicate that it does not always maximize returns (Smith, 1991; Kelly, 1995: 219-221). Social benefits to communal hunting may also be relevant, for instance, it may help to maintain good social relations, facilitate access to other cooperative hunting teams, or educate young hunters. Some collective hunting strategies employ a relatively large number of people, sometimes including people of varied ages, both sexes and different groups (Rai, 1990: 48; Puri, 1997: 265-266). People tend to engage in collective hunts to take advantage of animals concentrated by migration, to exploit animals when their fat content is high, and to obtain quality hides (Driver, 1990). At low latitudes, the scheduling of other activities may be more important. A number of tropical African hunter-gatherers are not documented as taking part in collective hunts (Lee, 1979; Silberbauer, 1981), and at higher latitudes solitary strategies with guns have replaced collective methods (Gubser, 1965). Collective methods involve the organization of a large number of people and thus may have particular features such as rules for behaviour (Puri, 1997: 357) or designating one person as leader (Nelson, 1973: 107).

There is marked variation in the number and composition of the species hunted by different groups: for instance, the Agta hunt 6 mammals, while hunting returns for the Penan include 28 species (Rai, 1990; Puri, 1997). The Mistassini Cree and the Kutchin are described as hunting 12 mammals, the Inujjuamiut 10 (Nelson, 1973; Tanner, 1979; Smith, 1991). This is primarily related to the species composition and biodiversity of the environment. Species diversity is highest close to the equator, but forested environments (particularly on islands) are low in mammalian, terrestrial biomass, and tend to have fewer large mammal species. Almost all foraging groups use more than 200 km^2 in a single year, and many cover more than 1,000 km^2 in that time (Kelly, 1995: 112-115). Because there is less energy available at higher trophic levels, hunter-gatherers with a greater dietary dependence on hunting tend to have larger home ranges (Kelly, 1995). Dietary dependence on meat increases with latitude. While human home ranges are larger than those of closely related primate species, even at low latitudes, they are comparable to those of large, gregarious carnivores (Marlowe, 2005: 63).

Hunting strategies can be described as particular ways of locating, disadvantaging, injuring or killing and catching prey. It is hard to compare the range of strategies employed by different groups based on the ethnographic literature, as some strategies can be defined in more or less general terms. Some strategies seem to be specialized, in that they focus on a particular animal and use knowledge of its characteristic behaviour, or require a particular skill. For example, one Penan strategy consists of imitating a pig-tail macaque in order to attract other animals: one person was recognized as an expert in this hunting strategy, and a somewhat limited group of people took part (Puri, 1997: 279). Other strategies seem more general. For instance, Ju/'hoansi hunt large game primarily by stalking or tracking and shooting with a poison arrow (Lee, 1979: 209-219). According to Lee (1979: 209), while the hunter may have particular game in mind, he does not neglect the possibility that he will encounter other game: this is reflected in the general nature of his toolkit.

There is considerable variation in hunting techniques among different groups and environmental conditions. Groups occupying higher latitudes tend to use a wider range of more complex technological aids, and also occupy larger home ranges. However, in addition to technology and strategies, many authors stress the importance of detailed knowledge in human hunting (Geist, 1978; Liebenberg, 1990; Frison, 1998; Roebroeks, 2001; Kaplan and Robson, 2002). Kaplan and colleagues (2000) argue that the relevant knowledge takes longer to acquire than other components of hunting skill such as marksmanship.

Hunting knowledge

Some ethnographic studies stress the breadth and attention to detail in hunter-gatherer's knowledge about animal behaviour (Blurton-Jones and Konner, 1976: 338-339; Tanner, 1979: 43). Others emphasize people's knowledge of signs of animal behaviour and how to interpret them. For instance, there are detailed descriptions of the data used and the information got from tracks by the Ju/'hoansi (Lee, 1979: 212; Liebenberg, 1990; Biesele and Barclay, 2001), and also by aboriginal Australians (Lowe, 2002). As mentioned above, many of these sources describe low-latitude groups. Frison (1998: 14578) argues that hunting knowledge may take a long time to acquire because it requires experience of predator-prey relationships and understanding of variation in animal behaviour in different seasons and conditions. This author also stresses the dynamic, interactive nature of the relevant factors (Frison, 1998: 14578). People know about seasonal variation in animal behaviour (Nelson, 1973: 86; Lee, 1979: 212). Some authors describe people's knowledge about the interrelatedness among animal species, and relationships between animals and plants (Tanner, 1979: 43; Nelson, 1983: 210-211; Puri, 1997: 357-360). According to Nelson (1983: 210-211), Koyukon understand relationships between species in a way comparable to modern biology: however, animal behaviour may also be explained or understood in terms of cosmological beliefs or anthropomorphism (Blurton-Jones and Konner, 1976; Tanner, 1979: 44-45; Mithen, 1990: 76). It is also possible to carry out more comprehensive studies of the ecological knowledge of a group of people, using interviews or questionnaires and various methods of identifying local experts (Davis and Wagner, 2003).

In some cases, knowledge about animals may be biased towards those of the greatest economic value (Silberbauer, 1981: 65-66; Mithen, 1990: 73). People may know in great detail about the behaviour of particularly significant game animals, for instance, the moose for the Kutchin (Nelson, 1973: 84-114). This can also be seen in the indigenous classification systems for animals and plants (Rai, 1990: 28; Puri, 1997: 448-466): for instance, the Agta use specific terms for animals they prey on and generic terms for several species of economically less important animals (Rai, 1990: 28). This would suggest that one of the aspects of hunting niches discussed above, the number of species taken, might affect information requirements. However, by contrast, the Eskimo can identify and name all bird species that are seen, including some that are not eaten (Nelson, 1969: 151-152). The !Kung and Eskimo are described as very curious about animal behaviour and other phenomena, noting a large volume of information about animal behaviour: in the former case the authors say this information may or may not be useful in hunting (Nelson, 1969: 305; Blurton-Jones and Konner, 1976). Mithen (1990: 74) suggests that in some cases people may employ a risk-buffering strategy of storing information that may be of use in the future, without having a clear idea of what role that information will play.

Knowledge of animal behaviour is seen as particularly important, but other possible factors include topography, vegetation, seasonality, and the other people involved in the hunt, or the larger social group. For instance, an important part of hunting knowledge may be landscape learning, both for navigational purposes and because many resources are associated with landscape features. People are described as being familiar with the habitats and landscape features of their region (Nelson, 1973: 275; Chapman, 1982: 21; Puri, 1997: 116). Some landscapes may be easier to learn about than others, based on the characteristics of topographic features and visibility (Nelson, 1973: 84; Kelly, 2003).

So far we have focused on descriptions of knowledge relevant to hunting. However, the suggestion that this knowledge plays an important part in foraging strategies requires further examination. Descriptions of hunting strategies and hunting episodes include information about what people know and also how they apply that knowledge in hunting. Hunters use knowledge of animal behaviour in predicting the appearance of an animal, for instance in searching for migratory animals. One Penan hunting technique involves ambushing migrating pigs at river crossings (Puri, 1997). This is preceded by observation of a range of signs that indicate that the migration might be about to start and from where, including observation of ecological associations between plant reproduction and animal migrations (Puri, 1997: 364). Once the migration starts, hunters make daily observations of the places and times they expect pigs to cross. In this case, it seems that knowledge is used to help locate the pig migration and to determine allocation of time to this hunting technique. In some cases, knowledge about animal behaviour and observation of cues may be used to decide when to move camp (Binford, 1979: 169; Kelly, 1995: 98), or where to hunt in the future – as much as a year in advance (Tanner, 1979: 133).

Such knowledge is also used to locate less gregarious animals and to search on a day-to-day basis. For instance, one Penan hunting strategy involves waiting in ambush at a salt spring (Puri, 1997: 334). Hunters use knowledge of prey, weather conditions and phases of the moon in determining when certain species are going to come to a salt spring to drink (Puri, 1997: 335). Knowledge about animal behaviour can be used to help catch an animal once it has been located. Kutchin tracking of moose provides a good example (Nelson, 1973: 106). When being tracked, moose circle away to get downwind where they can identify the intruder by smell, and Kutchin hunters use this to their advantage by searching downwind for a moose they have frightened. The knowledge used in catching animals is often very specific to prey species or conditions (for example, Nelson, 1969: 195-196, 238-239; Hill and Hawkes, 1983: 150). Knowledge of signs of animal behaviour and how to interpret them is used to locate animals, and to make repeated decisions about which ones to pursue (Lee, 1979: 212-213). It may also be used to locate a good place to set a trap or hunt from cover (Nelson, 1973: 109; Lee, 1979: 208; Tayanin and Lindell, 1991: 64; Puri, 1997: 339). On some occasions people demonstrably direct their activities towards getting relevant information. Arctic or subarctic hunter-gatherers, who are particularly dependent on hunting, may make specific information-collecting trips to determine the location of game (Kelly, 1995: 98). The intensity of sampling activity varies throughout the year, and is related to the need for information and the behaviour of specific resources, and also the amount of spare time available (Mithen, 1990: 57). For instance, searching for caribou by the Nunamiut normally takes place in the spring when their movement and location are most irregular (Binford, 1978: 169). These observations give some idea of the benefits of knowledge in hunting.

However, not all of the information used in hunting is based on detailed knowledge of animal behaviour and relationships between species. For instance, Mithen (1990: 65) describes the use of "calendar plants" as cues to seasonal changes in behaviour in other species by Australian aborigines. Similarly, the Penan use a range of cues to the timing of pig migrations including the reproductive behaviour of wild dogs and an abundance of honey in Penan houses (Puri, 1997: 358-360). Mithen (1990: 81) notes that these cues can be considered as "rules of thumb", as people make a decision to move to a new area or exploit a new resource based upon this single piece of information. This is an interesting point. While people are described as having large bodies of environmental knowledge, it seems possible that in some situations they make foraging decisions not based on rational choice and abundant data, but using rules of thumb, which could be learned from other people. In addition, not everyone in a group may know everything. This suggests another possible role for social solutions in foraging. It also raises a question about the quality of the data on foraging knowledge from ethnographic studies.

Social solutions in human hunting

The ethnographic literature gives some impression of the range of social solutions used in hunting. Above, I described the wide range of hunting strategies and weapons and other technology employed in particular groups and the global variation in these characteristics. The range of tools and strategies used by an individual hunter may be based largely on cultural learning; likewise global variation may be an effect of processes of cultural transmission. Cooperative hunting is widespread, and the benefits of joining or allowing other people to join a group may include education for young hunters, opportunities to join other activities in the future, and improving social relations. Children may learn hunting skills from other people by imitation, teaching or other forms of facilitation. People take social knowledge into account in planning a hunt, in cooperative hunting and keeping track of where other people plan to hunt that day. The demands for meat from the social group are another important consideration. Meat (and other foods) is shared by the hunter and other people, sometimes quite widely (Kelly, 1995: 161-181). People may share food to further a range of reproductive and social ends (Smith and Bliege Bird, 2000; Winterhalder and Smith, 2000; Smith et al., 2003).

In addition, social norms and rules are important in hunting behaviour, while the interaction with animals involved in hunting may be viewed as a particular type of social relation (see for example, Tanner, 1979). Finally, as Mithen (1990: 66-67) points out, foraging information is acquired from other people as well as by individual exploration. Thus, social solutions are important in human hunting; both hunting activity and the fruits of hunting are used concurrently to achieve social goals. Sharing information provides an example of the possible implications of social factors for human hunting, and leads into a discussion of the evolutionary implications.

Information is shared when someone returns from any type of hunting or traveling (Nelson, 1969: 193), or in consultations between prospective hunters and other people in the camp (Lee, 1979; Puri, 1997). Information gathered by a number of hunters over time may be discussed and eventually applied in a collective hunt (Tanner, 1979: 51). Informants may include women who cover the same ground while gathering (Silberbauer, 1981: 245; Biesele and Barclay, 2001: 78). By contrast, Eskimo hunters of northwestern Alaska gather information from other hunters, who are all men, after they have been hunting or traveling any distance (Nelson, 1969: 193). In this case, men cover much larger distances than women. The sort of information exchanged in these contexts includes the location of prey, fruiting trees and previous hunts (Puri, 1997: 381); reports on game sightings, game tracks, and weather conditions (Lee, 1979: 210); peculiarities of the behaviour of an animal, and also the presence of game or game signs (Nelson, 1969: 193). People devote quite a lot of time to such discussions (Lee, 1979: 210). These descriptions suggest that acquiring up-to-date information from peers is central to hunting strategies. Pre-hunt discussions may allow hunters both to update and to fill in their knowledge, and may also help people to remember the key facts or patterns (Mithen, 1990: 75). In addition, in many groups story-telling about past and recent hunts is a frequent occurrence (Gubser, 1965: 110; Binford, 1978: 182; Lee, 1979: 236; van Beek, 1987: 95; Tayanin and Lindell, 1991: 14; Puri, 1997: 386).

Learning to hunt

Some hunting skills can be learnt outside the hunting context. Adults provide children with toy or small hunting weapons (Gusinde, 1931, 1937, 1974; Ray, 1963: 107; Gubser, 1965: 102; Watanabe, 1975: 42; Marshall, 1976: 131; Lee, 1979: 236; van Beek, 1987: 94; Tayanin and Lindell, 1991: 16; Puri, 1997: 402). These are always scaled down and sometimes made of different materials from the adult version (Gusinde, 1931; Watanabe, 1975: 42; van Beek, 1987: 95; Healey, 1990: 89). Larger, more powerful versions are provided as the children grow older. This allows the children to play at shooting things, thus developing their marksmanship and ability to adjust their shooting to circumstances. In some cases children participate in games or exercises involving shooting at targets (Gusinde, 1931, 1937, 1974; Ray, 1963: 107; Lee, 1979: 236; Roulon-Doko, 1998: 101-102). In one case, this game was played by boys aged 9-10 and upwards (Lee, 1979: 236). Such games are interesting in that they provide a clear case of learning skills relevant to hunting that is not "on the job", i.e. a part of children's foraging.

A number of studies suggest that learning about animal behaviour also begins early, through individual observation (Lee and DeVore, 1968: 236; van Beek, 1987: 96; Tayanin and Lindell, 1991: 15). Young children play at tracking or hunting animals within a restricted area: in or around the camp or village (van Beek, 1987: 94; Puri, 1997: 325), and (sometimes when they are a bit older) around the fields or gardens and nearby paths (Watanabe, 1975: 71; van Beek, 1987: 95; Healey, 1990: 88). Young boys and girls may experience a wider area and encounter a range of plant and animal species when they are carried by their mothers on gathering trips (Berndt and Berndt, 1964: 133; Marshall, 1976), or taken out by both parents (Goodale, 1971: 35). In addition, children listen to stories about hunting told by the men (Gubser, 1965: 110; Binford, 1978: 182; Lee, 1979: 236; van Beek, 1987: 95; Tayanin and Lindell, 1991: 14; Puri, 1997: 386). These stories include details about animal behaviour and hunting techniques (Lee, 1979: 236; van Beek, 1987: 95). Children are described as beginning to acquire a range of hunting skills at an early age, including using hunting tools, learning about animal behaviour, and hunting with their peers.

Children and adolescents hunt in groups with older children or with peers (Gubser, 1965: 109; van Beek, 1987: 96; Tayanin and Lindell, 1991: 16; Puri, 1997: 402; Roulon-Doko, 1998: 128). Children also tend to accompany their fathers or other close male relatives on hunting trips (or to check untended devices such as traps) away from settlements and farmland (Gusinde, 1931, 1937; Gubser, 1965: 109; Lee, 1979: 236; van Beek, 1987: 95; Tayanin and Lindell, 1991: 16; Puri, 1997: 400). Penan and Bedamuni children start accompanying their fathers and other relatives at age 5 (van Beek, 1987: 95; Puri, 1997: 400). In the arctic, boys start to accompany their fathers as adolescents (Murdoch, 1892: 417; Gubser, 1965). As Kelly (2003: 47) points out, this does not seem to be related to the severity of the climate. Neither Ju/'hoansi nor Australian aboriginal boys start to accompany their fathers until age 12 (Berndt and Berndt, 1964: 133; Lee, 1979). It seems likely that this age trend is related to the commencement of the adolescent growth spurt. Due to various anatomical and physiological changes, the athletic ability, power and endurance of boys in particular increase greatly at adolescence (Harrison et al., 1993: 339). Thus, there appear to be constraints on learning to hunt through experience, which may be based on growth and strength. Skills in hunting small game may be established more quickly. Bedamuni girls and adult women chase rodents and catch spiders, lizards, snakes, flying foxes and fish. They are restricted from the use of bow and arrow or trap technology, and hunt primarily on an encounter basis in fields and gardens. According to van Beek (1987), the "female" way of hunting is firmly established by the early teens.

Instruction in hunting contexts is limited. Adults may point out plants or animals of interest, or signs of animals (Goodale, 1971: 38; Puri, 1997: 401), or tell children about animal behaviour (Tayanin and Lindell, 1991: 16). Liebenberg (1990) has described tracking skills as based on cooperative training. In a number of hunter-gatherer groups in Tierra del Fuego, adolescent boys (and sometimes girls) experience a more formal education in subsistence skills during initiation ceremonies (Gusinde, 1931, 1937, 1974). This includes supervised exercises and assessment of progress. Since examples of such formal education are restricted to one geographical area and period, it seems unlikely that this is necessary for hunting at higher latitudes. However, adults will alter their hunting behaviour to accommodate the limitations and learning requirements of children (Puri, 1997: 324-334). Adults and older children are described as being involved in children's hunting education in a wide range of ways, from providing tools to taking them on hunting trips, and may incur costs in doing so.

Other aspects of the human foraging niche

In this discussion I have focused on a potentially complex foraging skill, hunting. This raises a number of other questions. First, other foraging skills may be more complex (in which case a study of these would be more informative). Second, the demands of a foraging niche involving exploiting a range of food types using a range of complex foraging methods may be more important than any of those strategies considered on their own. In this case, it might be relevant to look at the complexity of characteristics of the foraging niche as a whole, such as the range of food types taken and home range size. This would produce different results for comparisons of some variables but not others. For instance, tools for processing vegetable products tend to be used more frequently at low latitudes (Torrence, 2001). Some contemporary or historic hunter-gatherers occupy very large annual ranges (Kelly, 1995). Range sizes are particularly large at high latitudes, and this has much to do with a strong dietary dependence on hunting. Thus, looking at the characteristics of the foraging niche as a whole makes a difference when considering technology but not home range size. It might also be relevant to look at the knowledge required for the foraging niche as a whole, and the time taken to learn a repertoire of subsistence skills rather than one skill area.

In terms of foraging complexity, the seasonal exploitation of different areas with contrasting characteristics of habitat and resources may be more important than absolute range size. The ethnographic literature can tell us more about what people know about their environments and how this relates to range size or the characteristics of the range. For instance, do people with larger ranges have a larger body of environmental knowledge, or do they know about the area in less detail? Comparison of two accounts of landscape knowledge suggests that the latter may be the case (Nelson, 1969, 1973). In addition, people with larger home ranges are described as physically covering the ground less thoroughly (Kelly, 1995). Information about home range characteristics and knowledge about landscape and resources for other groups would be interesting. Some of the hypotheses discussed above would suggest that there are higher benefits to gathering and using information in more variable environments. A number of groups of people are described as knowing about much larger areas than they exploit (Binford, 1983; Kelly, 1995). In addition, as discussed above, some groups of people are described as knowing about species of birds and animals that are not exploited. The ethnographic record could tell us whether groups with knowledge of additional areas or resources have to deal with complex resource fluctuations. The discussion of the role of social factors in human foraging applies to these hypotheses, too. For instance, an alternative way of coping with highly variable environments is to maintain strong social ties with people in neighbouring areas where different resources are available (Kelly, 1995: 150-151).

Conclusion and future directions

There is considerable variation in hunting techniques among different groups and in different environmental conditions. Groups occupying higher latitudes tend to use a wider range of more complex technological aids, and may also occupy larger home ranges. Some descriptions of people's ecological knowledge suggest that factors such as the range of prey species may indeed influence what people know about. Some ethnographic studies stress the breadth and attention to detail in hunter-gatherers' knowledge about animal behaviour, cues to animal behaviour and how to interpret them, relationships among animal species and between animals and plants. This suggests that human hunting strategies are learning-intensive. However, we need to establish that this knowledge plays an important part in foraging strategies.

The examples of how people apply knowledge in hunting discussed above suggest that it may be used to improve foraging decisions (including patch and prey choice), to reduce search or pursuit time, and to increase the chances of capturing prey: it may also contribute to long-term strategies of mobility. Optimal foraging models suggest that more information is needed when the movement and location of resources are very irregular (Kelly, 1995: 98). This is corroborated for contemporary hunter-gatherers by the timing of information-gathering trips, and also from descriptions of the information people use in hunting migratory species. A more detailed study would allow us to ask questions about the effects of social demands on information use, the knowledge associated with different methods and technology, and also the impact of environmental change on current strategies. However, the variety of ways in which information is used makes it hard to employ such models in combination with ethnographic data to suggest specific environmental contexts which would favour more knowledge-intensive foraging. An alternative outcome would be to use a similar analysis to help interpret the archaeological data in terms of skill or learning, for instance by testing whether hunting a particular prey species tends to involve a lot of knowledge about its behaviour.

Ethnographic data suggest that gathering information may be incorporated into foraging activities or may be done independently, in which case there is a trade-off between obtaining information and other activities (Mithen, 1990: 58). Thus, information gathering is likely to be done where there are low costs (for instance, when people have lots of spare time) or high benefits for information. Ethnographic examples suggest that people often share information before or after hunting trips, so that there is no trade-off with subsistence activities. In addition, people use rules of thumb that may be learned from other people as well as rational choice and detailed knowledge. This raises a question about the role of knowledge described in ethnographic studies in foraging strategies, and suggests another possible role for social solutions in foraging.

What implications do ethnographic data on the sharing of foraging information have for social and ecological hypotheses for brain and language evolution? People are described as devoting quite a lot of time to sharing information related to foraging, or as doing so frequently, confirming that sharing information is important. The ethnographic data also suggest that conversation covers a range of factors that change at different rates. On occasion people find out about quite rapidly fluctuating environmental factors, and this information may be more up-to-date than their personal experience; they also discuss characteristics of animal behaviour that may be relevant over the longer term. Based on social learning models, information from peers is likely to be useful for tracking resources that change relatively rapidly; where rates of change are slower, information from older people with lots of experience may be helpful (Laland et al., 1996, 2000). The ethnographic data suggest that learning from peers is very important, but story-telling could include information based on longer-term experience. In addition, some examples suggest that the people in the group who are treated as potential informants depend on how foraging activities are distributed and the distribution of resources within the area they are exploiting. The ethnographic data confirm that communication may lower the costs of knowledge-intensive subsistence strategies, and give people access to more up-to-date information. However, because communication occurs in such a range of contexts and between such varied people, it is difficult to highlight a likely selective ecological context for the evolution of social learning and communication based on this evidence.

Mathematical modelling of communication of foraging information incorporating information about group size, home range size and composition can be used to ask questions about the role of language in monitoring resources across a large home range, and possibly also resource specialization (e.g., Lake, 2000). This allows the modeller to vary environmental and social conditions in order to see where the gains are greatest, which would give some insight into possible evolutionary scenarios.

The ethnographic evidence on how children learn hunting skills is generally either anecdotal or generalized, and includes limited quantitative data (such as time devoted to learning and to teaching). It can be difficult to identify learning processes from the primary sources, given the different research interests of the authors. However, there is documentation of activities, children's ages, and the social context of learning, and this can be used to make some inferences regarding learning processes including social learning. The preliminary data described above give some indication of the costs and benefits involved in acquiring hunting experience. There seem to be growth constraints on learning some skills through experience, particularly those associated with hunting larger game. This is interesting given Kaplan et al.'s (2000) emphasis on learning during childhood: however, evidence for such a constraint would not conflict with their theoretical model. Comparison of a larger sample of groups could test the generality of this pattern and the nature of the constraints. Some skills are learned relatively early, but key elements are acquired through experiential learning after the child has reached a certain level of growth and strength. This is consistent with Bock's (2002) suggestion that growth and experience will interact, producing a step-like pattern in the acquisition of particular skills. Further data could be collected on the people involved in children's hunting education in different ways. This is of interest because it seems possible that adults incur costs related to children's learning: such costs might be a relevant factor in the evolution of learning and life history.

How useful is the ethnographic literature on foraging strategies for addressing dietary and ecological hypotheses about human evolution? It may provide better data on some subjects than others: for instance, methods and technology or learning compared with ecological knowledge. In using ethnographic descriptions as a source of inference about past conditions of selection, we need to account for changes (for instance, technological innovation) with possible effects on the character of interest. On the other hand, variation between groups may help us to explore the effects of changes. Some characteristics are relevant to comparisons with other primate species (for instance, home range size or dietary breadth). Other methods of testing evolutionary hypotheses should be used together with those discussed here: for example, the evidence from the fossil record for changes in brain size and life history, and the evidence from the archaeological record for diet and foraging techniques. The current summary of ethnographic data on foraging and learning poses more questions than it answers. However, this is potentially valuable, in that these questions could help us to refine current theories, particularly those concerning the interaction of social and ecological factors.

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Haak en Steek – The Tool that Allowed Hominins to Colonize the African Savanna and to Flourish There

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Introduction

Physical data from early hominins prior to the use of stone, some 8 to 3 million years ago, is mostly limited to bone fragments. Fortunately, indirect data and reasoned assessment can provide additional information about diets and life-ways of early hominins. This is possible because these hominins were phylogenetic relatives of ourselves and the other great apes, and as such we know many elements of their life: we know they needed to find secure places to sleep, that mothers carried small babies for several years, that males contested one another for status, that there were strong elements of group bonding, and so on. Of course these earlier hominins needed to obtain a nutritious diet, and did so in a context that included competition for both security and resources with many other species. And we know something about their unusual habitat.

When African savannas expanded in the late Miocene and early Pliocene, say, 8-10 million years ago, hominins were apparently one of many forest-adapted groups that ventured into this new habitat. Tied to the expansion of savannas there was an unparalleled explosion of large mammalian herbivore diversity. Hominins faced the same two problems that other mammalian colonists faced on the expanding savannas – how to take advantage of the abundant new food resources, and how to avoid becoming one of them. In this essay I will be applying recent refinements in our grasp of mammalian ecological and ethological fundamentals to reconstruct parameters of early savanna adaptations during these pre-lithic times. At first sight hominins brought rather odd talents from their primate ancestry to this transition: a modicum of cognitive skill, hand dexterity, and the ability to stand upright. But the combination of those capacities enabled the acquisition and employment of a special tool with which, I propose, hominins opened the savanna gate.

The forest-savanna transition for herbivores

Growing aridity is thought to be the central factor in shifting the predominantly forested African landscape toward savanna vegetation in the Pliocene (Partridge et al., 1995). This increasing aridity has been attributed both to general global causes, and more locally to moisture blocking from the topographic rise along the rift system of Eastern Africa. This was, however, an unsteady shift; the Plio-Pleistocene was marked by irregular swings of moisture and hence varying landscapes (De Menocal and Bloemendal, 1995). Thackery's research (1995) finds that today a peak combination of moisture and rainfall (means of temperature around 21° C and 750 mm rainfall) produces the most species-rich and densest large mammal communities. Those particular climatic settings result in a small-tree scrub savanna (Fig. 1). It seems probable that this same climate was more widespread throughout much of the world during the Pliocene, and particularly in Africa (Cerling, 1992; Thackeray, 1995).

The fossil record helps us to piece together some of this vegetational transition (Cerling, 1992). By the early Pliocene many forest plants had adapted to drier circumstances and were able to prosper in more open conditions. Along with the forest plants came a rapid radiation among forest-adapted herbivore groups, and ho-

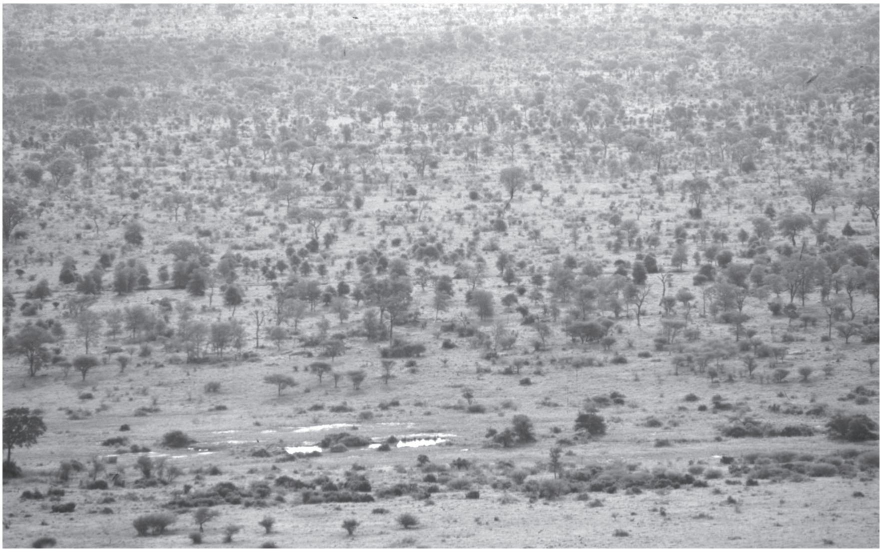

Fig. 1. Scrub savanna, Kruger Park, South Africa. This is one of the most productive landscapes in Africa for large mammals, and is probably the closest approximation of what much of Africa was like in the Pliocene - not the same species but a similar physiognomy - a productive grassland landscape dotted with short trees.

minins were part of that. The great apes were a Miocene forest radiation, with lives built around forest circumstances. So why did one or more lines of great apes leave the forest? Perhaps a more pertinent question is, what enabled a forest primate to successfully compete and survive in the expanding scrub savanna? That is my challenge in this paper: to present a credible connection linking hominins into a mesh of climate, savanna plants, herbivores and carnivores.

Modern comparisons allow us to reconstruct hominin forest ancestry as adapted to exploiting an arboreal frugiverous base (Leach, 1997) for carbohydrate energy together with an opportunistic use of protein supplemented from the forest floor. But protein is sparse in forests. Forests are on the whole nutrient limited. That was not true of the opening savannas, where the soils were much richer.

These more arid but nutrient-rich soils supported low-canopy plants with edible tissues that were in reach of large herbivores. A variety of invertebrate and small vertebrate herbivores found ways to exploit this highly seasonal productivity. Three herbivorous large mammal groups did so as well: artiodactyls, perissodactyls, and proboscidians. Each of these, originally dwellers among the forest openings, had special gut flora to enable them to digest the cell walls of plant leaves. The savanna scrub trees and rank grasses revolved around getting enough water, by growing seasonally, storing root water, keeping little above-ground tissue exposed to dehydration, and much else. Savanna plants kept plenty of protein and new growth tissue handy. Because they were not so protein limited, they evolved growth patterns in which fewer resources were allocated to chemical defenses. That was the key. The savanna vegetation afforded herbivores a nutritious and less chemically defended smorgasbord if they could but find ways to digest the tough structures that protected plants from desiccation. And they did (Walker, 1984; Vrba, 1995), reaching a diversity and biomass unknown throughout the preceding Tertiary or since.

My proposition here is that we can discover many basic elements of early hominin ethology and ecology by placing them in the context of the evolving Pliocene savanna community. This involves understanding herbivore competitors and potential predators. The fossil record can help us establish the overall setting of this problem, but it still affords scant details about hominin life strategies. So I will be drawing from the palaeoecological data and superimposing what we know of the comparative ethology and ecology of today's African species, to enrich our reasoned assessment. Of course the mammalian community the early hominins experienced was not the same as Africa today, but basic adaptive interactions do have some analogues among today's array of species. It is the best we can do, and not so remote as it sounds. We know, for example, that early hominins did not have an unlimited range of possibilities in regards to foraging and protecting themselves, only narrow adaptive avenues were likely available.

How did hominins fit into this taut herbivore community?

So let us begin by imagining these frugiverous pre-hominins observing herbivores venturing from the forests into the open scrub savannas, indeed, joining them. There were considerable new resources on these expanding savannas, but there were many more competitors as well. Remember, every species has a speciality, something at which they trump other species. That is the dictum of evolutionary community dynamics – two species stacked on the same resource are either pried apart or one becomes extinct. Such specialization dictates much of species' differences in body form, behaviour, and physiology (Gilchrist and Mackie, 1984). Species are shaped by evolutionary successes and failures shoulder to shoulder in a community of many other species. If hominins were herbivores, what kind were they?

Let us start with what we know. These hominins faced a complex guild of mammalian herbivores, which was remarkably diverse in Pliocene Africa, probably sufficient to have left virtually no unoccupied adaptive gaps. It is likely that short-term seasonal possibilities existed in which maturing fruit and nuts or termite emergence would have been so abundant as to overwhelm many specialists. But a species cannot live by serendipity alone, no species is completely an eclectic generalist, that niche does not exist. And hominins had some major limitations; they didn't have special detoxification systems (browsers have enlarged salivary glands to neutralize tannins), nor did they have a gastro-intestinal tract that could use a complex, incubating, chambers-using gut flora to neutralize toxins and to digest tough plant cellulose. This rules out most mature leaves, twigs, and stems. Grass seeds would have been sought after by many species of top-sward feeders existing at high densities, for example: zebra, horses, and hipparions (*Equus*). Roots were sought after by an array of root diggers, including a variety of baboons, *Papio,* many suids, *Sus, Phacochoerus, Nyanzachoerus, Notochoerus, Kalpochoerus, Potamochoerus, Hylochoerus, Metridiochoerus,* and other groups. Smaller vertebrates, the "crumb feeder" specialists, would soon have cleaned up fruit and insect pulses. The list of potential competitors is particularly apparent among large herbivores (Owen-Smith, 1982). Any theory as to how hominins fit into this guild has to describe a niche not already competitively held by another species. Though I have read works by a number of theoreticians, who have tried to elbow out other herbivores to find room for the hominin radiation, there seemed to have been no credible niche. The reason for this failure is that hominins were probably not a herbivore specialist. Accumulating data from a number of studies suggest that early hominins had to have relied heavily on animal resources (e.g. Aiello and Wheeler, 1995; Milton, 1999; and see papers elsewhere in this volume). Rather, I propose early hominins used a variety of plant supplements to round out their true speciality role as a highly competitive member of the large carnivore community. The question is, how were they able to successfully compete with other large carnivores?

The true savanna bounty for a simple stomach lay not among the herbs but among herbivores

Again, our two fundamental questions are: (1) what key resources were these hominins able to use to their ecological advantage on the savanna, and (2) what kept hominins from being eaten?

We have hinted at the variety of large herbivores which each had ways of transforming the bounty of grasses and shrubs into themselves. Transforming the coarse savanna forage into flesh worked best with a large composting gut. So, opposite to what we find in forests, large mammals flourished on the savanna at the expense of small herbivores. Mammalian biomass on the savanna was mostly in the form of large mammals, and it is here where the grand potential for a meat-eater lay. For a hominin with a simple stomach, no caecum, short intestines, simple bunodont teeth – a fruit and insect eater from the forest, able to occasionally kill and eat other forest vertebrates – this savanna large herbivore meat was edible and nutritious, rich in critical micro- and macronutrients, a generally compatible diet (Milton, 1999). But dietary compatibility was not sufficient.

The problem lay not in the eating, but in obtaining this herbivore bounty. Large carnivores bring exceptional capabilities to their niches: fantastic stealth, long endurance running, lightning acceleration, tremendous ability as scent followers, long sharp canines together with powerful neck muscles for killing, carnassials to scissor thick skin, and for the three main groups (lions, *Panthera*, spotted hyenas, *Crocuta*, and hunting dogs, *Lycaon*), elements of cooperation. These latter live in prides, clans, and packs, extended family groups that help ward off other carnivores with whom they compete and share the landscape, cooperate in the hunt for larger herbivores, and jointly defend their territory against conspecific neighbour groups.

But our newcomer apes lacked the outstanding physical powers of other carnivores. They undoubtedly did live in social groups (Hill and Dunbar, 1998), and they did have something else that was crucial. Opportunistic use of supplements to a frugiverous life in the forest had provided them with facultative flexibility and intellectual problem-solving skills. Smarts and group cooperation somehow broke the herbivore's defensive codes – hominins apparently found a way to make a living from catching, killing, pirating kills, and eating large mammals, with, of course, considerable supplements. But keep in mind that other carnivores were likewise using their physical skills, social cooperation, and considerable smarts to outwit large herbivores. Yet, hominins made a secure niche amongst that tough competition because they had a certain sort of smarts that could leverage tools to make up for physical deficits.

What was a boon to herbivores was a boon for carnivores

The skyrocketing Pliocene density, diversity, and abundance of herbivores afforded new opportunities for large carnivores. For example, in addition to lions and leopards, there were three species of large sabertooth cats (*Homotherium, Megantereon,* and *Dinofelis*). There was also a large bear, *Agriotherium,* the size of the largest Kodiak bears. Also there was a wolverine, *Plesiogulo,* the size of a small bear, likewise, species of large hyenids (*Chasmaporthetes* and *Pachycrocuta*), in addition to many of the extant carnivore genera. It was an incredible fauna (Hendey, 1982). The predator guild was densely packed.

The predatory techniques of these carnivores varied considerably. Canids and hyaenids became coursers, constantly testing herds for the halt and lame, and trying to catch individuals at some disadvantage that would allow predatory strengths of endurance and stamina to prevail in long pursuits. Large felids relied on stealth and special anatomy that allowed a drag-racer style of acceleration. The latter was bought with a loss of endurance, so felids had to start a chase at quite close quarters. To attain that proximity they evolved exquisite patience and stealth. Some, like hyaenids and canids, were scent trailers; others, like cats, developed penetrating nighttime vision.

Evolutionary pressures also honed herbivore fleetness and alertness, but defense against predators is quite expensive, and complete security is probably inaccessible. Evolutionary changes had only to keep the balance of recruitment vs. loss slightly in favour of the recruitment side. Every species can tolerate some density-dependent predation loss of adults (that is the basis of well-managed human hunting regulations). The adaptive life history of each species dictates what level that will be. Some species, like suids, can tolerate around over 50% annually, while others, like elephants, cannot tolerate more than around 4%. So how were these herbivore species able to walk out into the full visibility of the savanna and hold the line against predation?

Anti-predator defenses are an integral aspect of evolving herbivore behavioural, anatomical, and physiological design. Camouflage can still work out in the open, and smaller savanna species use a variety of cryptic coloration. Most species augmented fleetness via increased stamina and locomotor efficiency. Many altered the configuration of their social weaponry so that it could also be used for defensive purposes. This is best seen among buffalo. Today, African buffalo use the rounded frontal boss to clash with social opponents, and use their curved and sharp horn tips as a hook to dig at predators. The use of fangs, tusks, horns, and

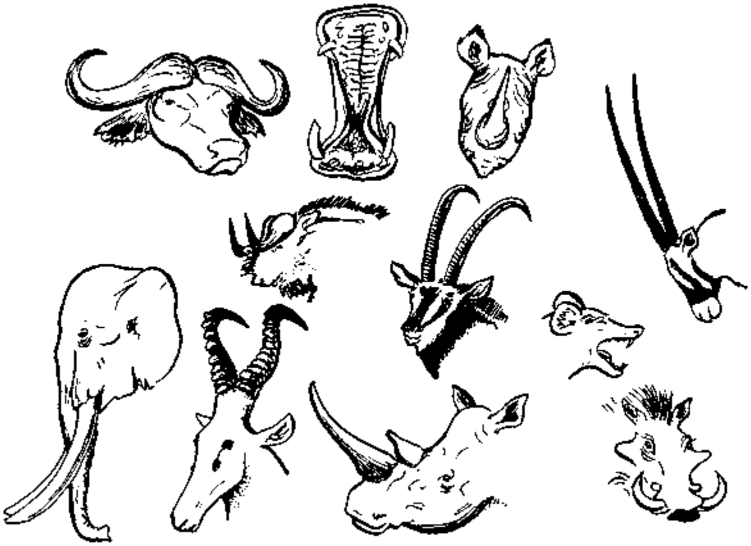

Fig. 2. Most African large mammals have sharp fangs, tusks or horns with which they fight one another, and also use as defensive weapons against potential predators. Carnivores have a long association with the potential dangers posed by long, sharp, bodily projections, recognizing these as extensions of the organisms. Carnivores would have recognized the hazards of hominin defensive tools in the same manner.

antlers for both social and anti-predatory defense is common among most extant large mammals, especially in Africa (Fig. 2).

That was probably true in the Pliocene as well among proboscidians (*Mammut, Deinotherium, Anancus, Loxodonta,* and *Elephas*). Suids used their tusks; gemsbok, *Oryx*, roan and sable antelope, *Hippotragus*, rhinos, *Diceros, Ceratotherium,* and buffalo, *Syncerus, Pelorovis* employed their sharp horns defensively; zebra, three-toed horses, *Hipparion,* true horses, *Equus,* and giraffes, *Giraffa,* aimed their powerful kicks at predators, and so on across a wide variety of species. Few other defences can compare with a large body size. Elephants, giraffes, buffalo, eland, and others, have evolved a trade-off of growing slowly and reproducing infrequently. Large body size itself makes predatory attack difficult and dangerous.

Another thing these large herbivores have in common is that they are smart, which is to say, they learn fast, have complex, yet flexible, social relationships and know how to discern situations in which predation attempts are likely. Once attacked, they often can figure out how to use their defences to best advantage to avoid being killed. For example, gemsbok and sable are known to back into a thorn thicket eliminating attack from the rear, while they successfully defend against a frontal attack with their long sharp horns (Apps, 1992). It sounds simple, but that strategy takes intelligence. Our lack of everyday familiarity with wild large mammals and direct exposure to domestic ones gives us a skewed view of how intelligent most wild mammals are. Domestic sheep have been selected to be placid, dull-witted, and to submit to human control. Wild Alaskan Dall sheep are anything but.

A comparative assessment of large mammal anti-predator effectiveness

In a roundabout way we can assess the Pliocene effectiveness of hominid defenses by looking at the efficacy of extant large mammals' defenses and reproductive capacity (Fig. 3).

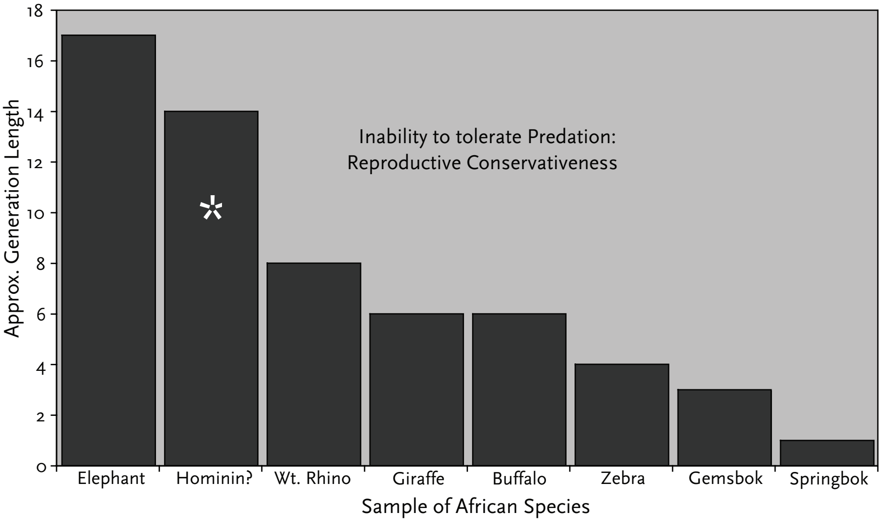

Fig. 3. Basically, hominins could have tolerated little predation. In that regard they must have been between ourselves and our nearest relative, chimps, in generation length. We can thus place them along a gradient of African species. Hominins would have fallen closer to elephants than other African large mammals in their degree of reproductive conservativeness.

If a species can reduce predation to 2% annually, it is using a comparatively effective defensive device or strategy. If predation kills 40%, the techniques are not so effective. To avoid extinction, the latter class has to have evolved compensations, say, in the form of higher reproductive rates (Hutchinson, 1978). Elephants are our gold standard here. Adult elephants essentially live predator-free. Once in a great while lions or hyenas take a juvenile. The risks are simply too high for lions to regularly attempt attacks on adult elephants. Many Pliocene herbivores were quite large. For example, there were several Pliocene species of large bovids. There were large baboons, including an enormous gelada species. Among numerous suid species two were truly giant forms. There were two species of rhinos, hippo, and several proboscidians, several equids (again one enormous one), many antelope species (three quite large) and three large giraffids that fit into that class of mammals which would have suffered little predation because of their large size.

Sable antelope, roan, and gemsbok use their long sharp horns in defence and are all known to occasionally kill lions (Pienaar, 1969; Schaller, 1972). As a result, the predation rate among these species is comparatively low for a medium-sized antelope – often in the less than 10% range. The powerful kicks of giraffes keep them in a similar category, as do zebra kicks. A zebra kick landing on the face of a pursing lion means dire debilitation if not death, and pursued zebra seem to try with all their being to land such a blow. Lions with mortal wounds of broken jaws have been seen in several lion studies (Schaller, 1972).

Buffalo generally provide too dangerous a defence to make them tempting for lions, but there are situations in which lions do bring down buffalo. Where buffalo are abundant, there are particular lion prides that are known to selectively exploit buffalo (Sinclair, 1977). In these buffalo-hunting prides, powerful male lions play a key role in joining the females in killing buffalo (Mills, 1991). Even so, seldom are more than 7% of the population taken annually by predators (Sinclair, 1977) but sometimes up to 50% for calves. Buffalo are very conservative breeders and cannot tolerate much predation, so they occupy the crease-line for our comparison.

Buffalo are almost, but not quite, able to reduce predation to the level required by a conservative hominin life history. A hominin defence had to be better than the violent force of a dig from a bull buffalo's horn or the hammer-blow of a zebra stallion's kick. How did these hominins achieve such a defensive effectiveness? What tool could they wield that would be of such power? Hominin reproductive rates and long childhood years could not have withstood much predation – a virtually predator-free life. Zebra and buffalo defensive force far exceeded that of any club blow that hominins could manage, by an order of magnitude. Yet their defensive might does not serve to keep adult zebra and buffalo predation below 2%, as a hominin life history would demand.

The large herbivore prey species we are discussing now have only one young at a time, thus we can look at such facts as gestation length, age at first reproduction, life expectancy, etc., as a rough comparison of conservativeness in life-history features. A general measure encompassing many of these features would be to compare approximate *generation length* in the female line (Fig. 3). Like elephants, hominins had a long generation length, so it would have been critical to virtually eliminate the threat of predation. What tool could hominins possibly have employed to achieve this effective reduction in predation?

Finding a defensive tool that would have protected hominins from all carnivores

The fossil record has left us few, if any, clues as to what this tool was. But the point I want to emphasize here is that we are not searching for a merely theoretical tool. We know hominins had to have used some defensive tool, and it worked well and consistently. First, however, I want to run through the attributes of an ideal tool and review some rejected candidates. Remember, we are searching for a tool that will stop a pride of hungry lions from attacking our group of hominins. Without this tool the hominins were virtually defenseless: remarkably un-fleet, with stubby canines, feeble kicks, and meekly muscled arms. Sleeping upright in a tree neither fits the newly emerging bipedal body nor, as we see from large baboons, does it guarantee escape from predation. Leopards often take baboons from their sleeping trees. Arboreal escape was not the answer, because using the scrub savanna often meant moving out of the range of large trees. A shrub savanna provides little

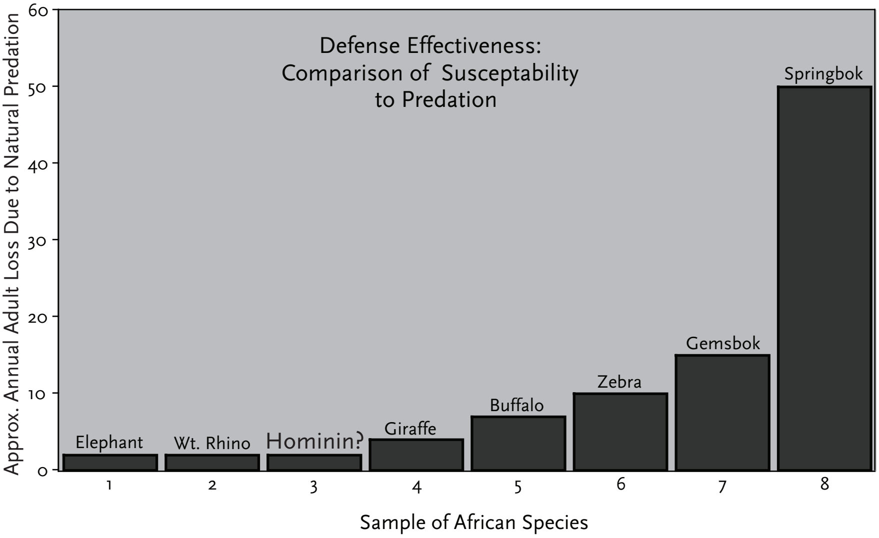

Fig. 4. Considering hominin reproductive conservativeness and inability to tolerate a high degree of predation, we can rank them alongside other African large mammals in the effectiveness of their defence and their susceptibility to predation. Lacking a natural defense away from trees, their requirement for tool effectiveness would have to have given them a high level of defense in the same range as elephants and rhinos. That is the standard by which we must judge the array of potential tools available to these early hominins.

relief. All savanna primates (except hominins) are built both for speed and for climbing, using cliffs or trees as suitable escape terrain. Baboons sometimes venture far from trees, but the troop is then defended by a group of large males sporting enormous canines (as long as those of a large carnivore). Unlike these other savanna primates, hominins had no obvious anatomical defence against large predators. There is thus a strong argument that early hominins would have had to make or discover some effective tool of defense ... if they could only have taken the trees with them (Fig. 4).

As the first step in our search for a no-fail defensive tool, we can begin by looking at the following, optimal criteria:

1. The tool was likely made from a commonly available substance.
2. The tool would likely have been available ready to use in a ready-made, or virtually ready-made form not requiring a great deal of work and forethought for its construction.
3. The tool would have been easy to use, that is, its use did not require a complex facility or months of practice.
4. The effective visual threat of the tool display would have been something that did not require previous experience, that is, predators innately and instantly recognized the tool as dangerous.
5. The tool could not only cause pain, but almost always guarantee a disabling or mortal wound.
6. The presence of this tool would arrest a running charge by a large predator; from hominin demographics we can assume it had to have been a tool that could not fail.
7. The best defensive tool would be light in weight and easily portable, so that it could at least be carried by a significant number of group members at all times.
8. The efficacy of this tool would have been enhanced and magnified if presented to the threatening carnivore in multiples through cooperative use.
9. Hominins could have capitalized on their unique biological adaptations, brought with them onto the savanna, in employing this tool.
10. No carnivore was able to make specialized use of such a tool nor has any since – that is, there was no competition for this niche among non-hominins.
11. There would have been direct uses of this tool as a means of obtaining large mammal resources.

What tool it was not

There has been surprisingly little focus or debate about the defensive tools early hominins could have used. A few published and unpublished suggestions have been offered, but the list is short:

1. Thrown pebbles or boulders
3. Large boulder swung as a hammer or axe
4. Wooden club or knobkerrie
5. Poisoned sharp stick
6. Long sharpened pole or spear
7. Sharp-pointed stone hafted to a spear
8. The threat of pain from a thorny branch
9. Stinky body odour

Circumstantial and physical evidence quickly eliminates these candidates. Let's put them to a test against a typical carnivore attack, say a charging lion.

Rocks and clubs, either thrown or swung as in a hammer blow, require a precisely aimed coordination that can only come with years of practice. Rounded rock surfaces spread the energy of the blow over a large area and do not regularly result in penetration of the skin. Wounds caused by such blows to the body tend to result in bruised tissue that regularly heals. Rocks and clubs could cause considerable pain, and sometimes significant injury if one was skilled enough to hit the lion exactly in a few places on the skull where bone lies just beneath the skin, but that is a small moving target in unimaginably terrifying situations. Pain alone is not a sufficient deterrent to predators; we know from fieldwork with lions that they necessarily must experience pain as a regular part of their violent mode of predation. Pulling down a kicking, thrashing zebra on the run by sticking one's head into the mayhem to make a killing bite is fraught with injury and pain. This predation is a high-risk affair, yet if one can regularly avoid mortal wounds, its benefits are immense. Holding a club or rock ready to throw or swing as the lion charges would have little deterrent value, as lions do not natively recognize a cocked arm holding a rock as potentially offensive behaviour. Each lion would have had to learn by experience, and hominin demographics could not have tolerated that kind of cost, even in the unlikely case of it occasionally being an effective deterrent.

Some of these same hurdles pertain to a poisoned stick as well. Poison is not intuitively threatening. Most poisons available to hominins were not lethal, and virtually all are rather slow acting. Poisons, likewise, would have involved learned behaviour on the part of every pride of lions, learning which would have to have been refreshed often. Remember that in the wild many, if not most, large carnivores ultimately are debilitated and die by starvation and in duress may take risks beyond the norm. Furthermore, there is a case to be made that the use of poisons involves complex reasoning and botanical expertise perhaps beyond the abilities of those first hominins coming out onto the savanna.

Spears or pikes, on the other hand, are effective defence tools, and were likely the staple tool throughout the history of our genus. I will argue in later pages that these devices grew out of the first tools, but to make effective sharpened spears or thrusting poles, one needs to have some tradition of stone working. One can sometimes find a naturally shaped spear point among thousands of stones, but these are rare and still probably not very useable. Stone for making spears, especially stone-hafted spears, has to come from stone working. There is no sign of stone working at the time of hominin entry onto the savanna, and none for the next several millions of years. Current evidence shows stone flaking probably began after 3 million years ago. Arguing in this way, there is an array of reasons to exclude the tools listed above.

Kortlandt (1980) proposed that a thorny branch could deter the largest predator because it offered the threat of pain. However, as I said, all kinds of violent predation regularly involves considerable pain to the predator. Simple momentary pain like needle pricks or blows with a stick would be a poor defense against a really desperate lion (Patterson, 1985). I'll return to this line of thought later.

Plagued by this theoretical problem of reconstructing hominin defence against predators, Leakey (1967) proposed that hominins were not edible because of their odour. Specialized anal glands are used by various mustellids and viverrids, but primates have no history of such potent scent organs. Until a more plausible hypothesis is proposed, we can only assume that an effective defence had to come from some powerful weapon. Without it, a large undefended hominin would not have survived long on the savanna (Kortlandt, 1980).

What tool can we not exclude?

There is one tool that fits the above criteria, and it involved acacia thorns as Kortlandt (1980) suggested, but I don't think for the reasons he proposed. No other exposed mammalian organ is so critical to survival as their delicate eyes, there was no evolutionary way around this undefended fragility among hominin's predators. Thorns are especially dangerous to eyes. The main weapon of attack and killing used by all large carnivores is their long sharp canines. Because of this, they have to attack head first, and that, as roundabout metaphor, was the large carnivore's "Achilles heel", when it came to their vulnerability to a hominin, weapon. Acacias, *Acacia*, are ubiquitous in African savannas and have a long history there. All species are well defended with thorns against predation by herbivores. Most thorns are long prongs, but some are short hooks. A typical prong is sharp and stiff, averaging around 10 cm in length. It is not just its size that is so effective. Thorn injuries on the side of the head or posterior parts of the body are an irksome sharp pain but seldom do sustained damage. That is not true on the face. Mammals are able to close their eyelids, but the lid protects the cornea surface from scratches or debris, not impalement. The skin of eyelids is thin and supple, not constructed as a shield from long needle-sharp thorns. A significant puncture into the inner orbit means blindness. Even if just one eye is injured, monocular vision for a carnivore is a great handicap, because critical actions are determined by assessment of spatial depth of combatants, prey, and its own body racing across an irregular 3-D landscape.

Imagine, if you will, hominins walking across the savannas when a carnivore races from behind cover and attacks. The hominin group raises their dry thorny branches toward the face of the attacking animal. Mammals have innate protection responses when it comes to their eyes. A lion, for example, would quickly recognize the implications of the approaching movements of a welter of thorns, both innately and from experience. Lions have grown up with thorny trees and experienced many thorn punctures, and would react to protect their delicate eyes. Though it would certainly be possible to crash through the thorns and make a kill, the likelihood of eye injury and blindness is too great. Large carnivores are intelligent creatures. There is no easy way around this thorn defence. The same equation works for a pride of lions and a band of hominins. Lions would not have to get face-to-face with the thorn branches each time they encountered hominins, for the same reason lions do not continually harass elephants or rhinos. Lions learn about futile and dangerous efforts from their mothers, who would have soon behaved with a body language that said: “leave those upright animals alone”. For hominins a thorn branch may have been a light-weight tool, but it was a heavy-duty defence.

How does the simple acacia thorn branch hold up to the eleven criteria we laid out earlier?

1. *The tool was likely made from a commonly available substance.*
   The widespread availability of thorny acacias is now, and likely has been for millions of years, almost unique to Africa. Thorny trees are not present to such an extent on any other continent, yet are omnipresent across the savannas of Africa. I will go into why that would be later.

2. *The tool would likely have been available ready to use in a ready-made, or almost ready-made form, not requiring a great deal of work and forethought for its construction.*

Shed acacia branches are common in savanna Africa, and these dead branches dry into a hard dense piece. Likewise, the thorns, while far from un-supple on the living tree, are especially dense and tough when dried. One has only to pick up such a thorn branch like a long-handled umbrella. In a curious way one is instantly well armed.

3. *The tool would have been easy to use, that is, its use did not require a complex facility or months of practice.*
   One has to do nothing to this acacia branch to make it into a defensive tool, though one might continue to upgrade, always looking for a more optimal form. Its use would have been intuitive and would require no skill, but perhaps some courage. However, confronted by a large carnivore the native response is to put something between you and the threat.

4. *The effective visual threat of the tool display would have been something that did not require previous experience; that is, predators innately and instantly recognized the tool as dangerous.*
   A bough of densely thorned acacia is something that every African large mammal understands. It does not take much cognitive depth to intuitively appreciate that the lion understands that the bristle of long thorns are nothing he would allow to be stuck into his face. A single sharp pole can be batted aside but not a whole branch.

5. *The tool could not only cause pain, but also almost always guarantee a disabling or mortal wound.*
   As I said, a long sharp thorn driven through the eyelid is tantamount to death for a wild animal that requires considerable 3-D visual acuity. Cats in particular have evolved refined stereoscopic vision by both eyes pointing forward. I argue the case for loss of one eye; of course they could lose both eyes by plunging their face into the bristle of sharp thorns. In that sense this tool could have been, at its historical outset, almost as lethal and threatening as one gets, maybe even more than a firearm, spear or bow, because the unintuitive power of their threat requires considerable experience.

6. *The presence of this tool would arrest a running charge by a large predator; from hominin demographics we can assume it had to have been a tool that could not fail.*
   Though not as physically arresting as 00-buckshot, no lion in its right mind would plunge face first into a thick array of acacia thorns. The real

power of an acacia thorn array is that it was unlikely to fail, no carnivore is so crazy as to plunge its eyes into such a structure.

7. *The best defensive tool would be light in weight and easily portable, so that it could at least be carried by a significant number of group members at all times.*
   Dried acacia limbs, despite the hardness and durability of wood and thorn, are not very heavy. Once lions understood the risk, a less massive branch would still be an effective tool.

8. *The efficacy of this tool would have been enhanced and magnified if presented to the threatening carnivore in multiples through cooperative group use.*
   Several individuals wielding these branches would create a more formidable functional defence, and an even more spectacular display of intimidation. This array could also have prevented a lion from circling in behind.

9. *Hominins could have capitalized on their unique biological adaptations, brought with them onto the savanna, in employing this tool.*
   I mentioned earlier some great ape assets: opportunistic talents, social cooperation, opposable thumb-forefinger, etc. This combination of traits were unique on the savanna, for example, the bipedal mobility from an upright posture of a big-bore tree climber (Lovejoy, 1981), and certainly flexible strong arms and precision fingers and power-grip hands (Richards, 1986), all of which would have allowed a secure and adroit wielding of an acacia branch. I don't want to look at the use of this tool too simplistically. Judging from what we know about our own hominin connections, the development of complicated defensive strategies employing this tool probably made it more effective than what we might first imagine.

10. *No carnivore was able to make specialized use of such a tool nor has any since – there was no competition for this niche among non-hominins.*
    The adaptive features in the collage of their great ape inheritance gave hominins an evolutionary edge in employing defensive tools. The adaptive commitments of fleetness created a legacy in which canids, felids, and hyenas could not easily stand up on their hind legs, grasp a sharp object with their forefeet and thrust it at competitors or prey.

11. *There would have been direct uses of this tool as a means of obtaining large mammal resources. How does this apply to acacia branches?*
    I will discuss this feature in the next section. But first is important to add a note here to this list of assessments of acacia thorn as a hominin weapon:

In addition to meeting these criteria, one very important additional angle of this tool's effectiveness is noteworthy. Large carnivores successfully avoid most thorns naturally on a daily basis, because their excellent stereoscopic vision enables them to place the thorns precisely in space. But that is true only if this threat is fixed – not an unpredictably moving haze of thorns as presented by a hominin wielding a branch. Shaking and waving such a branch toward the attacker's face would have made thorn position unpredictable and hence an exceptionally effective threat. Kortlandt (1980) performed an experiment that showed this clearly. Acacia branches placed around butchered meat and livestock had modest effectiveness in keeping well-fed lions away. However, when the acacia branch was kept moving by an electric rotating arm, the lions were very threatened.This result was curious to Kortlandt, and he observed (p. 99) that there was "*something excessive in this response to fast-moving thorn branches. Possibly these lions have had experience with wild-living porcupines.*" The functional aspect of the direct eye-threat from the thorns was missed by Kortlandt. In fact, he went on to say he was puzzled over why lions were so threatened by these moving thorns, especially because of "*the relatively small amount of injury that a thorn branch can inflict.*"

How could hominins have taken large mammals?

Unlike other carnivores, hominins had no sharp canines, were not fleet of foot, and were at an unusual disadvantage at night. How to approach a large mammal and kill it? Here we can imagine the offensive potential of a dried acacia branch. Occasionally, large herbivores are caught in circumstances where they are vulnerable. For example, managers of ostrich farms in the Oudtshoorn Valley of South Africa use an acacia branch to drive off large male ostriches from nests to gain access to eggs. Bushmen did similar things (Lee, 1979). When Bushmen hunters have killed a large animal with more meat than they can carry to camp in one load, they cover the stashed meat in thorn boughs until the next trip (Lee, 1979). Kortlandt (1980) believed acacia thorns were used by early peoples in Africa and, as I discussed above, experimented by surrounding a caged goat with acacia thorns overnight to show that the thorns would protect it from being eaten by carnivores. Of course, the outcome of this experiment would not have surprized Bushmen. Likewise, the use of thorny boughs for a corral, boma, to protect livestock was something African pastoralists are known to have done for millennia, and still do today on the thousands of bomas. Today, a thorn barrier is the strategy bush pilots use to protect the rubber tires and elevators of their planes from hyena chewing. A number of times I have helped to gather acacia boughs for a Cessna, a regular evening chore on the bush strip in the African wilderness.

I suspect an important hunting opportunity available to acacia wielders was newborn large mammals. Zebra and other species of plains bovids drop their newborns and protect these wobbly-legged young for the first few days. For a time these new calves and foals are unable to recognize their mother or even recognize conspecifics, which makes them vulnerable to predation (Fig. 5).

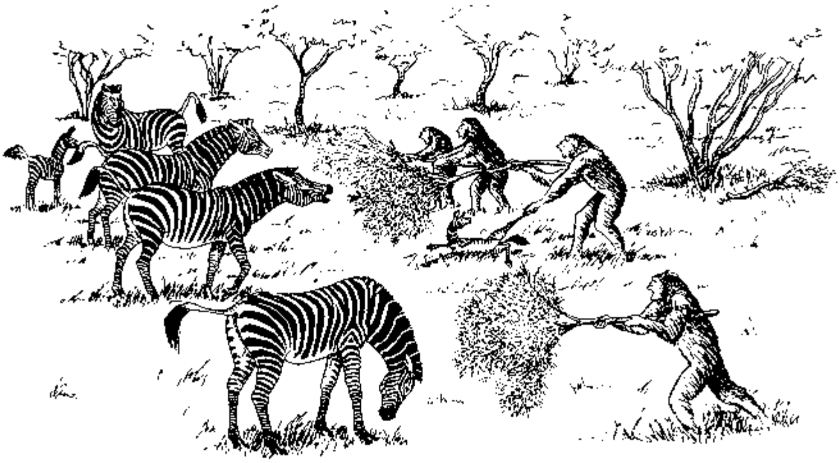

Fig. 5. The thorn bough would also have been threatening to large herbivores, allowing hominins to drive protecting parents away from newborn offspring. This would probably have worked on virtually all large herbivores except the largest pachyderms.

However, females (and protecting males) can put up a very credible defence and have every evolutionary reason to take high risks in doing so. But they are reasonable and would not take too great a risk. A wildebeest fights a hyena or jackal in defence of her young, but not a lion (Schaller, 1972). Likewise, she would not readily plunge face-first into a phalanx of bristling acacia thorns. Additionally, many species of herbivores "hide" their young and remain at a distance while feeding. They return occasionally to nurse. Mothers will race to the defence of hidden young, if a carnivore discovers the calf. Bushmen mimic the mother's calls to locate these hidden young. Because of the different adaptations of trees and grasses in the savanna year, the green season is lengthened, and as a result one species or another is having offspring year round (Schaller, 1972), quite unlike the highly canalized births in seasonal climates at higher latitudes (Fig. 6).

The skin and connective tissue of young animals would not be easy to tear apart for a modern human, but the dental row of early hominins was more formidable. Large tendon insertion scars on fossil skulls show early hominin masseter and temporal muscles were much larger than ours. The above suggestions probably

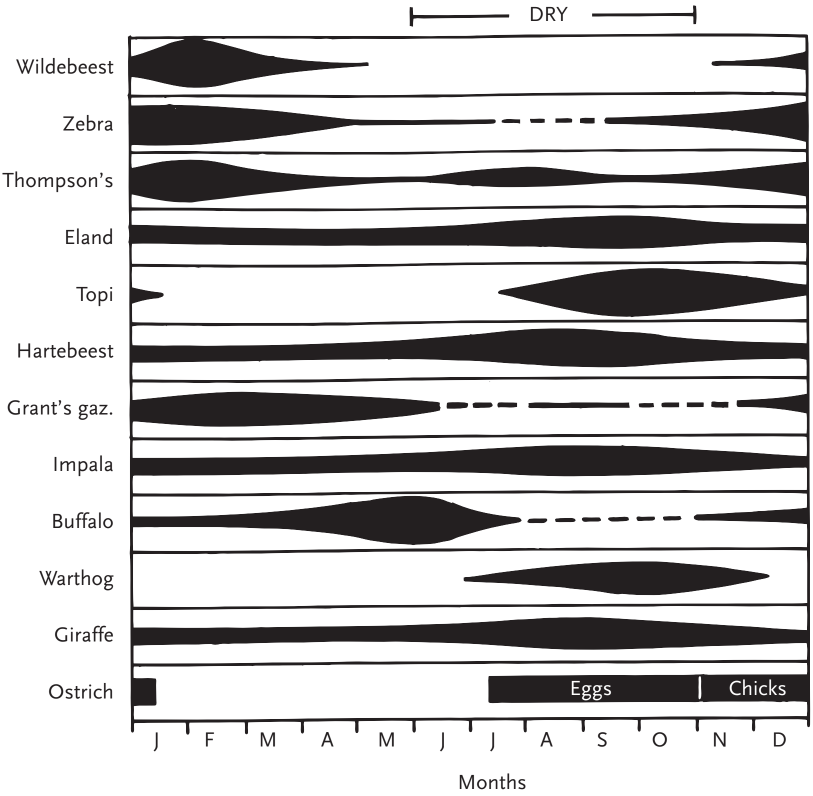

Fig. 6. African savannas have sufficient year-round range resources that allow a variety of species of large mammalian herbivores to reproduce year-round. Likewise, some species specialize in reproducing during the dry season and others during the wet season. This pattern of constant calving meant there would have been opportunities to hunt young animals over much of the year.

cover a small spectrum of the potential hunting opportunities provided by this kind of tool, and probably ranged widely from direct hunting to pirating. Circumstantial evidence would suggest that such a deadly weapon as an acacia bough would have been as effective as a direct way to gain food – as a hunting weapon. This is an aspect that Kortlandt (1980) did not envision in his paper on defence. But this is the key. I propose that it was the use of a thorn branch as a hunting weapon that allowed early hominins to compete favourably with other large mammal carnivores that were taking advantage of the increasing vast abundance of high-nutrient resources on the savanna.

The use of acacia boughs in defence blurs into using them offensively. For example, hominin groups could have used these boughs to drive some carnivores off of fresh kills (Fig. 7). Recall that it was a richer herbivore Pliocene community than

Fig. 7. In addition to providing a defence from predation, the acacia thorn bough could also have allowed Pliocene hominins to displace many (but perhaps not all) kinds of predators from fresh kills. Fresh herbivore tissue would have provided a great nutritional resource. Pirating of other carnivores' kills would have the benefit of an already-opened carcass (otherwise, a virtually impossible challenge for pre-lithic hominins). I picture them with long hair because they had to cope with cool night temperatures without a fire, likely had no roof shelters, and in the daytime were perhaps still dependent heavily on apocrine sweat glands associated with hair (like chimps) and not eccrine glands of exposed skin (like humans).

today, with twice as many large carnivore species, and perhaps more opportunity for carcass pirating, that is, more large mammals being killed. Large sabertooth cats did not have the post-carnassial dental anatomy for thorough carcass stripping, so sabertooths are thought to have essentially removed the viscera and major muscle masses. A fresh carcass of an adult animal thus obtained is even better than one killed by hominins, because the thick hide of the carcass would have already been opened by the other carnivores' powerful carnassials, no small point to pre-lithic hominins.

Two or more species of early hominins could all have used this kind of tool, simply exploiting different aspects of the complex savanna habitats and communities. The nature of those specializations is difficult to estimate. Trying to assess hominin diets using dental anatomy and surface microwear alone has some risks. Animals torn apart on the ground are not like store bought meat. It is tougher and usually has much grit attached. Large carnivores are not very adept at neat and tidy butchering. Unlike the large primates, the grit does not cause any wear stress on the teeth of felids, canids, and hyaenids. The latter three have wide throats and are adapted to swallowing large dirty chunks of meat whole. The thick enamel and "nut-cracker" tooth structure present in varying degrees among early hominins may not have been driven solely as an adaptation to rough vegetarian diets. It is probable that pre-lithic hominins would have had to use their teeth for considerable oral processing of gristle, ribs, immature long bones – using the robust teeth for thorough carcass use (the broad molars with thick enamel of sea otters, *Enhydra*, used on gritty skeletal tissues, are a possible analogue). The several species of hominins undoubtedly exploited different combinations of dietary staples and supplements in different proportions. Different uses of supplements could have significantly affected dental morphology and microstructure. A diet of 70% siliceous and fibrous vegetable material and 30% animal tissue would create considerable wear and coarse scratches, making the teeth appear those of a vegetarian, looking rather different than individuals eating 20% animal tissue and 80% soft plant tissue, yet both may well have been obtaining their main nutrients from animal tissue. *Enhydra* live almost totally on animal tissue yet have heavy teeth with quite thick enamel, very similar to those of early hominins. These wear rapidly because of the skeletal inclusions in their diets.

Studying other carnivores we can see that pirating fresh kills is not too different from hunting in function or product. Among a large carnivore guild of species, one's claim is always at risk of being challenged by another species. This is not at all the same as real scavenging, searching for left-over refuse. Protecting one's fresh kill and pirating those of others are part of hunting, always a risky affair. Large carnivores are especially belligerent about giving up their kills. A thorn branch threat likely would have been more effective against kills made by female and young lions as they have a much lower level of risk tolerance than males, and are more amenable to recognizing and avoiding risk. Smaller predators and scavengers like leopards, hyenas, vultures, and jackals would have been more easily driven off. Leopard caches might also have been occasionally targeted by hominins. Leopards are small and seldom eat a whole antelope, and stash the rest in a tree crotch. Early hominins came from a phylogenetic line of tree-climbing experts. Hominins had a great advantage among other possible leopard-kill scavengers, hyenas, jackals, hunting dogs, lions and perhaps sabertooths, and other extinct Pleistocene genera, all of which were not adept tree climbers (which is why leopards use tree stashes).

Hominin group cooperation was probably crucial in the tool's offensive effectiveness as well as its defensive uses. And sharing food thus obtained would have reinforced the group bonding. Most of Africa's large predators today are social species, but lions do fight over kills. Hyenas compete by seeing who can eat the most the fastest. In contrast, hunting dogs, like wolves, feed leisurely, not only regurgitating the food for their communal pups, but for the baby-sitter as well (Apps, 1992). The evolutionary trend in some carnivores seems to be toward more sophisticated cooperation and more equal sharing (even the small meerkats [*Suricatta suricatta*] behave more like wolves and humans in this regard, practising full cooperation and prey sharing).

If large mammal resources became the hominins' irregular staple, their opportunistic creativity probably meant that they also capitalized on seasonal and happenstance opportunities: finding honey, digging out medium-sized animals (like springhaas, *Pedetes*), termite emergence, locust flights, turtles, snakes, and pulses of edible fruits, melons, seeds, greenery, and roots. Based on several lines of evidence, Foley (2001) suggested that meat comprised up to 20% of the diet of these early hominins; note that meat makes up to 10% of the diet of some individual wild chimps (Stanford and Bunn, 2001). This high-quality protein and nutrients derived from animal tissue would have had a critical impact on health and reproduction (Milton, 1999). In combination with high-nutrient invertebrates and small vertebrates, plus some high-nutrient plant parts, savanna hominins would have been a primate species no longer limited by nutrients. Milton (1999) proposed that this increase in concentrated, easily digestible nutrients in the form of animal tissue would have extended the hominin dietary range into the high-calorie but low-nutrient plant materials that were formerly unacceptable or marginal.

A species smart enough to use acacia boughs would likely have also made opportunistic use of other simple tools. It is quite possible that stones and sticks were used to dispatch small prey. Such tools would likely have been ephemeral, as we have seen they would not have been effective defensive tools against large carnivore attacks, nor would clubs have been enough to drive carnivores from their kills or large-bodied herbivore mothers from protecting their newborns.

The difficult niche of being a large carnivore

Being a large mammal predator is a dangerous business. We can look at three aspects of predator biology to see this with more clarity. Firstly, although large carnivores are evolutionary specialists, individuals must often shift to uncharacteristic supplements. For example, in Alaska we sometimes see a wolf hunting lemmings like a fox. The unpredictability of their niche causes virtually all species of carnivores to be quite opportunistic. Few large carnivores survive solely on their own special skills of killing large mammals; at some time or other most exploit dietary fringes. This ability was likely an important factor in the evolution of hominins as well, and we will return to this point later.

Secondly, few large wild carnivores reach old age. Most starve or become mortally injured. The high reproductive capacity of large carnivores as compared to herbivores underscores the risk and unpredictability of the large carnivore niche (hunting dogs, *Lycaon*, for example have a gestation period of 2 months, lions 3 months, and African buffalo 9 months). African carnivores therefore have roughly less than one-third the gestation of the large herbivores we have been discussing (Asdell, 1966). Instead of having one young like large African herbivores, the large carnivores have litters. The life expectancy of large carnivores in the wild is much less than half that of larger herbivores (Schaller, 1972; Sinclair, 1977). On average a male lion can hold onto his harem for slightly over one year (Schaller, 1977). After that, hunting by himself, he is doomed to fail soon.

Thirdly, despite the large litters and tumbling piles of lion cubs in nature films, large carnivores are always rare (Colinvaux, 1978). They are always outnumbered by large herbivores by several orders of magnitude. No landscape can support very many large carnivores. Ecological demographics insure there is always considerable competition for carnivore jobs.

Due to the difficulty of the large carnivore niche, such species are intelligent, facultatively capable of reason and planning. Their days are made up of decisions of how-tos, when and why-nots, the best option, and the least dangerous one. Their social life is complexly intertwined within life and death dimensions, which are too complex to be resolved by instinct.

Large carnivores are themselves potential prey; they live amid a context of other species of large carnivores and active scavengers (Schaller, 1972). Lions and hyenas, for example, are often in direct competition and occasionally do kill and consume one another. Hominins would have been no exception to these dynamics.

The story behind acacia thorns

Several other tree genera in Africa are protected by thorns (e.g. *Balanites, Scutia*), but *Acacia* is the main protagonist in our story. The large herbivores moving out onto the savanna made use of abundant grasses and forbs, and the large body size of many species allowed them to reach up and consume the leafy new growth of shrubs and small trees (giraffes can reach to 5 m). Savannas are the product of seasonal rainfall combined with high aridity in a very warm climate. Graminoids compete for the new rain at shallow soil depths. The woody plants compete at lower depths. To survive this competition for water, woody plants are adapted to spread their roots well beyond the drip-line. This deep underground competition at the root level creates the above-ground polka-dot pattern of shrubs on savannas. Woody plants can use root-stores of water to grow and flower during the dry season (growth rings are difficult to find on African lumber). This off-season productivity forms considerable forage for tall browsers, but such browsing is detrimental to woody plants that have responded evolutionarily with physical defensive structures, particularly sharp thorns. Everywhere in Africa one sees this haze of thorns on tree branches (Fig. 8). Curiously, there are many acacia species, called “wattles” in Australia, but none of these have thorns, probably because of that continent’s different evolutionary history – the Plio-Pleistocene of Australia lacked an African-scale full complement of large browser species.

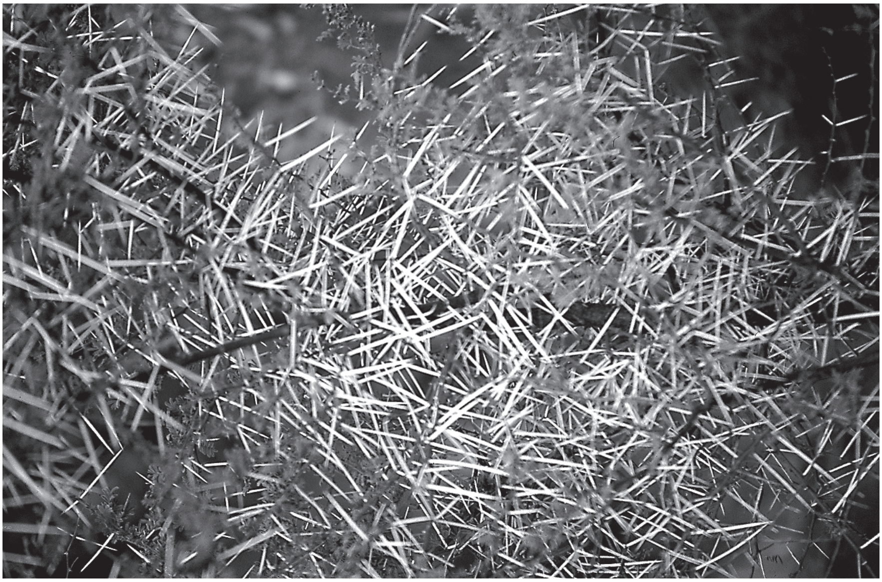

Fig. 8. A typical maze of acacia thorns on a living tree.

Acacia thorns are specifically a defence against large herbivores, and that is precisely why hominins could have used them so effectively. In addition to intense browsing by giraffes, the lower parts of the trees are browsed by impala (*Aepyceros*), gerenuk (*Litocranius*), eland (*Taurotragus*), kudu (*Tragelaphus*) and many other antelope. The characteristic 2-3 metre browse-line results in an umbrella shaped savanna tree. That is noteworthy here, because when a limb breaks from the trunk, it consists of a long bare shaft on its proximal part with a dense cluster of thorns on the distal end. It needs little modification for a tool as we describe it here.

Acacias are a legume tree, able to use symbiotic soil microbes to furnish considerable nitrogen to the roots. This gives them an edge on occasionally depleted soils. Their leaves are lacy thin because they grow in the open where there is little competition for sunlight. Small leaves interspersed with thorns can deter or slow browsers. Impala and other small savanna antelope are sharp muzzled, likely adapted to slip between the thorny branches to nibble at the filmy leaves (Smithers, 1983). Giraffes are also pincer-faced, taking the nutritious treetop new-growth leaves and twigs. These are more nutritious, and the new thorns are often still limber. Giraffes even manage to eat young thorns by adroitly aligning and crushing them with the molar row (Dagg and Foster, 1976). Acacia thorns are dangerous around eyes, and one-eyed giraffes are not rare. Of course, one does not see giraffes that have been blinded in both eyes.

Acacia species vary in their thorn engineering, often having both the *haak en steek* (short hook and long spike or prong); the hook holds while the prong punctures (Figure 9). *Acacia erioloba,* the camel thorn, is particularly dangerous. Moffat tells of a lion attacking a giraffe. The lion fell into a dense camel thorn thicket and was "impaled and doomed to a slow death" (Palmgrave, 1990). Burchell (after whom the common zebra is named) recorded being unable to extract himself and having to scream for help to be extracted from the hooks of *Acacia mellifera,* the hook thorn. The *Acacia karoo* of the sweet veld has the sharpest, longest, and woodiest thorns, up to 17 cm in length. Individual thorns of this species are sometimes used for sewing needles.

Mammalian analogues of thorn defence

Several species of mammals have grown their own thorny defences, so to speak. One lived side-by-side with early hominins, African porcupines, *Hystrix* (Fig. 10). They use their long quills for defence but can use quills aggressively if threatened. Quills are known to have caused mortal wounds to lions, leopards, and hyenas (Smithers 1983).

Fig. 9. Haak en steek. The two basic types of thorns, a tough long needle and a short stout fishhook. In this species, *Acacia tortilis*, both thorns occur together on the same branches.

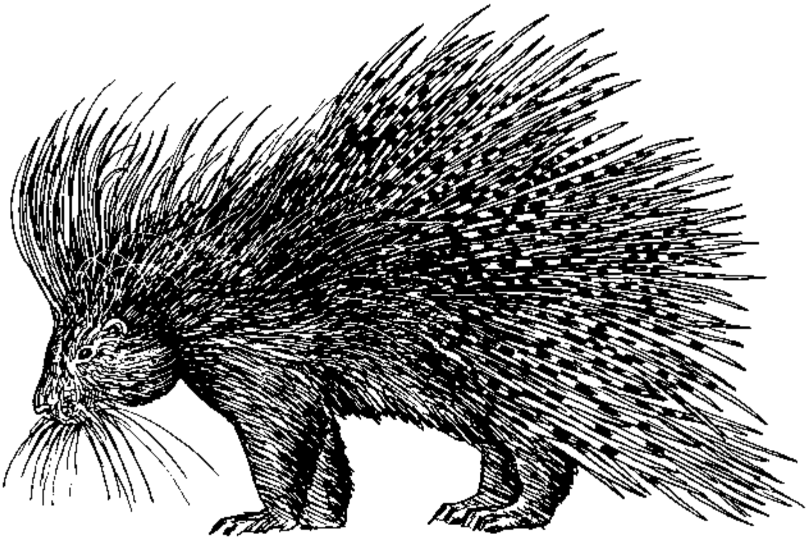

Fig. 10. Not only have plants evolved thorny protective devices, so have several phylogenetic lines of mammals. Here I picture an African porcupine, *Hystrix*. Even though these porcupines are nocturnal and are out foraging at the same time most large predators are out hunting, the large quills keep predation levels on these rodents quite low. African predators are accustomed to avoiding spiny creatures, a lesson hominins could depend on.

African porcupines are typically long lived and have small litters, a single young being the most common. Similarly, as part of a study of Alaskan foxes I have necropsied many foxes and found septic quills of American porcupines, *Erithizon,* involved in instances of debilitation and even death. Kortlandt (1980) theorized that early hominins could use acacia boughs because large carnivores had learned to avoid painful sharp objects from trying to kill porcupines. As I stated earlier, the innate response to eye threat combined with the learned exposure of lions to acacia thorns is probably sufficient for recognizing thorns as potently dangerous. Seldom do days go by in the scrub savanna without modern people experiencing punctures and scratches from these thorns, and that holds true for most active large mammals as well. In fact, the pelage of most large African mammals is adapted to minimize thorn injury (Smithers, 1983).

Where to spend the night? – behind a boma

> "*Each late afternoon when the caravan stopped there was a rush to collect thorn bushes for building the nightly berm, known as a boma, around camp to ward off carnivores*" (Dugard, 2003).

Most African carnivores hunt at night; however, the long evolutionary legacy of diurnal adaptations meant hominins were prevented from using that part of the day. Whatever they did, hominins had to do it in the daylight. So, how could early hominins ever have slept and still maintained defensive nighttime measures against lions, leopards, hyenas, and sabertooths? Throughout most of hominin history there were no campfires. Furthermore, one cost of bipedal efficiency is the loss of arboreal dexterity. The latter would have made tree sleeping inappropriate. Maybe hominins could have climbed steep cliffs or found the exact tree configuration to make tree houses, but such features are not easy to find. I cannot think of any nighttime defensive hypotheses better than a simple wall of ever-present dry thorn branches.

Thorn walls are still used in Africa (Fig. 11) as a night kraal (boma) to defend livestock from large predators. No herdsman needs to stay out with the sheep, donkeys, goats and cows to protect them, the livestock are safe inside the boma. Historically, when a man-eating lion was on the rampage, the whole village would move behind the boma, and in those rare situations when lions were so desperate as to cross the boma, it became a legend (Patterson, 1985). The native guides of African explorers, like Stanley and Livingston, followed the pattern of building protective bomas at night (above quote).

Fig. 11. Bomas are protective corrals of dry thorn branches used as nighttime protection for domestic livestock against lions and other large carnivores. The bomas in this picture are a modern relict of what was once a universal technique of Bantu pastoralists.

Spears – a megathorn

In this paper I have been working to imagine hominin life prior to the archaeological horizon of worked stones and hearths. Hundreds of thousands of generations of our early ancestors and their species' relatives roamed the scrubby savannas of Africa before the Pleistocene. Daily and nightly they were involved in the gritty dramas of a complex community of large mammals. These hominins were not us, but if transported back to those times we would probably recognize their relatedness, and appreciate their many discoveries, love life, family and social interactions, fortitude and vitality – and many of the same predator-prey dynamics. Up to now I have stressed the defensive utility of a branch of thorns, but thorns are not a good killing tool. For dispatching, say, young calves, hominins may have used their bare hands, but possibly also a club or large rock, or maybe even a sharpened stick – perhaps a predecessor to the thrusting spear. We have the archaeological data to suggest that whatever its origin, the spear ultimately became the hunting tool of choice (Movius, 1950; Oakley et al., 1977; Thieme, 1997). The prickling sharpness of a thorn branch may have been the logical antecedent to a pike or thrusting spear (Fig. 12). The latter was like a branch with a single sharp "megathorn".

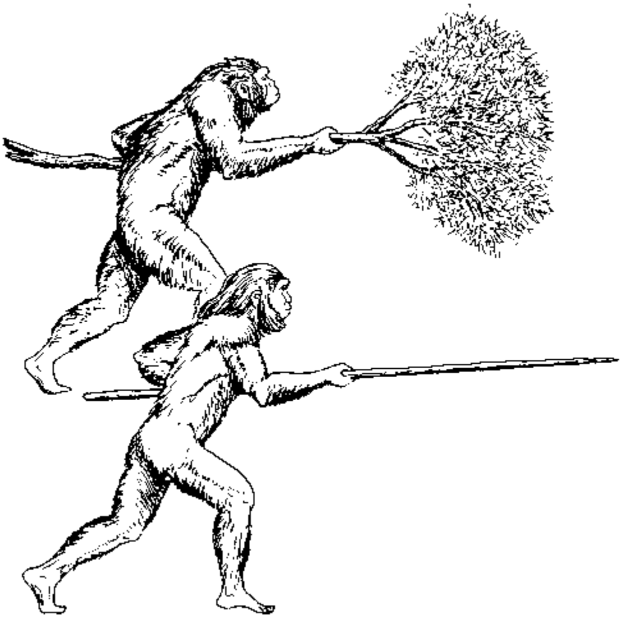

Fig. 12. Hominin use of acacia boughs as a defensive/offensive tool may help account for the transition to some sort of spear. Such a megathorn is an important step away from a thorny bough, but a rather simple one in principle.

There is a close link between a branch with thorns and a naked sharp stick. As with the acacia branch, a long sharp "thorn" or "horn" capitalized on a predator's recognition of menace. The innovation of the spear seems to be that it was a better offensive tool, one that could be driven deeply into the thorax to cause death in a matter of minutes. Sharpening was perhaps the problem that had kept the idea of a spear undeveloped for millions of years. That and of course the comprehension of how effective it would have been as a hunting tool of offence. At some point a new horizon was crossed. "Don't just drive off the attacking mother wildebeest with our thorns, we can kill her".

The breakthrough was in the discovery that a sharp broken stone edge could contour the pike, sharpen it, and keep it sharp. And that same sharp stone edge could also be used to open the tough skin of a mature large mammal, skin with which hominin teeth could not cope. This tool change was probably simple on the surface, not much different in cognitive scale than the sea otters first beginning to carry around their own stone to break open otherwise impenetrable shellfish. But the hominin's broken stone had tremendous repercussions. All the varied and complex strategies of its potential uses depended on a creative owner and a learning power that transmitted complex accumulated information to following generations. The new opportunities afforded in this technological shift of tools would have raised the bar in terms of cognitive behaviour and perhaps group size and complexity (McHenry and Coffing, 2000, also see Aiello, this volume), though it is not easy to sort out cause and effect. (One could even surmise that between two hominin species, acacia branches were a poor protection against the species that carried sharp poles – a great subject for a Jean Auel style novel?) Whatever that story line, this new revolution of a pointed pole likely accompanied the transition into something we designate as the genus *Homo*.

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Women of the Middle Latitudes. The Earliest Peopling of Europe from a Female Perspective

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The earliest human peopling of Europe so far documented occurred in the southern fringes of the continent, namely Spain, France and Italy (Roebroeks, 2001; Dennel, 2003; Langbroek, 2004). I will briefly review the evidence, with a focus on Italy as a case study. Then I will shift to examining the colonization of the middle latitudes from the viewpoint of the female, child-bearing half of human society. Female fertility and success in raising young are the demographic bottleneck of any stable or expanding mammal population. This is even truer of primates, including humans, which usually give birth to a single offspring. Accordingly, I will examine the likely impact of a non-tropical environment on women's wellbeing and physiology. I will then model a scenario of the social adaptation – if any – required to buffer the constraints of the middle latitudes and of a new habitat. I will also discuss how the archaeological and anthropological record fits into this proposed reconstruction.

The archaeological and palaeontological background

Of the middle latitudes of Europe, the Italian record is one of the most complete and best dated, with earlier sites than in many other countries. No human signature, however, has been discovered so far at any of the late Villafranchian palaeontological deposits of Italy (Palombo and Mussi, 2001, 2006). The earliest archaeological site mentioned in the scientific literature, supposedly dating close to the Jaramillo Subchron, is Monte Poggiolo, in the northeast of the peninsula (Peretto, 1992, 2001), at which abundant lithic implements were unearthed, but no faunal remains were preserved. After correlation with better dated stratigraphic sequences of the same region, an age of 1 Ma was put forward. At Ceprano, in central Italy, an archaic-looking calvarium was discovered, and an age close to the Matuyama-Brunhes boundary was hypothesized (Ascenzi et al., 1996; Manzi, 2004). The human remains of Ceprano, too, are dated by indirect stratigraphic correlation, as it is a find without any direct association. The age and meaning of this piece of evidence has been discussed at length elsewhere (Mussi, 2001; Villa, 2001). Suffice it to say here that the proposed date is far from uncontroversial.

Scanty evidence pre-dating the Brunhes normal epoch also comes from Le Vallonnet, on the Mediterranean shore of France and adjacent to the border with Italy (Echassoux, 2001). Even counting Le Vallonnet with the Italian sites, the earliest record is definitely more firmly dated in Spain: in the Iberian peninsula, at latitudes similar to the Italian ones (Fig. 1), the sites of the Orce basin give evidence of groups of humans living in southern Spain before the Jaramillo Subchron, while Atapuerca, further north, is in the range of 1 Ma, or slightly later (Carbonell et al., 1999; Oms et al., 2000; Martínez-Navarro et al., 2004).

There is a radical change in the archaeological record around 650-600 ka bp, after re-dating of the major sequences of Isernia La Pineta and Venosa Notarchirico. Both are multi-layered sites in inner fluvio-lacustrine basins of south-central Italy, with an outstanding preservation of lithics and faunal remains (Peretto, 1994; Piperno, 1999). There is little doubt that Notarchirico is of early Middle Pleistocene age, even if different dating methods have given some discrepant results (Rhodes and Grün, 1999). A date of more than 640 ka is retained by Piperno (1999) for the beginning of the local archaeological sequence. After a recent re-assessment, Isernia has a quite similar age, as a sanidine crystal from a layer capping the deposit is dated to 605 ±10 ka by Ar/Ar (Coltorti et al., 2000). New archaeological evidence also turned up at Pagliare di Sassa in central Italy: a single flint

Fig. 1. The distribution of early archaeological sites at north Mediterranean latitudes: 1. Dmanisi; 2. Visogliano; 3. Monte Poggiolo; 4. Pagliare di Sassa; 5. Venosa; 6. Isernia; 7. Ceprano; 8. Le Vallonnet; 9. Atapuerca; 10. Orce basin.

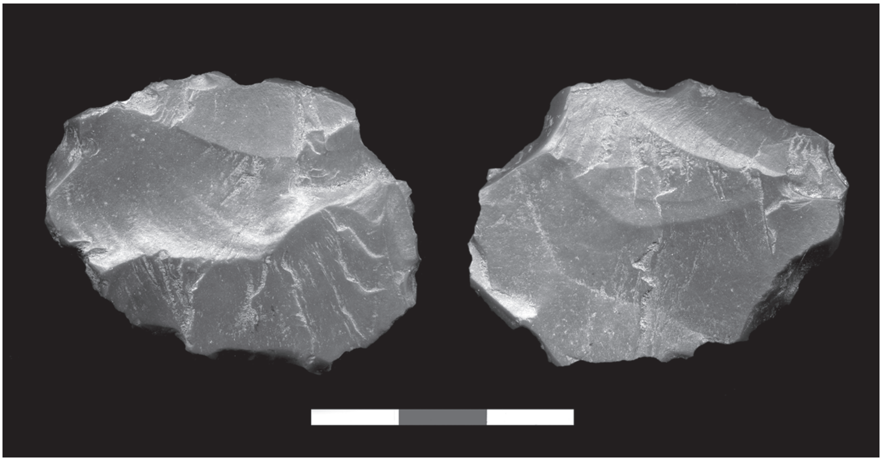

Fig. 2. Flint implement from the site of Pagliare di Sassa.

implement (Fig. 2), and an artificially modified bone fragment were discovered in association with a Galerian fauna. The inferred age is close to that of Isernia, but after a recent revision of the micromammals, a greater age cannot be ruled out (Palombo et al., 2001; Di Canzio et al., in prep.).

Fontana Ranuccio is the next chronological landmark (Biddittu et al., 1979). At this site, in the volcanic region southwest of Rome, a rich Acheulean level was found to be 458 ± 5.7 ka old after K/Ar analysis. This date is bracketed by a determination of 366 ± 4.5 ka higher up in the stratigraphic sequence, and by 487 ± 7.5 ka at a lower level. At ca. 500 to 400 ka, humans also settled the northern part of the Italian peninsula, after the evidence of Visogliano, in the Karst of Trieste (Abbazzi et al., 2000): the lithic industry is scarce, but faunal and palynological evidence suggest correlation either with MIS 13-12, or with MIS 11-10. Further archaeological evidence also exists at Middle Pleistocene sites which are less firmly dated than those mentioned above (see Mussi, 2001, for a discussion). Then, starting with MIS 9, the record is rich and complex, and will not be mentioned further below (Mussi, 1995, 2001; Villa, 2001).

Accordingly, the Italian record fits well into a model of two-phase or multiple-phase colonization of the middle latitudes, as reviewed and summarized in recent papers and books (Roebroeks, 2001; Dennell, 2003; Langbroek, 2004). There seems to be some kind of consensus about a sparse and intermittent human presence in southern Europe starting around 1 Ma, and about a much more widespread and continuous occupation of the continent after 600-500 ka bp.

Environmental constraints have been put forward as an attempt to solve the puzzling question of human groups documented much earlier “at the gates of Europe", as at Aïn Hanech in North Africa and at Dmanisi in Georgia, but not settling yet into the continent (Gamble, 1995). Italy is, again, a suitable case study. After Mussi and Palombo (2004), in this Mediterranean peninsula a scenario of delayed human peopling makes full sense when correlated with changes both in the carnivore and the herbivore guild. During the Early Pleistocene, the carnivore guild was richer and more diversified than the herbivore one, and included both formidable flesh eaters, and carcass destroyers. At the end of the Early Pleistocene, there is a renewal of the carnivores: some species disappear, such as the hyper carnivore, pack-hunter *Canis falconeri*, and the super-predator felid *Megantereon*, possibly allowing for some human colonization. Furthermore, the prevailing carnivore and herbivore taxa suggest that more open landscapes develop. This is the time of the putative earliest, sporadic archaeological remains. The scenario, however, was still rather unfavourable, and competition with mighty social carnivores, such as giant hyena, would have been hard for any human group. A faunal turnover occurs later, in the early Middle Pleistocene. Carnivores decline: *Pachycrocuta* is nearly extinct, the spotted hyena is only sporadically documented, the dogs of the group *C. arnensis* (or *C. mosbachensis*) are probably not such a threat, even for archaic humans. Then the herbivores increase, progressively including more and more middle-sized taxa – that assumedly were more suitable prey than larger ones. The biomass, furthermore, is also possibly higher. To no great surprise, when this favourable temporal window opens, large archaeological sites are well documented, starting with Isernia and Venosa.

Hunting and meat eating

The timing of the colonization is of some interest: humans enter the scene for good not only when middle-sized herbivores increase, as said, but also just when two new carnivore species appear, *Panthera leo fossilis* and *Panthera pardus*. The common driving force might well have been an increasing availability of suitable prey (Mussi and Palombo, 2004). At Isernia and Venosa, meat and marrow consumption is documented by artificial bone breakage and cut-marks (Anconetani et al., 1993; Piperno, 1999). No direct evidence of hunting, however, is available from the Middle Pleistocene sites of Italy.

Even if there is only circumstantial evidence, I assume that the earliest settlers were already capable hunters. My assumption is based on several lines of reasoning. First of all, at middle latitudes, seasonal contrast means that plant productivity is low, or even non-existent, during part of the year. After a review of 229 modern hunter-gatherer groups by Cordain et al. (2000), 58% obtain at least 66% of their energy intake from animal food, compared to 4% who get at least 66% from plant food. There is a threshold around 40° N or S: animal food markedly increases at higher latitudes where, during winter months, plant food can only be collected in small amounts, mostly as unpalatable and scarcely nutrient food. The seasonal lack of productivity is also reflected in the diet of other primates living under contrasted climates with a cold season: *Macaca fuscata*, the Japanese macaque, shifts in winter from leaves, shoots and fruit, to bark (Melnick and Pearl, 1987); while the Barbary macaques similarly survive by eating the bitter needles of cedar trees, when the snow falls on the mountains of Morocco and Algeria (reported in Whitten, 1987). In the Pleistocene, scavenging may have been an option, but primates only eat fresh meat (Telecki, 1981). Furthermore, as discussed elsewhere, at Mediterranean latitudes scavenged meat may well have been available neither in sizeable quantity nor on a regular basis (Mussi, 1999).

Aiello's (1998; this volume) well-known "Expensive-Tissue Hypothesis" further emphasizes that modern human body proportions are already found in early *Homo erectus*, and that a high-quality diet and increasingly large amounts of animal-derived food were necessary for increasing encephalization at this stage of human evolution. Leonard et al. (2003), in turn, underline that *Homo erectus* is characterized by a substantial reduction in craniofacial and mandibular robusticity, as well as in molar tooth size. They conclude that the diet included less low-quality plants and more nutrient-rich animal tissues, which is also consistent with the much higher energy requirements they hypothesize. Ungar (2004) suggests likewise that, according to dental topography, early *Homo* relied on tough and elastic food, probably meat.

A long history of meat eating is also embedded in modern gut morphology, and in the development of exclusive parasites such as *Taenia saginata*, while isotope ratios in early hominins suggest significant meat intake (Henneberg et al., 1998), in good accordance with the evidence of butchering activity at Bouri, the 2.5 Ma site in East Africa (De Heinzelin et al., 1999). Regular hunting of large game is actually part of the European scenario during the Middle Pleistocene, after the evidence discussed by Roebroeks (2001), and most notably after the extraordinary finds of Schöningen (Thieme, 1997).

The overall implications are that the earliest peopling of Europe occurred when humans were already relying on meat and marrow in everyday life, and I assume that they had to hunt frequently. As discussed above, after the Italian record this was a successful adaptation of the mid-Middle Pleistocene, when the number of great carnivore species was declining, and middle-sized herbivores were found in increasing numbers. I contend, however, that the development of reliable hunting techniques can be equated with overall increased diet quality. Unless every group member is a capable hunter, after the kill and before consumption, there is a major problem to be solved: the negotiation of whether and how food must be shared. This is crucial for the wellbeing, or even survival, of non-hunters. I will examine below the disadvantaged segment of society involved, not through bad luck, but because of anatomy and physiology.

Among modern hunter-gatherers, hunting is mostly or even exclusively a male business. At archaeological sites, techniques allowing us to sex human predators have not been developed – at least, not so far. Accordingly, I will use circumstantial evidence to evaluate who caught and killed animal prey during Middle Pleistocene times. I will also discuss the implications, if any, of a hunting way of life for the females of the earliest groups settling into Europe.

The dependent female

Among primates, relative neonatal brain size, which is a measure of the brain growth in the mother's womb, is negatively correlated with postnatal brain growth (Harvey et al., 1987: 193) – that is, either the newborn has a relatively large brain, which will not develop much further; or it has a relatively small one, that will rapidly grow during a short period after birth. Modern humans are unique in that a high neonatal brain size is coupled with a high postnatal growth index. A high rate of postnatal brain growth is also retained for longer than in any other primate. As a consequence, during the first year of life, while "the human neonate continues for some time to function more as a fetus than an infant" (Rosenberg and Trevathan, 1996: 166), and the brain is still developing rapidly, a very high investment in parental care is required. Secondary altriciality characterizes modern human growth.

There is some direct evidence related to *Homo erectus* brain growth. A reassessment of the skull of the Modjokerto child suggests a pattern closer to apes than to modern humans, and only a short period of brain maturation after birth (Coqueugniot et al., 2004). The age of this find is controversial (Langbroek, 2004, for a discussion), but an age of more than 1 Ma can be retained. Ruff and colleagues also conclude that, after the juvenile individual WT-15000, brain growth after birth was faster in *Homo erectus*, compared with the modern human condition (Walker and Ruff, 1993; Ruff, 1995). A similar signal comes from dental development (Dean et al., 2001). Nonetheless, in early *Homo* the process was slower than observed in African apes and assessed in australopithecines, thus proving that a pattern of delayed postnatal growth was already established at least 1.6 Ma ago.

Circumstantial information can also be gained from pelvis dimensions and morphology, allowing for hypotheses on brain size at birth and on the birth mechanism. So far, however, very few reasonably complete *Homo* fossil pelves pre-dating the last interglacial/glacial cycle have been found. After Ruff (1995) and Walker and Ruff (1993), the WT-15000 pelvis and skull, while being male, suggest a rotational mechanism of birth, similar to the modern one. A rather complete pelvis from Sima de los Huesos (Atapuerca, Spain) is dated to more than 200 ka (Arsuaga et al., 1999), and to a time period in the range of 400-600 ka after recent re-dating (Bischoff et al., 2003). This is another male pelvis, but the birth canal would have been perfectly adequate for the parturition of a modern baby. By implication, this was even truer of any female pelvis of the same human group. Cranial capacity in the adults of Sima de los Huesos is relatively small (c. 1200-1400 cm^3), while a foetal head as big as, or even bigger than, its modern counterpart would pass through the birth canal of a female. Arsuaga and colleagues conclude that the neonatal brain size was as large as, or larger than, in modern humans. The pelvis morphology, furthermore, suggests that parturition would have happened following the complex, modern mechanism, with the foetus rotating within the birth canal.

Overall, the palaeontological record, incomplete as it is, proves that the development of secondary altriciality was already well under way during the early to mid-Middle Pleistocene, the time of the peopling of the middle latitudes. By then, female behaviour and life cycle would have adapted accordingly.

The energy expenditure of a modern pregnancy is estimated to be 75-80,000 kcal, and 126,000 more kcal are needed during the 9 months of lactation (Picciano, 2003). Additional energy intake, including approximately 70 g of protein per day, is recommended during the second and third trimester (340 and 450 kcal/day, respectively), as well as during lactation (500 kcal/day): by then nutritional needs become even greater, as in their first 4 to 6 months babies double their birth weight accumulated in the previous 9 months. Vegetarian women can and do have babies, but dietary supplements are recommended for complete vegetarians. It should be underlined here that modern complete vegetarians eat protein-rich pulses, soy beans, nuts, etc., which were hardly available, or not available at all, during the Palaeolithic. Overall, undernourished women conceive more rarely, or not at all, have more difficulty throughout pregnancy, and deliver children who face more health problems.

Energy requirements were lower for archaic women, after Aiello and Key's (2002) modelling. The pattern, however, is the same, with increased caloric intake during gestation, and even higher caloric requirements during lactation.

The need for extra, high-quality food would have been compounded in any human group, if pregnancies did not happen randomly during the year but peaked seasonally. This is known to occur amongst the few primates living at middle latitudes, i.e. the macaques of northern Japan and the Himalayas, which experience a birth pulse of two months in the spring (Melnick and Pearl, 1987), and the macaques of North Africa (Whitten, 1987).

In humans, this would stem from seasonal amenorrhea and from menstrual syn-

chrony. The latter has long been known to occur in women living together (McClintock, 1971), as timing in ovulation happens in response to pheromone production (Stern and McClintock, 1998). Winter amenorrhea is reported among Polar Inuits of the late 19th century (Malaurie, 1976). Around 1950, most Inuit babies were still conceived in late spring, when the sun shines again and more resources are available. Before the age of electricity, admittedly, the physiology of people living at 80° N would have been much more dependent on light (or the lack of it), i.e. on photoperiod, than among more southern human groups. Female fertility, however, is also highly dependent on energy intake, and most notably on fat, and on body mass, both among hunter-gatherers and among Western, industrialized people (Frisch and McArthur, 1974; Kolata, 1974; Kurzer and Calloway, 1986).
It is reasonable to assume that, at middle latitudes, the seasonal change in insolation and food availability would have influenced female fertility. This, coupled with menstrual synchrony, could have prompted a peak in fertility from late spring to autumn (Fig. 3). If my hypothesis is correct, the period of conception would have been later among the Palaeolithic inhabitants of Europe than among recent Inuits, who rely, during winter, on the flesh and fat of marine mammals, either fresh or stored. Terrestrial animals, on the other hand, are lean in spring, and much fatter in late summer/early autumn. At middle latitudes, conception would rather have peaked during this time of the year.

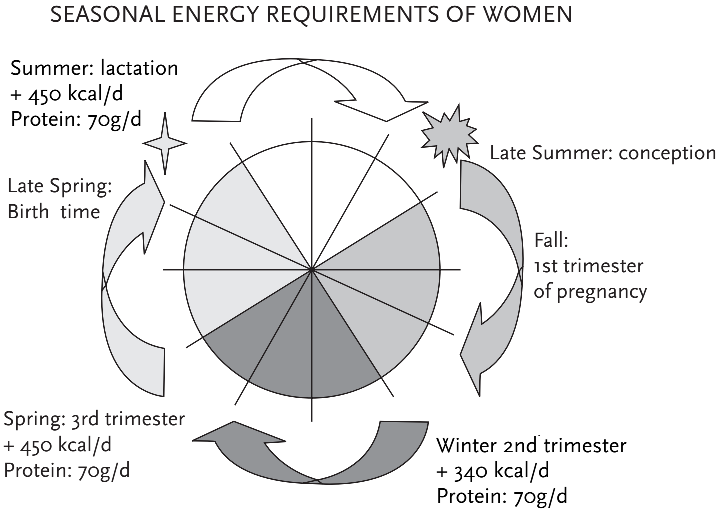

Fig. 3. Seasonal energy requirements of fertile women, assuming (1) that fertility was controlled by photoperiod and diet, and (2) that energy requirements were similar to those of modern women (see text).

This implies, in turn, that pregnancies would have been well under way during the winter months – the second and third trimesters most notably, when an extra intake is badly needed – would have coincided with the darkest, coldest and less productive months of the year. Then, parturition would have happened in spring, allowing fresh food intake for nursing mothers. Some months of milder weather would also have greatly helped in maintaining the critical body temperature in the notoriously poorly thermo-regulated neonates.

During the winter months, meat consumption would have been a required option, or nearly so, for women in their second and third trimester of pregnancy. Meat would also have been of great value for lactating women in spring and summer. However, it is difficult to imagine 3- to 9-month pregnant women, or women nursing a newborn infant, regularly and successfully hunting.[1] If this scenario is correct, the success of human reproductive strategies would have been greatly enhanced by a social organization including male hunters provisioning pregnant and nursing women.

The provisioning male

Among baboons and chimpanzees that catch sizeable prey, females occasionally prey upon mammals, but hunting is predominantly a male business (Telecki, 1981; Strum and Mitchell, 1986; Melnick and Pearl, 1987; Mitani and Watts, 2001). This makes sense considering that different feeding strategies among sexes are adaptive and reduce competition for resources. I surmise that, among archaic humans, just as among modern humans and other modern primates, most of the hunting was done by men.

Non-human primates only prey on animals smaller than themselves, however, and a ratio of 1 kg of prey to 8 kg of predator is fairly standard, from prosimians that catch insects to baboons[2] and chimpanzee that capture and kill mammals (Telecki, 1981). In other terms, the ratio is 1 kg of predator to 0.125 kg of prey. At Schöningen, where horses were hunted (Thieme, 1997), even using extremely conservative estimates the prey would have weighed 200 kg or more. Even assuming that European Middle Pleistocene *Homo* weighed as much as 90 kg, as suggested by Arsuaga et al. (1999) after the evidence of Sima de los Huesos, we are left with a ratio of approximately 1 kg of predator to *more than* 2 kg of prey. The result is similar at Isernia, if the adult *Bison schoetensacki* were not just scavenged, but also hunted. That is, the prey/predator weight ratio is at least 16 times higher with archaic Europeans than with modern non-human primates.[3]

Human hunters cannot restrain unimpeded animals larger than themselves, or inflict a lethal blow with bare hands or teeth. To spot, track and kill fairly large-sized prey on a regular basis, a well-organized party must work with well-designed tools. When the animal is dead, more tools are needed to cut the hide and reach the flesh. Then, the next problem to be solved is what to do with the huge amount of meat. Even figuring a large party, the human gut is of restricted capacity and cannot accommodate much meat at once. In the Middle Pleistocene of Italy, or of other parts of Europe, ravens would quickly congregate around carcasses, signalling them to the many competing carnivores. A sustained and co-operative effort makes little sense if it ends in provisioning lions, hyenas, and the like.

Sharing the meat with more people is an option. Among non-human primates, meat is to some extent consumed by non-hunting individuals, including females, who pirate, beg, recover dropped fragments, and even sometimes get a voluntary share. The prey animals are relatively small, however, and can be quickly dismembered and ingested by those that happen to be on the spot. It is of some use to focus on large herbivores, ambush and/or stalk them, and eventually make the kill, only if a relatively large troop is expected to quickly congregate, participate in the meal and even defend the carcass, before more large carnivores arrive.

If I am correct in assuming that the hunters *à la Schöningen* were men who foresaw the provisioning of an extended group, then my scenario of dependent women can be implemented. Pregnant and nursing women of the European Middle Palaeolithic could have expected some high-quality diet intake even during winter months, and the road would be paved for a slow but real demographic expansion.

Discussion

Women of reproductive age could also have sought help from other females. It is well known that females share collectively part of the reproductive burden, not just among bees and other social hymenoptera, but also among mammals: wolf "nursemaids" or "dry nurses", for instance, have been observed in the wild (Mech, 1981: 146). The most extreme example is probably to be found among *Suricata suricatta*, a cooperative mongoose of southern Africa, as the non-breeding females commonly lactate and nurse the pups (Clutton-Brock et al., 1999). Helpers, however, exist at the cost of inhibited or suppressed fertility: not only in bees and ants, but also in mammals, which experience interference in mating attempts and/or infanticide, as reproduction is monopolized by a dominant pair of breeders (O'Riain et al., 2000).

Female helpers, and in particular helping grandmothers, have been hypothesized in the well-known "grandmothering" model elaborated by Hawkes et al. (1997, 1998). There is mounting evidence, however, that grandmothers could only provide limited, anecdotic support to their daughters. To start with, if well-developed hunting capacities were required to survive and expand at middle latitudes, the older members of the group were probably not the fittest to catch prey – mostly inexperienced old women, who had spent their youth raising their own children; then there is positive evidence that, before *Homo neanderthalensis* and *Homo sapiens*, only a few individuals survived to an old age, evaluated at twice the age of puberty or more (Caspari and Lee, 2004). Aiello's model and analysis of mortality profiles are also fitting, as they underline that only a limited number of daughters would have a living mother able to assist them at the time of their reproductive career (Aiello, this volume). Furthermore, as predicted by my survey of animal behaviour, this was at the cost of suppressing the fertility of helpers, in this case the grandmothers' fertility. To overcome this shortcoming, the alternative was to tap the male reservoir which, amongst primates, and most notably amongst apes, is largely irrelevant for reproductive success once the mating process is over.

Concluding remarks

Among great apes, mammal hunting never occurs among gorillas – which have a one-male social organization – nor among the solitary orang-utan. It is developed only among baboons and chimpanzees, both of which are characterized by multi-male groups. Males that live in multi-male groups are even known to threaten and sometimes attack predators to defend the group (Cheney and Wrangham, 1987).

After a thorough analysis of chimpanzee behaviour, Mitani and Watts (2001) conclude that there is no statistical evidence for hunting arising in response to a seasonal shortage of food, or for being primarily motivated to obtain meat and swap it for mating. Hunting rather reinforces social bonding among males, who reciprocally share meat for social purposes.

Following a different line of reasoning, O'Connell et al. (2002) argue that at the Plio-Pleistocene archaeological sites of Africa, large carcass remains were the result of scavenging (not hunting) by *Homo ergaster*, in the context of competitive male display.

Both models refer to tropical Africa and are not directly relevant to Middle Pleistocene Europe. However, they are of interest because they suggest that meat consumption and/or hunting may have started for social more than for nutritional reasons among the male segment of primate populations living in the tropics.

After my own line of reasoning, the development of hunting techniques is the prerequisite for the colonization of middle latitudes, and would have happened before any successful attempt of peopling Europe. Provisioning male hunters would have been selected for, because it is adaptive for women, during pregnancy and lactation, to get access to meat, a high-quality food.[4] This allows women to externalize part of the cost of the reproductive system, characterized by large neonatal brain size and high postnatal brain growth.

My review of the archaeological record is in full agreement with Aiello and Key (2002: 561) who suggest that "a change in reproductive strategy and social organization was essential if *Homo erectus* females were to meet the increased energetic costs of maintaining larger body mass and caring for their large-brained, large-bodied infants". At middle latitudes, the need for increased male cooperation, and a higher level of paternal care, would have been definitely compounded by the scarcity of gathered food during the winter months, at a time of a possibly increased energy requirement for many adult women. Aiello and Key also model a reproductive strategy for *Homo erectus* females allowing them to bear and grow many more offspring than australopithecine females. This fits into the evidence of a human population expanding outside Africa and peopling the middle latitudes. The archaeological and palaeontological record, however, is not consistent with their timing of this major change as early as 1.8 Ma: a major Out of Africa dispersal, as opposed to "occasional visits", first occurred substantially later, and the successful colonization of middle latitudes is of Middle Pleistocene age (Dennell, 2003; Langbroek, 2004).

There is concurrent evidence pointing to a long evolutionary stasis after 1.8 Ma, and to a major threshold at 600-500 ka, the time of a marked increase in encephalization, after estimations of body mass and brain size based on total cranial volume (Dunbar, 1993), femoral head dimension (Ruff et al., 1997), and posterior tooth surface area (Leonard et al., 2003). Larger group size and the development of socially focused language have also been hypothesized at this critical time (Aiello and Dunbar, 1993).

There is little doubt that most of the anthropological evidence of the Middle Pleistocene age is the outcome of research focusing on the European continent, a sampling bias which inevitably affects different lines of research. Circular reasoning is a risk. For archaeologists, however, it is of interest that the mid-Middle Pleistocene breakthrough, and human peopling of Europe above 40° N, is paralleled in other fields of research. At middle latitudes, meat, a high-quality food, was the key to overcoming seasonal shortages in plant productivity. To allow a successful peopling, it had to be available on a regular basis, and provisioned by capable hunters to the extended human group, including pregnant and nursing women. Accordingly, much more was required than increased physical strength, larger problem-solving brains, and technical improvements: a thorough social change and lasting cooperation between the sexes had to develop before archaic humans were fit to successfully disperse into temperate Eurasia.

Sharing among the sexes of part of the burden of a costly reproductive system was also a further step in the externalisation of the anatomical and physiological constraints which characterize human evolution, and which includes the use of tools to cut hides and gain access to otherwise unavailable meat; and cooking to reduce the energy expenditure of the digestive system, and allow brain expansion. Most importantly, male-female cooperation would have been a way to solve an evolutionary stalemate, at a social level.

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Notes

1. After Nicolson (1987: 331) "the vast majority of the primates carry their infants on their bodies throughout the day. With a few exceptions, this task falls to mothers". The effort of carrying babies should not be underestimated. Amongst tamarins and marmosets, individuals carrying babies rarely forage or even eat (Wilson Goldizen, 1987). Transporting human babies is particularly difficult. The reflex to grasp or grip (palmar grasp as well as plantar grasp) is one of the so-called "primitive reflexes" which develop during uterine life, and are gradually inhibited by higher centres in the brain during the first months of post-natal life. The past evolution of this and other reflexes cannot be estimated, but even a well-developed grasping capacity is of little use if the mother has no fur coat. On top of a need for close attendance and careful handling, babies must be fed frequently because human milk has a relatively low fat and protein content (Hinde, 1987; see also Robson, 2004).
2. Baboons (*Papio anubis*), for instance, "can only eat prey which is small enough to restrain since they do not deliver a death blow. Lacking the teeth and jaws of a true carnivore, they have great difficulty getting at the meat and bone through the thick hide of larger or older prey" (Strum and Mitchel, 1986: 92).
3. A less conservative estimate of 400 kg for the horses of Schöningen, and 75 kg for archaic *Homo*, both probably acceptable, would end with a much higher ratio.
4. After statistical treatment of the evidence provided by modern hunter-gatherers, Marlowe (2001) also concludes that: (1) males contribute more to female diet at higher latitudes; (2) greater male provisioning allows increased fertility.

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The Diet of Early Hominins: Some Things We Need to Know before "Reading" the Menu from the Archaeological Record

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Introduction

What should we know when we research phenomena from the past for clues to identifying and/or mounting robust arguments regarding the type of diet of early hominins? A scientist should demand that we begin by discussing the "initial conditions" that may be assumed to be both germane and common to the phenomena (i.e. hominins) before and after the appearance of stone tools, with their impact on diet.

On the topic of diet, one important question we must consider is, how have the diets of our biological ancestors and predecessors changed and/or diversified during the course of human evolution? For instance, today, humans eat a wide array of species and parts thereof, and this huge inventory is geographically partitioned, ethnically differentiated, and found to be variable even at the individual level of comparison. I think that we not only want to address the issue of the "normative" diet through time, but what generally conditioned the patterned geographical and/or seasonal differentiation in dietary habits, as this may be manifested in archaeological site assemblage variability.

Part I. The issue of initial conditions

Before addressing these fascinating issues, we must look into the past to investigate the initial conditions at the time stone tools became common adjuncts in food procurement behaviour. I will assume that the hominins at that time were biologically omnivores, that is that they were capable of ingesting and digesting both animal and plant parts. Put another way, I will assume (1) that they were feeding omnivores (2) subsisting upon a diverse array of natural foods obtained directly from both the plant and animal kingdoms. It should be pointed out that omnivores are relatively rare in nature and that a similar condition was likely to have been so in the African ancient past. A recent comparative study of modern tropical rainforest African and neotropical faunas (Fa and Purvis, 1997: 100-101) confirms that feeding specialists outnumber omnivores by a ratio of 2 to 1 among tropical rainforest species, excluding primates. On the other hand, among primates, omnivores outnumber feeding specialists at a ratio of five to one. Omnivores are thus exceptionally common among primates, a point made some time ago (Harding, 1981) for very different reasons. Of the larger body sized non-human primates, baboons are the most omnivorous, with the chimpanzee and gorilla practising a reduced omnivorous feeding pattern.

One can say that feeding on both plants and animals is a strong part of our phylogenetic heritage, making it not unlikely that the earliest hominins in our lineage were omnivores at some unknown but probably variable plant to animal ratio, depending upon the environmental setting. Technically, they were hunter-gatherers. If this is accurate, then at least part of what we want to know is, what conditioned a patterned diversification of diets across space and through time among hominins? The latter features could stand as the initial patterned dietary conditions, out of which our species of hunter-gatherers (*Homo sapiens sapiens*) appeared in the ancient past. Given the historical trends in body size and brain development, I think that most would agree that there should be a parallel, a trend towards the consumption of higher-quality foods, which would primarily be fruits, insect by-products such as honey, and animal products such as marrow, blood and meat.

Part II. Comparing "us" to "them", a framework for learning

It's a challenge to fill in the information gap between the vague assumptions of the initial conditions and the actual patterns of dietary diversification and changes that are characteristic of modern humans. Just as it would be nice to know the actual details of hominin diet that we begin with as initial conditions, we must also seek to understand the factors conditioning dietary variability among modern human hunter-gatherers. Such knowledge is important for reasoning about the factors that may have inured dietary diversity in the past. This insight is critical to any evaluation of the differences between "us" and "them".

Let's begin with two kinds of data: information regarding dietary differences related to the environment, and information regarding diverse tactical strategies facilitating these feeding habits among ethnographically documented hunter-gatherers. With such information, we may then seek to recognize deviations from the documented patterns as indicative of differences between behaviours in the past and those of known modern hunter-gatherers. In addition, such a strategy may yield clues to the ecological relationships differentially conditioning our diet, as hunter-gatherers, and at least introduce the issue of whether similar factors were operating upon ancient hominin populations.

The second important domain of needed information focuses our concerns upon the species available versus the species (and/or biomes) actually exploited on a regular basis by ancient populations. This focus moves our inquiry into the domain of strategies and tactics employed by the ancients for obtaining food, which also implicates the feeding pattern, the organization of labour when feeding, as well as processing products for transport. Finally, we want to know about variability in the techniques employed when preparing food for consumption.

As an initial probe into the above issues, I will explore the broad dietary differences documented among near modern hunter-gatherer peoples. I will focus on recognizing any accompanying consequences for time trends as well as organized geographical variability that may be helpful when considering the past.

The property space in Figures 1 and 2 is defined by effective temperature (ET) displayed on the y-axis and the log 10 value of net above ground productivity (LNAGP) shown on the x-axis. Effective temperature is an estimate of the warmth at the beginning and the end of the growing season in degrees centigrade (Bin-

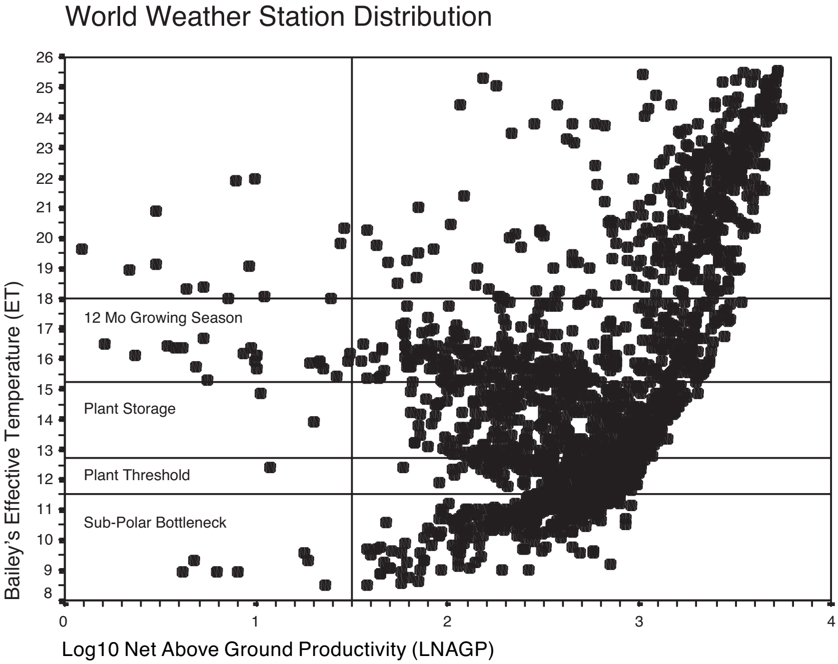

Fig 1. Global distribution of effective temperature measures relative to net above ground productivity (NAGP) values (see text for explanation).

ford, 2001a: 58-59). It is a more informative measure of geographical variability in warmth from solar radiation than many other familiar measures, such as latitude, which is not variable with altitude as regards temperature. ET was developed by Bailey (1960) as an analytical measure of warmth particularly germane to differential productivity in the plant community. An ET value of 8.0°C represents the coldest place on earth. A value of roughly 10 suggests the boundary between boreal forest and the polar regions. A value of 14 approximates the earth's mean biological temperature, while the values that exceed 18 mark the transition to regions with a 12-month growing season, i.e. the tropical and equatorial zones.

Net above ground productivity is a measure (in grams per square metre of land surface) of the amount of new cell life produced by the plant community annually (Binford, 2001a: 78-80). It is a measure of biotic production and varies primarily in response to annual differences in the amounts of solar radiation and rainfall delivered to a given location.

Figure 1 displays the global distribution of effective temperature measures relative to NAGP values. One can think of this distribution as describing the terrestrial biological variability of the earth as regards plant productivity. It is like a map of terrestrial plant productive differentials over the earth. Keeping this pattern in mind, we may now turn to Figure 2.

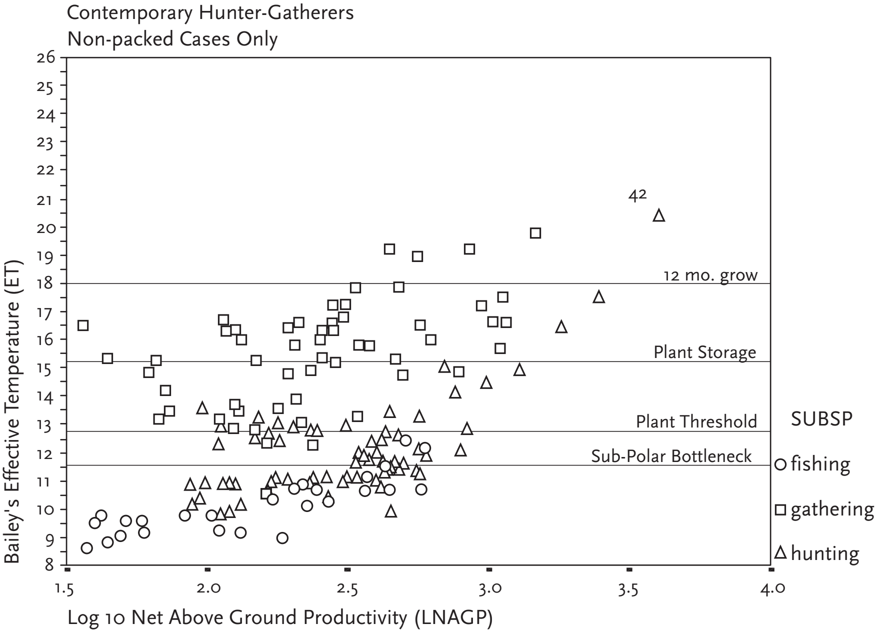

Fig. 2 Environmental distribution of near contemporary hunter-gatherers with population densities less than 9.098 persons per one hundred square kilometres.

Figure 2 shows the environmental distribution of near contemporary hunter-gatherers who have population densities less than 9.098 persons per one hundred square kilometres. The latter value was found to mark a threshold (between hunter-gatherers who strategically rely on residential mobility to insure their well-being and those who have intensified their land use through specialization and/or expanding the diversity of their subsistence base).

Perhaps the most obvious feature of this distribution is the strong concentration of cases that are dominantly dependent upon aquatic resources in environments colder than the Cool Temperate zone (i.e. concentrated in settings colder than the "plant threshold"). The latter threshold was found empirically to mark the coolest setting below which few, if any, cases are found that were primarily dependent upon terrestrial plant resources. In short, all but one non-packed hunter-gatherer case primarily dependent upon aquatic resources are found in settings colder than the ET value of 12.75°C. On the other hand, in settings warmer than the 12.75°C are found all of the documented non-packed hunter-gatherer cases primarily dependent upon terrestrial plant resources.

The exception to the above generalization, case no. 42, is the Guato, who lived in the upper Paraguay River Basin of Brazil. They were swamp-adapted people who have been very poorly documented (Simoens de Silva, 1930; Schmidt, 1942; Métraux, 1946). These people are, nevertheless, interesting particularly in light of the large number of swamp-living peoples from New Guinea, who appear to have been hunter-gatherers in the recent past (Zegwaard, 1959; Van Arsdale, 1978), and the Miskito of Nicaragua (Nietchmann, 1973). Such cases need to be included in the comparative study of near contemporary "hunting and gathering" peoples. However, for now the Guato remains the lone exception to my generalizations.

Now let's turn to the people whose food is predominantly obtained from terrestrial animals, remembering of course that we speak only of people with a very low population density, below 9.098 persons/100 square kilometres. It should be noted that most of the cases exploiting terrestrial animals are found mixed with aquatic resource-dependent people (Fig. 2), which when viewed together describe a "V"-like distribution. The base of the "V" converges at the sub-polar bottleneck with an ET value of 11.75 or roughly 55 degrees latitude both north and south. The terrestrial animal hunters exhibit a biased distribution along the inside of the "V", which corresponds to the environments with the lowest NAGP. Along the higher NAGP edge of the case distribution, which reverses at the sub-polar bottleneck, are concentrated the aquatic resource-dependent people. Only one case[1] is found in settings warmer than the threshold at an ET value of 12.75°C. The latter is coincident with the ET threshold where the shift to dependence upon terrestrial plants may occur, particularly in moderate to low NAGP settings. On either side of this threshold, across a considerable spread of NAGP setting, we see scattered cases where terrestrial animals contribute 50% or more to the total diet. These are found primarily in modern grassland settings.

It is in high NAGP environments warmer than or essentially at the plant threshold that we note a major change in the setting where terrestrial animal hunting is concentrated; such cases are found exclusively in the highest NAGP locations (greater than a log 10 value of 2.8 for NAGP). These are with one exception located in warm temperate and/or subtropical settings. The one exception is the Yuqui who are reported to be the remnants of a society of hunting specialists (Stearman, 1987), possibly mutualistically articulated with more complex horticulturalists before discovery (Stearman, 1984).[2] This case is easily visible on the chart, as it is the only terrestrial animal hunter case in settings warmer than the ET 18 (12-month growing season) threshold. It is directly to the right of the Guato (no. 42). If the Guato are misclassified and the Yuqui are the remnants of an economic specialist segment formally part of a larger society, then it is probably important to note that there are no terrestrial animal-dependent or aquatic resource-dependent hunter-gatherers with population densities at or below 9.098 persons per 100 square kilometres known from the modern world in equatorial or tropical climates. All known low population density cases from regions with a 12-month growing season are terrestrial plant-dependent, recognizing of course the two "exceptions" noted above. This, by the way, is the situation also with the New Guinea swamp dweller cases mentioned above. The latter are all predominantly dependent upon terrestrial plants. This general lack of people predominantly dependent upon food sources other than terrestrial plants is also true for the sub-tropical and temperate zones, with a few minor hunting exceptions in the transitional region indicated along the plant threshold in Figure 2 and the narrow line of hunting cases found in high productivity settings which runs almost to the 12-month growing season indicator at ET 18.

If we are looking for modern human living conditions as they vary with demography and environments that approximate the probable range of adaptive forms known from the past, prior to demographically driven intensification, the information in Figure 2 is a provocative guide.

As an additional means for making very explicit the dietary biases among low population density, near modern hunters and gatherers, I have prepared the following two illustrations. The basis for these illustrations are projections obtained by running multiple regressions between the three variables treated independently, "hunting", "gathering" and "fishing" (Binford, 2001a Table 5.01, 118-129), with the full suite of environmental variables I reported (Binford, 2001a: Tables 4.01, pp. 60-67, and Table 4.07, pp. 86-93) for only cases with population densities below 9.098 persons per 100 square kilometres.

The equations obtained were quite impressive. The projected value of hunting dependence, derived from one equation based upon seven environmental variables, anticipates the percentage dependence upon terrestrial animals. When these projected values are compared to the actual values for the cases to which the equation was fitted, a correlation coefficient R = 0.917 was obtained, with R2 = 0.840. The highest correlation coefficients between observed and expected values were obtained for the projected percentage dependence upon terrestrial plants R = 0.954, the R2 value was 0.911. The latter equation was based on six environmental variables. Finally, the percentage dependence upon aquatic resources was anticipated by a multiple regression equation based on six environmental variables that yielded a fit between observed and expected values as evaluated by an R value of 0.887 and an R2 value of 0.787.

These equations were then used to obtain projected values of the three basic sources of foods for the sample of world weather station locations, where values for the equations discussed above could be solved using weather data. The results are, of course, projected percentage dietary estimates at the location of each weather station. These percentage estimates were then mapped with isoplith lines connecting equal values for percentage contributions to the diet by terrestrial animals, terrestrial plants, and aquatic resources, respectively. A global summary of such values is presented in Figure 3. Figure 4 follows with a more detailed view of projected food source values for Western Europe. It should be kept in mind that these maps are based upon equations for low population density hunter-gatherer people only, not the complete set of known hunter-gatherers as was the case for analogous maps previously published (Binford, 2001a: Figs 6.04, p.190, 6.07, p.193 and 6.09B, p.194). These low-density, near modern peoples were fully capable of exploiting aquatic resources effectively. This is something that needs further investigation since the issue of dietary alternatives that includes aquatic resources may not have been a part of the ancient hominin behavioural repertoire. This point should be kept in mind when viewing Figures 3 and 4, where modern human behaviour is projected geographically.

Figure 3 graphically illustrates the projected behaviour for low population density, near modern hunter-gatherers onto the contemporary (interglacial) climatic conditions of the earth. On the global scale it is clear that Eurasia exhibits huge areas where terrestrial animals are projected to provide 50% or more of the diet. This is also true of North America as well as much of South America. In dramatic contrast are the continent of Africa, as well as the islands of southeast Asia, and most of Australia where the values below 40 dominate the isoplith maps for percentage dependence upon terrestrial animals. These indicate greater dependence upon terrestrial plants together with aquatic resources. Western European hunter-gatherers are projected at the global scale of comparison for essentially interglacial settings as obtaining not much more than 50% of their diet from terrestrial animals.

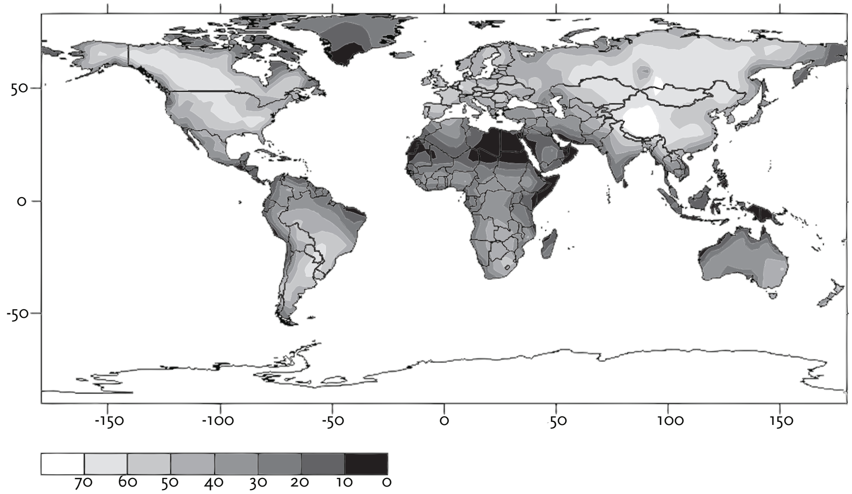

Fig. 3 Projected behaviour (percentage dependence upon terrestrial mammals) for low population density, near-modern hunter-gatherers onto the contemporary climatic conditions of the earth. See text for explanation.

The latter suggests a more diverse subsistence base, which appears to indicate, other things being equal, a more secure subsistence base for hunter-gatherers than that enjoyed by most specialized subsistence feeders.

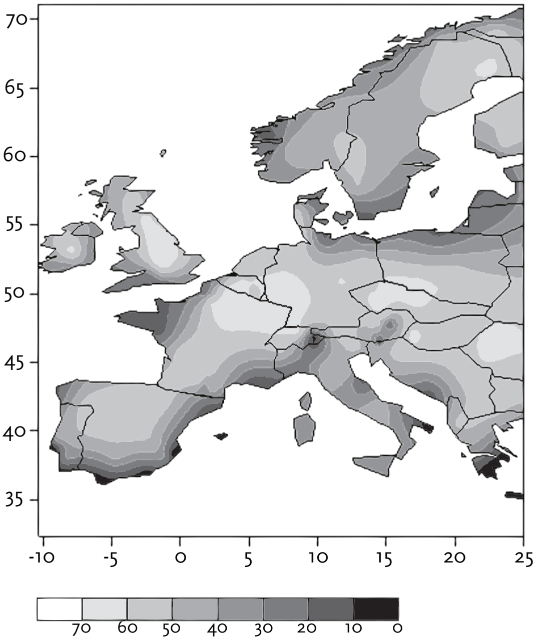

Fig. 4 Projected behaviour (percentage dependence upon terrestrial mammals) for low population density, near-modern hunter-gatherers onto the contemporary climatic conditions of Western Europe. See text for explanation.

My interest in this paper is particularly focused upon Western Europe, thus Figure 4 was prepared using a richer sample of weather stations per unit area, providing us with a more detailed view of hunter-gatherer behaviour as projected from the low population density cases of near modern hunter-gatherers.

The greater breadth in diet mentioned above is characteristic of modern hunter-gatherers, who regularly use aquatic resources. This is particularly true of the more northern regions, as shown in Figure 4. On the other hand, inflated values for hunting terrestrial animals may occur along the southern boundary of this 50% dependence zone. Modern hunter-gatherers gain time utility from "large kill" strategies coupled with storage. The boundary between aquatic resource "specialists" occurs at and above the sub-polar bottleneck as shown in Figure 2. For much of the ancient past this aquatic dependence zone would have been uninhabited (see Fig. 5).

The southern boundary of this region, with 50% terrestrial animal food dependence, becomes vague since one expects increasing use of plant resources across the land along the northern fringe of the Mediterranean Sea. Yet during glacial events, the line for 50% or greater dependence upon terrestrial animals may well dip down such that it runs east-west along the North African coast, turning slightly northward so that it crosses Israel and the southern tip of Syria. Thereafter, it runs across Iraq and along the northern border of Iran, turning south toward the coast of Pakistan. The area south of this line is where modern hunter-gatherers with a diet of 50% or greater dependence upon terrestrial plants would have lived. The northern fringe of the Mediterranean Sea would have been the "transitional" zone between terrestrial hunters and terrestrial plant-dependent people. This "transitional" region in the south should have exhibited considerable diversity and strategic chronological shifting over time as the environments changed in response to glaciations. Hominin groups behaving like modern hunter-gatherers should have been hunting terrestrial animals largely as Figure 4 suggests for interglacial stages. During glacial stages, however, the hunters may have been distributed southward into the Mediterranean drainage area, as suggested above. There would be a greater extent of uninhabited region extending south of the Baltic Sea area and around mountain areas, considerably south of the distribution shown in Figure 3.

It should be noted that a geographic ordination of hunted food use coming close to what is seen across Europe is also found in South America (uninhabited during the era of interest here) as well as South Africa, and Mozambique. The latter region has much in common with the "transitional" zone along the northern fringe of the Mediterranean.

The above material may be thought of as a baseline for orienting our expectations regarding hominin behaviour in the ancient past. I would be very surprised if the

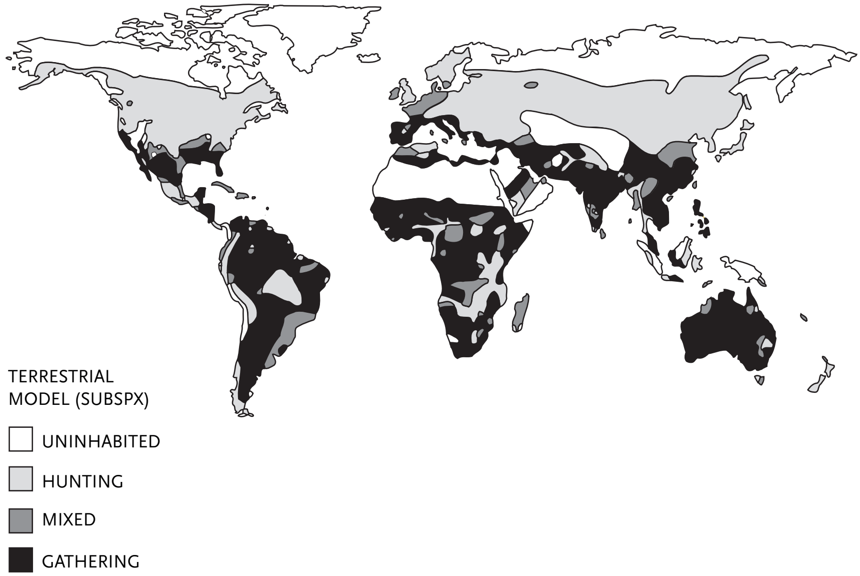

Fig. 5 Global projections from ethnographically documented hunter-gatherers for primary source of food (terrestrial model subsistence bias). Source: Binford 2001a, Fig. 6.04.

ancient populations of our relatives and ancestors could out-perform the accomplishments of the fully modern human hunter-gatherers whose behaviour is projected here.

It should be noted that the distribution of expected subsistence dependence is not homologous with the ancient Palaeolithic data from Europe. For instance, regular exploitation of aquatic resources prior to 60,000 years ago is at best poorly documented, although not unknown, at least in the Mediterranean region, and even up the west coast of the Iberian peninsula. Nevertheless, the Middle Palaeolithic indications of aquatic resource exploitation are consistent with "picking things up" along the beach and at low tide (Stiner and Kuhn, 1992: 322), while an extractive set of strategies common to *Homo sapiens sapiens* utilization of aquatic resources is not thus far evidenced for the Middle Palaeolithic.

Focusing again on the distribution patterns given in Figure 3, one should recognize a strong connection between the pattern of terrestrial plant dependence projected from low population density, near modern hunter-gatherers and the area occupied, or at least penetrated by hominins dated earlier than approximately 500,000 to 600,000 years ago. In fact, current thinking suggests that demographic probes by early hominin populations did not succeed in peopling Europe until roughly 500,000 years ago, and subsequently there appears to have been a continuous presence of hominins in Europe (e.g. Roebroeks, 2001). During the latter period indicators for diet should not escape a comparison to the area indicated in Figure 3 for a dominant dependence upon terrestrial animals. This area should correspond to the regions unoccupied by populations of *Homo* prior to the Middle Pleistocene. It should, however, correspond to much of the European evidence for obtaining food from large-bodied animals by the survivors of the successful radiation into Europe at about 500,000 to 600,000 years ago. The honours for initially penetrating the northern boreal and polar regions of Europe and Eurasia goes to *Homo sapiens sapiens* during the relatively recent, late and immediately post-Pleistocene era. This late event was anticipated nicely for interglacial episodes similar to the present by the "Terrestrial Model" (Binford, 2001a: 192-195). Figure 5 reproduces the information from Figure 6.04 in (Binford, 2001a: 190). The contrast between the terrestrial model and the projections from low population density hunter-gatherers of the near modern world (Fig. 3) is simply that the latter is a projection from data, while the former is a predictive model built on the assumption of no major technological aids to food procurement. The diet is modelled as conditioned directly by the availability and relative presence of different consumable resources in the world's biotic communities. Additional assumptions were that the consumer was a terrestrial creature, omnivorous, and would only access foods that it could reach and/or overpower physically and/or as regards animal products obtain by scavenging. Finally, it was assumed that no aquatic resources were regularly accessible except along beaches and in tidal pools, etc. The implications of the projections and modelled predictions of the dominant sources of foods, not the actual diet and its likely complexity and variability across different regions at different time periods in the past, should seriously be considered by those who tend to sensationally cite evidence for "meat-eating" to be sufficient evidence to infer a predatory hunting adaptation in the warm tropical early home ranges of our hominin ancestors. Modern, technologically aided, fully capable *Homo sapiens sapiens* did not have such diets and consumptive specializations except in the zones of very short growing seasons. These are also the settings which require many additional "necessary resources" (for clothing, housing, etc.) than are required for people living in warmer, more continuously productive settings. The area uninhabited until recently includes regions that the models and projections do a very provocative job of anticipating. The archaeological data we have at present tend to confirm the predications and projections. Secondly, the gross fit between the models and projections with the geographical patterning indicative of early radiations is encouraging. Differential changes within regions over time, when the early populations of "*Homo*" in Europe occupied the northernmost edge of the *Homo* range, are yet to be well understood. However, geography as a means to recognize a differential response to environment is not enough to begin speaking of diet. Let's expand our horizons somewhat.

Part III. Looking again to modern humans for clues regarding weapon use and procurement strategies

The issue of tactics for obtaining food is probably more closely related to diet than are the documents of discrete animal death sites or the imagined activities of early hominins advanced by many archaeologists. How do we accurately infer tactics and strategies of food procurement from the archaeological record? I will focus specifically on the issue of "hunting" and the use of weapons as well as techniques for disadvantaging animals prior to weapons use. Some years ago I accumulated a data file to aid in addressing the issue of the probability that Middle Palaeolithic "hunters" regularly killed cave bears (Binford, 2002). I have continued to add information to that database and will use it to provide a knowledge baseline for reasoning on the issue of weapons and hunting tactics. I will begin, however, in Table 1 with data accumulated by Churchill (1993) supplemented, as noted, from my data.

Table 1. Weapon type and effective ranges.

(Data taken from Churchill, 1993)

Weapon type	Range (in metres)	Standard deviation	Number of cases
Thrusting spear	Physical contact	Not available	(26)
Hand-thrown spear	5.7-7.8	2.2-0.9	14
Atlatl spear	39.6	5.5	9
Bow and arrow	25.8	2.4	25

Note: Values in parentheses come from my research and refer to the number of species. The number of cases refers only to the number for which range was a measured observation.

Churchill's data dramatically illustrate that the range effectiveness of the thrusting and hand- thrown spear is so much less than that of the atlatl and bow and arrow. We can reasonably expect that people lacking the atlatl and/or bow and arrow were forced to rely less on "at a distance" shock weapons than the majority of hunter-gatherers known from the relatively recent past. The spear, as a hunting weapon, is severely limited relative to the shock weapons used most commonly by recent hunter-gatherers. In this more modern context, the thrusting spear and the hand-thrown spear have rather specialized uses in most areas. The hand-thrown spear or "javelin" is commonly used for throws directly at specific animals who are commonly already disadvantaged or disabled. If the javelin is used by a group of hunters, most often engaged in a game "drive" or surround, a high arching simultaneous throw is made so a "rain" of spears comes down in the area where animals are congregated. This is not uncommon in Tasmania where wallabies are hunted using fire drives from one direction, and men concentrate along the side of the fleeing animals anticipated to be their escape path. The hunters surprise the animals by blocking their escape, and in the confusion may successfully kill a number of animals with javelin and thrusting spear.

Churchill (1993) noted the strong association between the use of the spear in conjunction with techniques designed to disadvantage the prey animals prior to the delivery of a, hopefully, killing blow.

> "Disadvantaging is highly dependent upon physiographic features for success, requiring natural or man-made traps such as narrow arroyos, box canyons, corrals, swamps, snow drifts, or bodies of water, or the assistance of dogs to surround and impede an animal so that the technology can be employed. The relationship of hand-delivered spears to terrain dependent hunting techniques in northern latitudes suggests that, prior to the development of long-range weapons, hunters may have been restricted to places in the environment where the technology was most effective for the hunting of medium to large size terrestrial game" (Churchill, 1993: 18-19).

In short, hunting with thrusting spear and javelin was largely restricted to where the animals were most disadvantaged. As a follow-up to Churchill's insights, I have summarized data from my larger sample of 131 ethnographic cases regarding hunts and specific kills (Table 2) and the way the animals were disadvantaged prior to the use of killing weapons.

Table 2. Context in which game may be disadvantaged relative to the hunter when using the full range of weapons listed in Table 1.

Context	Number of cases	Percentage
(1) Water	19	14.5%
(2) Snow	7	5.3%
(3) At dens	22	16.8%
(4) Use landforms	5	3.8%
(5) Trapped or poisoned	21	16.0%
(6) Exhaustion	11	8.4%
(7) Not disadvantaged	21	16.0%
(8) Missing data	25	19.1%
Total	131	99.9%

In 80% of the documented cases of hunting tabulated in Table 2, the basic strategy was to initially disadvantage or disable the game prior to the delivery of "killing" blows with weapons. All such techniques, except possibly no. 5 "trapped or poisoned", are possible components of the Middle Palaeolithic hunting bag of tricks. Of the cases tabulated as "not disadvantaged", thirteen were examples where the hunter exploited some known prey weakness or common response to being approached that put the hunter in an advantageous position for using the weapons available. For instance, in Central Australia a common kangaroo hunting technique is to hunt during mid-day when the animals are "shading" under brush and/or small trees. The hunter observes the way the animal is facing and positions himself so that he is directly in front of the shading animal. He begins to approach the animal, standing fully erect, nude so no clothing will move in the wind, with arms rigidly positioned relative to his body. He slips one leg at a time forward so there is no change in his silhouette as seen by the animal. As the animal begins to get nervous by what appears to be something approaching, but with no change in its silhouette, it will jump slightly to one side or the other to get an oblique angle view. The well-practised hunter knows this little trick and is waiting for it so that when the animal jumps, so does the hunter, but forward as well as obliquely, so that he comes down again directly aligned with the animal's line of sight but much closer to the animal. The animal detects no clear movement but remains nervous. This deadly dance continues until the hunter is close enough to quickly use the atlatl to spear the kangaroo, or the kangaroo detects movement and runs away. I used the term "spear" in conjunction with the word atlatl since the object propelled averages 12 feet in length, is made from tree roots, not fletched in any way, and importantly not tapered as is the thrusting spear, or even modern javelin as known from Olympic distance competition.[3]

When working with hunter-gatherers, researchers are always impressed with the enormous detail that the hunters have learned about the prey in their region. They know every small detail of the animals' responses to being hunted, and their reactions to the presence of both hunters and other animals, seasonal shifts in behaviour, differential feeding habits depending on the location, and social state of the prey population, etc. This detailed body of observation-based lore is the hunter-gatherer's "knowledge capital", the means to success or, if used poorly, failure. I might even suggest that the less sophisticated the technology, the greater the necessary dependence upon a complete knowledge of prey behaviour for insuring a steady food supply. With an AK47 you don't have to know so much!

It is quite likely that the first successful occupants of glacial Europe had to have accumulated considerable knowledge about the behaviour of animals and learned to use this knowledge to their advantage. It is also probable that the early populations of European arrivals at about 600,000 years ago had already developed some learning skills from hunting, even though it is quite likely that their primary sources of foods were commonly obtained from terrestrial plants, as was suggested earlier based on the behaviour of low population density, fully modern human behaviour (Figs. 1, 2, and 3).

There is another interesting domain that is rarely talked about when discussing hunting, namely the material aids that may be used by hunters to insure advantage over potential prey. Table 3 summarizes the frequencies with which some common aids are used by the modern hunters to secure an advantage over their prey.

Table 3. Hunting aids used to secure an advantage over prey.

Hunting aids	Number	Percentage
Fire for driving	10	7.5%
Use of dogs	22	16.4%
Use of snowshoes, skis, etc.	7	5.2%
Organized drives with construction	38	28.4%
Riding a horse	8	6.0%
Moving in boats	17	12.7%
Use of dog or reindeer sled	8	6.0%
Aids unreported	24	17.9%
Total	134	100.1%

Note: If more than one aid was used, the most difficult to build or organize was tabulated.

Organized drives with construction is the most common hunting aid used by modern hunter-gatherers, followed by the use of dogs in game surrounds. It is a bit sobering to realize that the use of fire with an early "*Homo*" organized surround and minor constructions on the landscape to direct game towards ambush locations are the only hunting aids on the list that Middle Palaeolithic hunters may have used, or seem likely to have used, given what is known about the other aids ethnographically.

When modern hunter-gatherers are examined for patterns of weapon use across major environmental regions, some basic relationships are revealed (Table 4).

The bow and arrow is the dominant form used in all environments except among hunter-gatherers living in deserts, where the atlatl and throwing spear are most common. The thrusting spear is very close to being used with equal frequency to the bow and arrow in both the Arctic and the boreal forest. Data reported elsewhere (Binford, 2002) show that the thrusting spear is primarily used as a defensive weapon among modern hunter-gatherers, not only in the Arctic but in all environments. Its "offensive" role is for dispatching wounded or disabled prey. The throwing spear is known among hunters of the Arctic, boreal and temperate

Table 4. Use frequencies for different weapon use across environmental zones.

Habitat type	Thrusting spear	Throwing spear	Atlatl	Bow & arrow	Poison b.&arrow	Row total
Arctic	08 (42.1%)	01 (05.3%)	01 (05.3%)	09 (47.4%)	00 (0.0%)	19 (12.75%)
Boreal	12 (44.4%)	01 (03.7%)	00 (0%)	13 (48.1%)	01 (06.3%)	27 (18.12%)
Temperate	15 (25.0%)	02 (03.3%)	00 (0%)	38 (63.3%)	05 (08.3%)	60 (40.27%)
Desert	03 (20.0%)	04 (26.6%)	04 (26.6%)	02 (12.5%)	02 (12.5%)	15 (10.06%)
Tropical	08 (28.6%)	07 (25.0%)	01 (03.6%)	10 (35.7%)	02 (07.1%)	28 (18.79%)
Column total	46 (30.9%)	15 (10.0%)	06 (04.0%)	72 (48.2%)	10 (06.7%)	149

zones, but it is rarely used in hunting. On the other hand, it is used more commonly in desert and tropical settings than in any other setting. Without question, ethnographically documented hunter-gatherers living in deserts used the most diverse array of hunting weapons.

Tropical settings are second on the weapon diversity scale. The temperate zone is the most specialized in the use of the bow and arrow, using the thrusting spear only slightly less than people of the deserts and in tropical settings. The boreal forest and the Arctic regions seem to share a common set of weapons usage patterning. The thrusting spear is almost as commonly used as the bow and arrow. Game in this region are mostly moderate to large creatures, and the size of omnivorous predators is large. The bow and arrow with its greater effective range (see Table 1) may commonly wound an animal, but the thrusting spear is regularly used to dispatch it.

This comparative exercise produced few surprises; the weapons known to have been available to the pre-*Homo sapiens sapiens* populations of Western Europe were generally less effective than those available to near modern hunter-gatherers. This situation promotes the idea that sustaining a population that is more than 50% dependent upon terrestrial animal resources in a glaciated European setting was a challenging and a relatively high-risk (of failure) situation. The one aspect of this situation that makes success feasible could rest upon the tactical means employed in predation. One possibility could be a dramatic difference in the "athletic" performance by Neandertal hunters (Trinkaus, 1983, 1986)[4]. Another might be to focus on the regularities in species-specific behaviours that might well be unknown to most of us. This latter focus would be on reliable "weaknesses" characteristic of different species in different contexts. What I have in mind is well illustrated by the distribution of caribou bones on the bottom of every lake I explored in arctic Alaska. From observing how they got there, I can testify that the bones on the bottom of the lake would vary between evidence of wolf kills and consumption to human kills and consumption. Why? One reason is that wolves can outrun caribou on ice, while caribou can generally outrun wolves in moderately deep snow. The result is that wolves will follow caribou, walking in the trails they make in the snow until they approach a river or lake. Then the wolves split up and some rush ahead to the ice on the lake or river, while others continue "driving" the animals along the caribou trails. As the caribou get closer to the ice-covered lake or river, the wolves charge the caribou and "herd" them towards the ice. If successful, the "advanced party" of wolves will almost certainly make one or more kills on the ice. They may feed for some time to "fill up" before the carcass freezes. The remains stay on and are absorbed into the ice until the melt in spring, when the bones drop to the bottom, particularly in lakes. Rivers may carry the bones to point bar accumulations, etc.

Humans also set up hunting blinds around lakes and on the ice where they may fish and also keep an eye out for wolf-driven caribou, and even have cooperating hunters driving animals toward lakes. What makes this a successful strategy is that caribou slip and slide on the ice. Anything that frightens them tends to also make them try to rapidly change direction, generally insuring that they lose control and fall down. They can be killed when they are so disadvantaged. The bottom of the lake accumulates all the remains from ice fishing, including food remains consumed there, as well as remains from butchering episodes and wolf kills. It would be my guess that any "hard-hoofed" species would have similar problems running on ice, and predators almost certainly know such things.

Many species have very regular movement patterns. Reindeer or caribou are a good example. They regularly move out of the winter range – in the forest – to more open landscape in the spring. The cows generally migrate off the winter range the earliest, initially moving slowly but increasing their speed as birth becomes more eminent. When they leave the forest, they may continue to feed, but once the herd size increases and the activity of the foetus increases, they stop feeding and move day and night toward the calving area. When the cows leave the forest, they may be accompanied by some of their calves born the previous spring, but many will leave their mothers as the rate of cow herd movement increases. The calves join male groups who are feeding and moving very slowly toward the summer range. The Nunamiut Eskimo report that they would never hunt at the calving area. When asked why, they replied with a laugh that there was always better hunting in "other places". Wolves, however, do travel to the calving areas where they prey on newly borns, as well as females and calves of the year in poor condition. It is interesting that the migration paths to and away from the calving areas may vary, but the actual location of the calving area tends to be relatively stable. It is generally located in the same place year after year if the size of the breeding population is large. The wolves take advantage of this reliably repetitive behaviour. In this case Eskimos appear to be targeting prey for optimal return when the wolves are targeting prey for reliable returns.

In other cases of exploiting "disadvantaged" animals, reliability versus optimality considerations are not necessarily primary. For instance, in the western part of North America, it is well known that horses, either wild or raised on the range, will generally run uphill if frightened. To prevent them from injury or sometimes killing themselves, range managers will frequently fence off box canyons that have loose or large boulder scree talus slopes so that horses that might enter are not frightened by coyotes or other predators, thunder storms, etc., to run up the talus slopes and break their legs. Hunters could both "encourage" or drive horses to such topography and then frighten them up slope.

Horses are not the only animals that tend to run uphill when frightened. This tendency was also characteristic of caribou and was the basis for a regular hunting strategy employed by the Nunamiut Eskimo for taking male caribou migrating north in spring. The Eskimo tactics required only a small group of hunters, frequently teenage boys, and with wind-blown snow smoothing the appearance of the slope, the deceived caribou, when surprised by the hunters, regularly ran uphill, slipped between boulders and either broke their legs or could not extract themselves from the deep snow patches among the boulders. These animals made easy prey for the hunters on snowshoes.

Good hunters take advantage of their prey's regular behaviours. In the examples given above, the only weapons needed would be a thrusting spear to dispatch the wounded or "caught" animal. While these tactics sound simple and reliable, they all depend upon the behaviour of the prey, not the ability of the hunter to take prey on his terms, such as when he needs food or when he encounters prey "unexpectedly". This means that the mobility patterns, the seasons of use for localities, as well as the size and character of groups might vary less with the specific distribution of shelter or landscape positioning tactics common among hunters equipped with reliable shock weapons.

> Proposition 1. The mobility and activity rhythms of the prey, as well as the prey options available at different seasons or locales, should condition very directly

> the land use patterns of hunters unequipped with effective shock weapons.
> Proposition 2. Poorly equipped people living in less challenging environments where there are more food options relative to any given location should be expected to exhibit greater redundancy in land use patterns. That is, greater redundancy than among peoples where there are few food options and thus less diet breadth during any given season of the year. Among the latter, expedience and the opportunity accommodations to relatively unique situations would make for greater variability in the scale of land use patterns.

One suspects that these two propositions would have been particularly germane to predominantly hunting-dependent populations or even seasonal hunters of Europe during the Middle Palaeolithic. Variable patterns are anticipated across Europe where the hunting of animals contributes differentially to the diet, as is suggested in Figures 2-5. Variability can be expected seasonally in geographic site patterning in response to the tactics of animal exploitation and, in principle, also to stone tool raw material accessibility. The latter might also be expected to co-vary with seasonality.

> Proposition 3. Assemblage content should be responsive to the above factors as well as the distribution of sheltered locations for sleeping, etc. Shelter access could vary with shifts in species dependence seasonally, at least partially. On the other hand, as potential diet breadth is likely to be reduced with more challenging climatic change, we may observe opposite trends toward greater redundancy in the use of specific places in the landscape to correlate with more extreme climatic conditions.

Let's explore briefly what I have in mind. I propose that:

> Proposition 4. Neandertal hunting strategies should, other things being equal, favour tactics that are reliable over those that are "optimal".

Proposition 4 should apply to the quality and/or the quantity of food. For instance, smaller prey may be favoured over larger prey only if the former can be obtained more reliably and in adequate numbers.

> Proposition 5. The dietary role of preferred species in "climatically stressed" environments can be expected to shift seasonally, dependent upon the relative reliability or feasibility of "known" hunting tactics accessed among the potential prey species available simultaneously by season.

Shifting of game targets would condition a pattern of land use very different from more “modern” hunting strategies where the emphasis is upon the taking, for instance, of large numbers of animals in fall, preparing them for storage and consumption over a much longer period than they are actually accessible in a given location (Binford, 1978). Thus far, storage cannot be warranted as part of the tactics used by Neandertals. It should be noted, however, that the storage-linked behaviour cited above was the likely phenomenon that has led many archaeologists to suggest that the hunting by Upper Palaeolithic humans was “specialized”. Insofar as this is correct in a dietary sense, storage is most certainly implicated. There is, however, no evidence that Middle Palaeolithic populations practised tactical storage. Thus, the citation of kill sites where only one species is involved is not evidence for “specialization” in the sense used with respect to recent and Upper Palaeolithic hunters. I should also caution that patterns of land use or “settlement patterns” vary among *Homo sapiens sapiens* hunters with group sizes as conditioned by tactics and the availability of alternative resources. We need to understand more about Neandertal “settlement patterns” if we are to understand their diet and the social aspects of the adjustments to their territories.

I have briefly introduced some ideas derived from my knowledge of modern hunters to be used as a baseline for comparison and even some expectations regarding the procurement strategies of terrestrial animals by Neandertals. We all know that the evidence we might cite to warrant an argument as to the diet of Middle Palaeolithic populations must rest with the sophistication with which we can argue for “indicative” properties in the archaeological record. How do we make provocative, or ideally compelling, arguments from the archaeological data? Let’s explore some data from a Middle Palaeolithic site.

Part IV. A Middle Palaeolithic site: Combe Grenal of south-central France: A case study dealing with the question of Middle Palaeolithic diet

I will begin by making available some of the basic data from this important site. It was excavated by François Bordes (1972, for a review). It spans, essentially continuously, all of Marine Isotope Stages (MIS) 4 and 5. The well-preserved deposits are estimated to start between sub-stages 5.4 and 5.51 with a likely beginning date of 113,000 years ago. The rockshelter is essentially filled by sub-stage 3.31 or approximately 53,000 years ago. Thus, the archaeological sequence from this site runs as a continuously accumulating deposit over the span of 60,000 years. All but one recognized level contained artefacts, animal bones and other evidence for what appears to represent regular use by Neandertals from the beginning to the end of the sequence. There are an impressive 144,189 lithic artefacts from the site, of which 18,904 are retouched tools. There are a minimum of 553 individual animals evidenced in the deposits by 12,121 identifiable bones and teeth recovered intact. In addition to the removable artefacts, there are 127 documented small hearths and 19 large ones. The only additional features were seventeen small pits and one large one documented among the levels at the site.

These statistics are certainly impressive, and we could learn much from the basic data summarized above. However, for the purposes of this paper, I shall focus upon the animal remains and any relationships we may uncover about the way in which the Neandertals exploited different species. One way is to relate how Neandertals treated species, places, and situations about which we have good descriptions of how such phenomena were treated by *Homo sapiens sapiens*.

For instance, I developed arguments elsewhere from the patterns of adaptive variability documented among near modern hunter-gatherers and formulated a generalization about diet breadth and systems security. The generalization (Binford, 2001a: 419) states that:

> Proposition 6. If generic hunter-gatherers successfully radiate into environments with very low terrestrial productivity, the majority succeed through specializations which condition a relatively narrow niche breadth.

Extremely specialized cases occur in environments in which there are few resource alternatives when viewed from the perspective of environments with abundant terrestrial plants, aquatic resources, as well as terrestrial animals. We need also to keep in mind that proposition 6 refers to modern *Homo sapiens* where specializations can be due to extreme seasonal variants (such as the Central Eskimo where seals are consumed during winter and fish with caribou during the warmer months). Neandertals living through eras of glacial development across northern Europe would be expected to behave in accordance with the principles of the above generalization. However, the specializations would be expected to be executed in a more fine-grained manner and in the context of species behavioural shifts, not the consumer populations' food management strategies, e.g. storage, characteristic of our species. For instance, Figure 6 demonstrates some interesting patterns in the degree that specialization on a relatively few species across time is documented at Combe Grenal.

High values of the diversity index signal specializations on a single or a very few animal species. Examining the pattern formed by the lowest specialization indices, there is an approximate normal curve beginning at level 45, rising to around level 26, and then more rapidly going down to about the same value, at the lumped levels of 1-3, as where we started the increase at level 45. This pattern is temporally

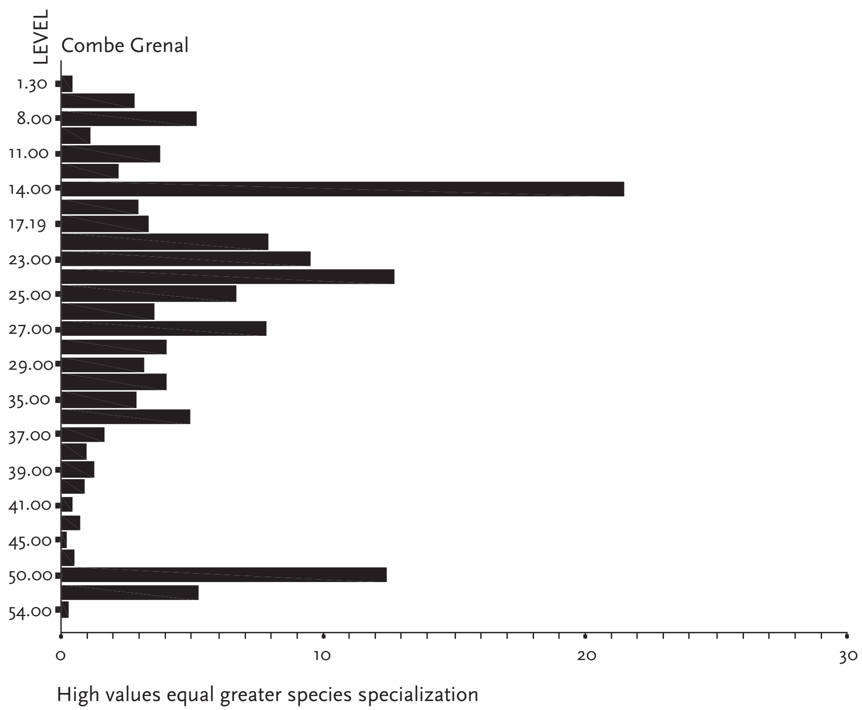

Fig. 6 Diversity index signal for Combe Grenal sequence, levels 54 to 1. See text for explanation.

distributed across oxygen isotope MIS 5.51 at the bottom of the sequence to the beginnings of MIS 5 at about level 28.

From level 28 through level 8 is the very cold MIS 4, and the cool interval between cool stage 3.31 to 3.3 is indicated by a return of reindeer dominance in Bordes levels 7-8, before the sequence at Combe Grenal was complete. An interesting area of the graph spans from early MIS 4, level 11, through the most recent three levels of MIS 5 or the coldest period in Europe prior to the onset of the most recent glacial episode between 24 and 16 thousand years ago. We note a regular pattern of increasing specialization on fewer species extensively exploited. The most extreme cold of the MIS 4 glacial episode is represented in Combe Grenal by levels 17-28. The specialization which drove the lower regular pattern, as well as most of the high spikes prior to the peak cold of MIS 4, was upon reindeer. The latter faunal dominance peaked with the coldest phase of MIS 4 (see Fig. 7). I should also point out that coincident with the peak of the MIS 4 cold, there was a massive roof-fall, which changed dramatically the usable space within the cave and accordingly could have conditioned change in the way the rockshelter was used. Leaving this

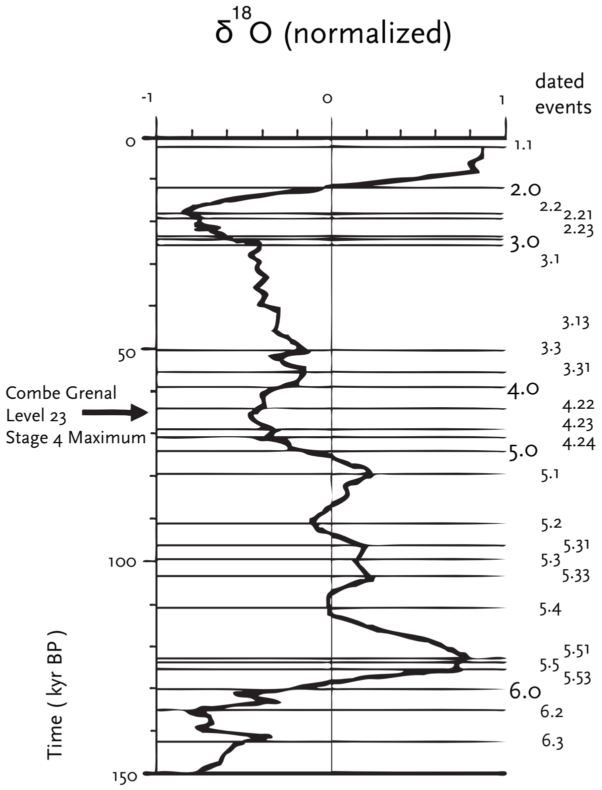

Fig. 7 Global Oxygen Isotope 18 fluctuations in the last 150,000 years, with Marine Isotope Stages and sub-stages referred to in the text.

issue aside for the moment, we need to continue our consideration of the patterns of species use at the site.

We see in Figure 8 that horse contributed around 25% to the animal component of the diet during the warmer phases prior to level 38, thereafter horse was a reduced contributor all during the ascendancy of reindeer as the dominant source of animal food. Bovids (primarily bison, Delpech, 1999: 82) tended to fill the gap between reindeer and elk or red deer as the glacial episode of MIS 4 progressed. On the other hand, after the peak cold period and with the onset of a declining role for reindeer in the diet of the Neandertals, horse played a prominent dietary role during the period of glacial retreat and associated amelioration in climate. Horse moved into a significant dietary role beginning at level 20 and shifted to a dominant dietary role in levels 16-14. Bovids (bison) then moved into a dominant role in levels 11-13. Thereafter for a brief period, in levels 4-8, bovids dramatically reduced as reindeer made a brief reappearance at around 50,000 years ago (see Figs. 5 and

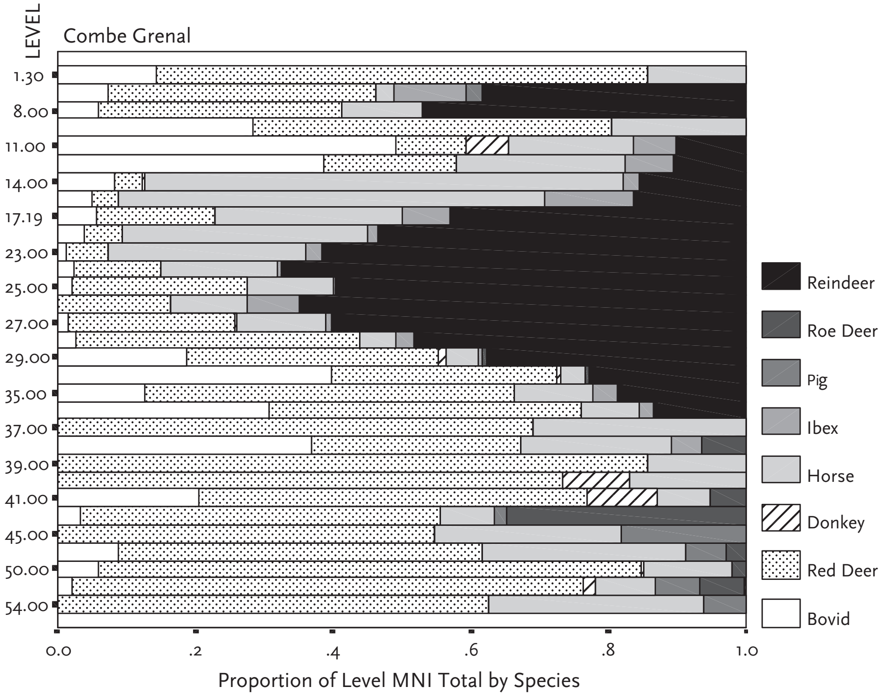

Fig. 8 Proportion of level MNI Total by Species for the Combe Grenal sequence, levels 54 to 1.

6). I should comment that all during the cold period, the "bovids" were dominantly *Bison priscus* (Delpech, 1999: 69). The important role for the bison during the most recent levels of Combe Grenal fits well with their chronologically increased importance at sites such as Mauran, the lower levels at La Ferrassie and Camiac (Delpech, 1999: 69). Bison also played a significant role in the diet of Neandertals during the warming phases after the climax of the MIS 4 cold period. Horses seem to play the role that red deer had occupied during the build-up of glacial conditions. Their prominence probably documents a greater reliability for hunting horses and bovids after the maximum cold of MIS 4 than was realized during the high-stress years leading up to the maximum cold of MIS 4. More likely, however, natural ecological dynamics were at work among competing populations of animals. Namely, populations of both bison and horse built up at the expense of red deer during the era of increasing cold. This pattern may in all likelihood be translated into a slower shift to grassland and steppe relative to the established forest biomes favoured during the pre-MIS 4 era of MIS 5. As the post-glacial maximum era started, the more ecologically established species outcompeted the re-establishment of species otherwise more successful during the warm to temperate settings of the early MIS 5. Open habitats with high biomass turnover rates tend to outcompete forest biome establishment, both with high wind settings (greater desiccation of tree seedlings) and a greater role for fire in the destruction of young tree growth.

I think that the basic gross environmental context for a closer look at Neandertal behaviour has been established, and the empirical material summarized in Figures 6-8 support general Proposition 1. The latter was derived from our knowledge of near modern hunter-gatherers, extrapolating to a population facing dramatic shifts in climate-driven environmental changes, particularly cold-stressed environments. Namely, increased specialization upon reduced numbers of species.

We have not dealt with propositions 2-4, however, nor have I treated the issue of Neandertal diet relative to Neandertal tactics for food procurement. Let's begin by exploring some aspects of the relationships between food procurement and biased prey selection. It was suggested (Proposition 4) that, other things being equal, Neandertal hunting strategies should favour tactics that are reliable over those that are "optimal". What do I mean by this, and is there any empirical support for such a suggestion?

Table 5 summarizes the relative frequencies of reindeer of different age categories represented by dental characteristics in the various excavated levels at Combe Grenal. Optimal in this case would conventionally refer to the greatest caloric return relative to the energy expended in procurement. Since we have no realistic way of evaluating the latter, a bias in favour of prime age adults, assuming whole animal carcass introduction, will be considered tactically optimal. This is a position consistent with arguments by Stiner (1994: 371-379) resulting from her comparative work with Italian materials.

Table 5. Age variability of prey: Reindeer.

Combe Grenal level	Juvenile	Prime adult	Old adult
7-8	20%	40%	40%
11-20	30%	35%	35%
21	65%	10%	25%
22	63%	27%	10%
23	20%	20%	60%
24	10%	90%	0%
25	25%	55%	20%
26	25%	59%	16%
27	26%	54%	18%
28	52%	30%	18%
29-36	35%	45%	20%

Examination of Table 5 shows that reindeer were being exploited in an increasingly optimal manner (increasing percentages of prime age adult prey) from level 36 up through level 24, which was the maximum cold of MIS 4 based on the focal procurement upon reindeer (Fig. 7). Level 23, however, documents a dramatic shift to old individuals immediately after the MIS 4 maximum cold. This could reflect a change in reindeer behaviour associated with the climatic cold conditions peaking during the formation of levels 24 and 25. Alternatively, it could reflect a change in the season of occupation with an associated tactical shift by Neandertals, or the general tactics of prey exploitation, such as hunting vs. scavenging, etc. Immediately after this dramatic shift to the exploitation of old adult reindeer (level 23), there follows another drastic shift in favour of the primary exploitation of juvenile reindeer during the occupations constituting levels 22 and 21.

Several features of this table are revealing. Level 23 in Combe Grenal was deposited as the first level after the apex of dependence upon reindeer during the maximum cold of MIS 4 dating to approximately 67,000 years ago. This is also the first level after a major roof collapse, which restructured the spatial character of the rockshelter. We see that the dominant fauna in level 23 was reindeer and approximately 60% of those animals were old individuals, well past their prime of health. Such a "hunting" bias is not an optimal meat nor fat returning strategy. On the other hand, the same level exhibits the first major increase in the numbers of horses introduced to a location since the onset of the colder climates documented at the beginning of MIS 5 – approximately 72,000 years ago (see Fig. 8).

These horses were 54% prime adults, and the remainders were dominantly juvenile (see Table 6). The pattern noted among the horses was partially analogous to the pattern characteristic of reindeer during the era of increasing cold that led up to the glacial maximum culminating at Combe Grenal with level 24. The shift in reindeer exploitation tactics seen in Table 5-level 23 contrasts dramatically with the levels above and below. Why did the Neandertals begin taking older reindeer after the glacial maximum? Why were old and prime age adults equally represent-

Table 6. Age variability of prey: Horse.

Combe Grenal level	Juvenile	Prime adult	Old adult
1-10	02%	97%	01%
13	10%	88%	02%
14	16%	80%	04%
23	38%	54%	08%
21-28	42%	48%	10%
29-47	05%	65%	30%
49-55	44%	54%	02%

ed above level 11 or until reindeer were apparently no longer present in the region? Why the dramatic shift to juvenile individuals immediately above level 23?

These contrasts marked major changes in the hunting tactics employed with regard to obtaining reindeer. They also reflect differences in diet, assuming changed ways of using animals of different sizes and ages. In turn, the latter could implicate changes in the character of occupations with attendant different food needs by occupants organized differently. I have in mind age and sex differences with attendant different group-related roles.

Let's leave aside the latter possibility for the moment. We need to consider possible changes in the exploitation of reindeer and how their behaviour could have impacted hunting tactics. If reindeer behaviour changed, that could have influenced how the Neandertals hunted them as well as other game. As I have emphasized, the change was immediate in the content between levels 24 and 23. The change of interest followed chronologically after level 24, where almost all the reindeer were prime age adults (7 of 8 animals). According to proposition 3, stress should result in a dramatic change in strategy in the direction of increased reliability rather than an attempt to achieve an increased return rate on the labour invested, which would hardly be possible given the bias toward prime adult animals documented for level 24 as well as levels 25-27. Understanding the tactical shift is further enlightened by the behaviour of the Neandertals as implicated by the contents of levels 22 and 21. Immediately after the climatic conditions that influenced the behaviour behind the facts of level 23, further instability is suggested for levels 22 and 21. There is a dramatic increase in the number of horses exploited coupled with a strategy for exploiting reindeer not previously recognized.

The tactics used on reindeer suggest that Combe Grenal is now geographically positioned close to the reindeer calving area. This appears to be the case during the entire decline of the glacial event marked by the MIS 4-3 transition, which also was accompanied by a marked decline in the exploitation of reindeer. This era is informally characterized by the heavy exploitation of juvenile calves of the year as well as adult females accompanied by the presence of foetus remains. This combination of animals could only have been exploited along the spring migration of females to their calving area or even at the calving area itself. It is quite likely that the route was up the Dordogne valley leading towards more "open" grazing areas bordering the hills and ridges of the margins of the Massif Central. Reindeer and caribou females do not feed as they get closer to the calving areas, but they frequently leave the winter range earlier than the bulls. The bulls move slowly toward the summer range feeding all the way. As the females get closer to the calving area, they stop feeding and begin to move both day and night until the calving area is reached. When they stop feeding, some of the calves of the previous year tend to leave their mothers and join with the smaller, slower moving male groups that feed over a much wider area in their migration toward the summer range. This means that males and some calves of the year are generally in much better condition, nutritionally speaking, during the spring movement to summer pasture. On the other hand, bulls are much more difficult to find in spring, requiring a considerable search time to locate their small groups as they drift toward the summer range. In marked contrast, the females are generally in very poor nutritional condition with little stored fat left after the foetus has been the privileged nutrient recipient all winter. They are, nevertheless, easy to find. As mentioned earlier, wolves, not uncommonly, hunt at the calving areas, probably for the same "reasons".

It is interesting that the Neandertals chose to exploit the female spring herds, in a poor nutritional state, and further disadvantaged by pregnancy. The recurrent presence of calves of the year in the faunal assemblage with foetus and exclusively female antlers strongly indicates that the end of winter and the beginning of spring was, as is generally true in temperate to arctic settings, one of the worse times of the year for reliable terrestrial foods including animals. The fairly predictable behaviour of the female reindeer herds, coupled with the late April to May period of probable movement by females toward the calving area, supports the earlier propositions (3 and 4) regarding favouring reliability over optimal returns under conditions of stress.

I draw the reader's attention again to Table 5, where the tell-tale presence of juvenile as well as adult cows (identified by antlers) characterizes the reindeer faunal remains until at least level 11 in spite of an ever diminishing contribution by reindeer to the overall diet (Fig. 8). Exploiting early spring female herds en route to or at the calving area lasted until reindeer were no longer taken. When reindeer briefly reappear in the upper levels of the site (levels 7-8), they are rare, and the majority are represented by adult individuals, reminiscent of the pattern seen at the onset of cold as indicated in levels 25-27. Tactically speaking, this represents still another exploitative strategy used by the Neandertals, but the environmental conditions were very changed, and the character of the site at Combe Grenal was, at the time of levels 4-8, an open site.

As the reindeer disappeared in response to warming climate changes, first horse, then bison and finally red deer increased relative to one another until the site of Combe Grenal as currently known was no longer used by Neandertals. Bison were unrelentingly represented by prime adults, while red deer and horses exhibited a pattern of exploitation more like reindeer during the cold period. The latter pattern of exploitation differed from the reindeer in the fact that prime age adults were most common in all horse-bearing levels, but they were accompanied by a regular presence of juvenile and newly born youngsters, suggestive of summer kills. The pattern seen in Table 6 shares with reindeer the greater exploitation of juvenile individuals during the coldest period. However, horses were similarly exploited during the warmest period levels, e.g. 49-55. The latter facts suggest that the vulnerability of pregnant females and females with young was a major "disadvantaged" situation, exploited by Neandertal hunting tactics whenever possible, regardless of species.

Modern hunters view pregnant and very young animals as undesirable because of the poor nutritional state of the adults, and the lack of bulk food on a yearling. At the same time, the skin of the female and the yearling reindeer at least are in very poor condition, commonly full of holes from the hatching of insects whose eggs, implanted in the ungulate the previous fall, eat their way through the skin in spring. Hunting spring females and yearlings, with a foetus "bonus" is certainly not an optimal hunting strategy. It does, however, seem to have been reliable. This further supports the general strategy advanced in Propositions 3 and 4, namely, that reliability was favoured over the optimizing of caloric returns.

Finally, it should be pointed out that after the glacial climax of MIS 4 was reached, the climate began to shift in favour of warmer environments. As conditions ameliorated, more species, including plants, were likely to have become available to the Neandertals. Their tactics certainly should have changed as suggested earlier in Proposition 5. That is, when species diversity goes up, in general, the potential subsistence security also increases. Such an expected trend is, however, difficult to evaluate from the Combe Grenal data, particularly more recent data than level 11. Levels 1-10 at Combe Grenal were deposited against the cliff face after the rockshelter was filled with depositional materials. In other words, Combe Grenal became an open-air site, not a truly roofed shelter as it had been for so many years previously. It is likely that this change would have conditioned a very different pattern of use at the Combe Grenal location even if the warming trend documented at Combe Grenal had not occurred. In short, one of the features of the site of Combe Grenal changed dramatically. Prior to the formation of level 10, the "rockshelter" characteristic of the site was reasonably considered a constant. Not so for levels 1-10. They are most profitably compared to other open sites. Certainly the Mousterian of Acheulean Tradition (MAT) identity for the contents of most of the latter levels compares favourably with other "MAT" assemblages that are also most commonly known from open sites (Mellars, 2004: 34).

I am confident that the issue of tool variability in the archaeological record at Combe Grenal will, upon further study, at least partially reflect variable food procurement tactics. Nevertheless, such suspected functional variability with tactical implications is a long way from placing us in a position to read off a "menu" of the Neandertal diet.

Looking at the archaeological record on a more detailed scale, what was a meal like? What conditions change consumption patterns?

Much discussion of the Middle Palaeolithic era has focused upon scavenging versus hunting, and bias in the types of anatomical parts actually targeted for consumption by Neandertals. I will use a single indicator of bias in the anatomical parts introduced to the site of Combe Grenal. Bias in the anatomical completeness of animals introduced to the site could implicate diversity in diet among different active segments of the Neandertal population, gender differences for instance, and/or different conditioners for the differentiated use of the Combe Grenal shelter itself. Let's see what we can learn.

The measure employed is a ratio introduced into the literature by Stiner and Kuhn (1992: 318). It is simply the minimum number of bone elements indicative of the presence of heads divided by the minimal number of elements tabulated from the basic bone units from the remainder of the body. Stiner and Kuhn report that 0.30 is the expected value of this ratio for a complete deer skeleton. My data are tabulated in terms of proximal and distal elements for long bones and even phalanges, as well as distinctions between right and left. Because of this different organization

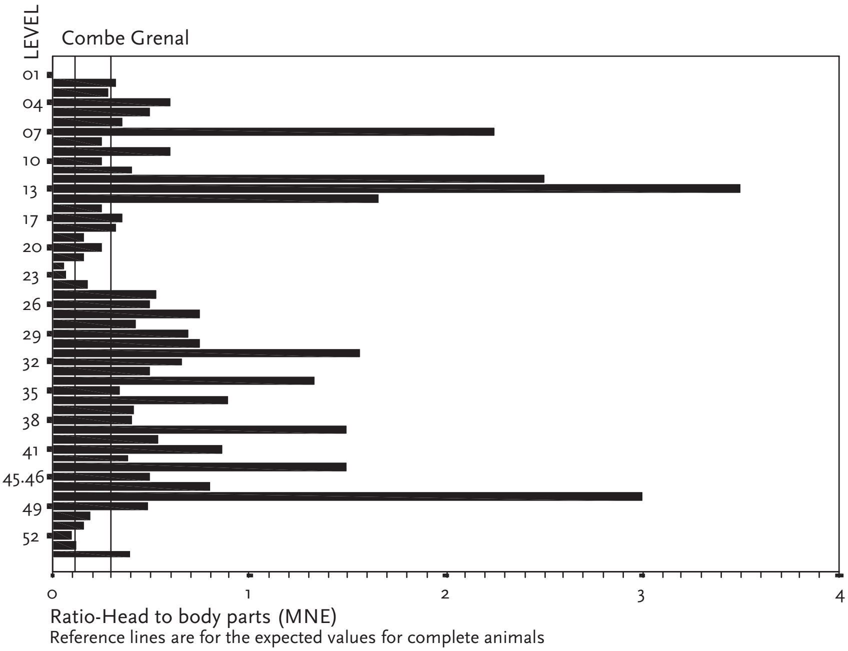

Fig. 9 Combe Grenal: plot by level documenting the ratio head-to body parts (MNE). See text for explanation.

of the data, I recalculated the ratio using my system of tabulating bone elements (originally done for different reasons) for the total ungulate skeleton distinguished as my data was differentiated. I obtained an expected ratio indicative of a complete skeleton of 0.11. The other issue is teeth, and I accepted the suggestion that head parts only be estimated from anatomical elements of bone. This removed the preservation bias in favour of teeth when bone destruction could be a confusing issue regarding variability among deposits. The data used were for both reindeer and red deer, the two species of moderate body size exploited across the full range of environmental conditions documented in the deposits at Combe Grenal.

Figure 9 is a bar graph plot by level documenting the proportion of head parts expressed as a ratio to the minimum numbers of elements of the head divided by the minimum numbers sum of all other skeletal parts. The graph has two references lines originating on the x-axis where the ratio values for head to body parts are plotted. The line to the left identifies the 0.11 ratio value indicative of complete animals being introduced. I have also included the 0.30 ratio value used as a standard by Stiner and Kuhn (1992) as mentioned above.

It is strikingly clear that there are only two episodes during the entire approximately 60,000 years of Neandertal occupational use at Combe Grenal when complete animals were being regularly introduced to the rockshelter. The earliest is during the moderate but wet period between levels 55 and 49. These moderately thick levels almost certainly represent palimpsests of multiple use episodes. In spite of the likely lack of occupational integrity within each level, there does nevertheless appear to be a regular pattern of occupational re-use during the formation of these levels. At the same time, Figure 9 indicates that red deer were introduced to the shelter as complete animals in very few other levels (none more recent than level 49), in spite of the fact that red deer were present in all levels more recent than level 49.

The earliest of the levels being considered here[5] are all levels classified by F. Bordes as "Typical Mousterian". They are also levels in which the sediments suggest extensive rainfall, particularly in summer. Levels 50 and 51 show evidence of increasing rainfall in all seasons. Thereafter, in level 52, this changes to equitably high rainfall all year around.

The other levels in which the head/body ratio clearly indicates the introduction of complete animals to the site are levels 21, 22, 23, and 24. Besides representing the maximum cold achieved in Europe prior to the last glacial maximum at around 18,000 years ago, evidence from the sediments strongly supports a moisture regimen of high winter snowfall, followed in more recent levels (19-1) by relatively dry and warming seasonal conditions.

We have seen that the level 23-24 comparison documents a major shift in hunting tactics as regards the age and maturity of animals taken at the very climax of the MIS 4 glacial event. What is common to the two tactically differentiated levels is the bias for complete animal carcasses introduced to the site regardless of the procurement tactics utilized. They were maximizing return rates when deciding what to transport to the site. It is also likely that the kills were very near the site, given the demonstrable homogeneity in transport decisions.

The places in the sequence where the introduction of complete animals is recognized correspond to (1) the highest rainfall indicated at Combe Grenal (levels 50-54) and (2) the coldest temperatures experienced during the accumulation of the deposit (levels 24-21), which also saw the greatest precipitation during the winter. I think that we may infer that shelter was the major factor favouring occupation under the climatic conditions inferred. There were severe weather conditions that would have limited mobility, yet in both situations whole carcasses were returned to Combe Grenal regardless of the species taken. Lithic industries were dramatic in their connection with these two uses of animals as well as the associated environmental contexts. Quina Mousterian was the type found during the cold period and Typical Mousterian during the moderate but very wet period.

If we look at the other suggested contexts of site use at Combe Grenal as indicated, for example, by those levels where heads of animals are associated primarily with lower leg and foot bones, or other properties of the animals that may permit us to identify the provisional month of dominant occupation, we might obtain a further clue to diet as well as other aspects of Neandertal behaviour.

Table 7 utilizes an estimate of the season of occupation developed from the tabulation of observations on both eruption and wear on teeth – properties which inform us about the animal's maturational state. Eruption data are well documented regarding the age of animals when different teeth erupt and when milk teeth are lost. Wear on the latter as well as on permanent teeth, when a large sample of teeth from a single species is available, do provide the basis for estimating the average month of death for the assemblage of individuals represented. I should comment that without exception the clustering of age indicators informs us that occupations were relatively short and, when multiple in a given level, were redundant as regards the season of occupation when examined from a single species perspective.

Table 7 is organized in terms of the percentage of teeth derived from the mandible divided by the total number of teeth from both the mandible and the maxilla. In short, the value is the percentage of the total teeth from the mandible. Low values indicate few mandibles with a corresponding dominance of maxillary teeth, and by implication, the complete head having been commonly introduced to the level. A value of 50% indicates that complete heads were present. Values lower than 50% signal a bias in favour of crania lacking mandibles. As suggested above, this is suggestive of scavenging with the brain being the component most likely to

Table 7. Mandible and cranial transport into Combe Grenal, seasons of deposition, and assemblage associations.

Animal	% of teeth = Mandible	% Season of death	Highest % of case types	Median % of case types	Low % of case types
Reindeer	86.4%	100% early spring	36.9% Quina	26.3% Typical	21.0% Denticulate
Red Deer	77.0%	66.6% winter, 38.2% early spring	46.6% Typical	20.0% Denticulate	16.0% MAT
Horse	82.0%	57.1% spring	29.0% Quina	29.0% Typical	29.0% Denticulate
Bovid	57.0%	50% spring 30% winter	46% Typical	23% Denticulate	23% Ferrassie

Note: In the case of columns 4, 5, and 6, the percentages do not add up to 100 because low frequency assemblage forms were not included in this table.

have been consumed. It is recognized that "other things being equal", differences in the percentages inform us regarding (a) possible exploitation of scavenged carcasses, (b) biased exploitation of the brain – it is high quality food and good for baby food, (c) bias introduced through transport cost considerations, and finally (d) bias arising from limited food alternatives available to the Neandertals. "Other things" that could also condition variability in the table are factors not recognized in the above list that arise from environmental variability through time either seasonally or with respect to occupations that occurred at different time periods, each being conditioned in turn by variability in the particular species available for reliable exploitation from Combe Grenal.

As an example of the phenomena suggested in "c" above, I offer some observations made among the Nunamiut Eskimo. The tongue, frequently butchered out with the mandible, is a choice meaty part, and is the part most commonly immediately processed and consumed in spring Nunamiut residential camps (Binford, 1978: 196). The skull is the anatomical part most commonly abandoned at Nunamiut kill or butchering locations in spring (Binford, 1978: 216). It may be cooked and eaten there as well as simply abandoned unprocessed at kill butchering locations. Another consideration is the weight and bulk of the head relative to the amount of consumable material. If humans-hominins are the transport agents, it seems unlikely when faced with a complete animal that the transport of the head would be a priority. We may speculate that, like the Nunamiut field parties, the head would be consumed very close to the kill or when it was one of a very few usable parts remaining of a carcass which was scavenged when food was scarce. I might add that such consumption is likely to have been by the persons obtaining access to the carcass. The transport of body parts for consumption by individuals other than those obtaining the carcass or parts thereof might be expected to be biased in favour of parts with larger quantities of meat and marrow relative to the bulk or overall weight of the part as butchered prior to transport. Similarly, differences in the body size of animals should condition the frequency of transport of complete heads, such that it would be more common with smaller animals, less common with large animals. The information summarized in Table 7 permits us to evaluate the potential relevance for some of the features found in the above suggestions, all of which derive primarily from ethnographic observations.

Perhaps the first observation of interest is that season may have more to do with the return of heads as opposed to the relatively light mandibles with tongues probably attached than does body size. If the latter was the primary conditioner of transport, we should see less mandible dominance among reindeer, certainly the smallest animal on the list, and the greatest percentage of the teeth coming from the mandibles of bovids, the largest animals represented. Clearly, the reverse situation is what is documented at Combe Grenal. The highest percentage of mandibles derive from reindeer and the lowest percentage from bovids. Body size hardly seems to be the conditioner at Combe Grenal.

The importance of season is further suggested by the comparison between reindeer and horses, where both show a high percentage value for mandibles relative to crania, and both animals were primarily killed in early spring or later in the spring. This is of course the season in the temperate zone when the least food is generally available for humans and other animals as well. Nevertheless, mandibles were returned to Combe Grenal with the highest frequencies among the four animals considered here. In spring when food is least abundant, we might have expected more marginal parts with higher transport costs to have been transported. They were not!

It will be recalled that the spring exploitation of reindeer and horses was observed to have changed dramatically as regards the ages of animals taken and the tactics for killing them, namely the exploitation of reindeer at the calving area or at least very close to it, and a parallel exploitation of pregnant horses and newly born foals. The latter patterns were cited as supporting Proposition 4, which stated that Neandertal hunting strategies favoured reliable hunting tactics over optimal ones. In addition, there does not appear to have been any practice of storage, so very short-term considerations of “abundance” may have ruled the economics of the Neandertal consumer population represented. Another possibility is that there was regular consumption by the entire local group at the procurement location. Instead of transport of parts to consumers not present in the “hunting party”, consumers may have travelled to the procurement location for initial consumption if relatively close to Combe Grenal. If consumption preference was given to parts with high transport costs, as was for instance the case among the Nunamiut Eskimo, then transport to the "camp" would be biased in favour of parts with lower transport costs. The latter certainly seems to be the case at least as regards the head parts of animals.

Examination of the red deer and bovid remains tabulated in Table 7 shows that red deer were killed primarily during winter and secondarily in early spring, while bovids were killed primarily in spring and secondarily in winter. The latter documents an overlapping shift from red deer in winter to bovids in spring. This is consistent with greater diet breadth expected in warmer environments, certainly a dominant condition during the warmer phases of occupation at Combe Grenal, when red deer and bovids were exploited most commonly.

The information summarized in Table 7 demonstrates bias in the types of Mousterian assemblage associated with mandible dominated assemblages. The exploitation of reindeer was associated with Quina, Typical, and Denticulate in decreasing frequencies. Horse, on the other hand, was associated with identical percentage frequencies among Quina, Typical and Denticulate assemblage types. The occupations during warmer settings at Combe Grenal exhibited a different but consistent pattern of assemblage type associations. Such associations nevertheless differed consistently in the forms of assemblage found with red deer and bovids. Red deer were associated with 46.6% Typical Mousterian assemblages, 20.5% Denticulate and 15.4% Mousterian of Acheulean Tradition. Bovids (dominantly bison) were associated with 46.2% Typical Mousterian, 23.1% Denticulate, and 23.1% Ferrassie assemblages. These facts stand at present as interesting, but there is no clear causal basis given our current understanding of Mousterian assemblage variability. One suggestion, however, might be to explore the bias in tool-making potential (Levallois cores) being transported when game such as bison was being hunted. Bison cover much larger range areas than do red deer.

These assemblage-related patterns do provide patterning from the facts of the archaeological record that is in need of explanation (Binford, 2001b). How does raw material variability relate to these patterns? How does raw material usage indicate differential ranges of land use, and of scales of landscape coverage? How do such characteristics relate to seasons of occupation? The research reported here represents the tip of the iceberg as regards research designed to expand our knowledge of the Mousterian.

What can be drawn from this short exercise in looking at the archaeological record for clues to the Neandertal diet? For instance, what about consumption patterns? Are meals consumed by "families", gender-differentiated groups, individuals, all of the above but in different social contexts? The organization of food consumption will certainly condition differential patterning in the archaeological record.

Among most species, other things being equal, we can see parallel associational patterns where the males and females move together in feeding. Other species exhibit some degree of mutually exclusive feeding strategies, as seen among orangutan where males and females feed independently much of the time. This latter pattern has the advantage of insuring that males and females do not compete for the same food resources and/or patches. One can find examples of yet other species socially organized so as to prevent males from competing with their mates for resources. Some costs, either in mobility and/or mating opportunities, must accompany varying ways of organizing male versus female subsistence. Asking the rather non-specific question of diet, when we have little to guide us in thinking about the character of the consuming unit relative to the procuring unit, makes the challenge a bit stiff. I have every confidence that we will begin to be able to diagnose not only procurement strategies as illustrated here, but also how the producers and consumers were organized and what conditioned variability in the size of associational groupings. Understanding diet is a more challenging problem than arguing that the ancients killed animals, scavenged for food, and seemingly lived in minimal social units. The basis for the latter inferences already seem in place. Solving challenging problems like the issue of diet should make our understanding of the past much more sophisticated than what is currently available.

Notes

1. This case is the Guato who lived in a deep South American swamp and heavily exploited aquatic resources as well as swamp fauna. At the time of actual observation, they practised some horticulture. The subsistence values used were based on a “memory culture” reconstruction. Nevertheless, it is my impression that deep swamps do foster hunter-gatherer adaptation of some stability. It appears that horticulture was a very late arrival in the swamps of southern Louisiana, USA.
2. If so, they would not be an independent society but a specialist group within a larger cultural system. They would be more akin to caste groups than independent hunter-gatherers.
3. The comments have reference to the recent claims for the sensational wooden spears recovered from Schöningen, in Germany (Thieme, 1997).
4. The arguments by Trinkaus regarding Neandertal athleticism have recently been challenged by Lieberman – “Rethinking the Fossil Evidence for Behavioral Differences between Neandertals and Modern Humans”, paper delivered April 4, 2004, at the 69th Annual Meeting of the Society for American Archaeology, Montreal, Canada.
5. Levels which Bordes considered to be Riss in age and levels essentially eroded away prior to level 54 in Bordes’ original numbering system are not included in this analysis and discussion.

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Diet Shift at the Middle/Upper Palaeolithic Transition in Europe? The Stable Isotope Evidence

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Introduction

In the study of hominin dietary evolution, much attention has been focused on the latter end of this long process, reconstructing the subsistence strategies of Neandertals and modern humans in Palaeolithic Europe. Of particular interest is the period of "transition" between the Middle and Upper Palaeolithic periods, where it is possible to contrast the strategies employed by these hominins in generally the same environmental context. Much of the dietary research in this period has been based on faunal evidence, but recently applications of bone chemistry, specifically stable isotope analysis, have added to our knowledge of Palaeolithic subsistence. The advantage of isotopic studies is that they provide a direct measure of diet, with a clear contextual link between the dietary information and the hominin of interest. However, where zooarchaeological analysis can provide high resolution pictures of past dietary strategies, even single events, isotopic analysis can only provide broad general views of diets over the longer term.

This paper will review the isotopic evidence for diets in Middle and early Upper Palaeolithic Europe. There are intriguing patterns in the limited data, pointing to different dietary strategies between Neandertals and modern humans, and the possible implications of these differences are discussed.

The isotopic method of dietary reconstruction – explanations and limitations

Isotopic analysis, in the context of palaeodietary reconstruction, refers to the measurement of the stable isotopes of carbon (the $\delta^{13}C$ value) and nitrogen ($\delta^{15}N$) in bone collagen extracted from hominin bone. These isotopic values can be used to determine past diets, specifically to see how the hominins, as omnivores, fit into a past food web. This is done by comparing hominin isotopic values to those of contemporary fauna from the same (or geographically close) archaeological site (Fig. 1).

Current knowledge indicates that the $\delta^{13}C$ and $\delta^{15}N$ values are indicators of dietary protein, with the $\delta^{13}C$ value being a good indicator of the consumption of marine vs. terrestrial protein, whereas the $\delta^{15}N$ value is an indicator of the trophic level of the main protein consumed. Bone collagen isotope values are long-term averages of diets, indicating the sources of perhaps 10 to 20 years of dietary protein (for general introductions, see Katzenberg, 2000; Mays, 2000; Sealy, 2001).

In Holocene Europe isotopic analysis is relatively straightforward, but in Palaeolithic Europe there are a number of confounding factors that make the use of isotope analysis somewhat more difficult. Firstly, the climatic shifts that occurred had dramatic effects on the background isotopic values, raising or lowering the absolute (but not relative) $\delta^{15}N$ values of herbivores, carnivores and omnivores. In order to make an accurate comparison between the isotope values of hominins and fauna, it is very important to ensure that they are indeed contemporary. This means that radiocarbon dates become almost essential, making isotopic studies in these time periods expensive and time consuming. These problems have to be taken into account when interpreting Palaeolithic isotopic results, but are not insurmountable. Recently, studies of the variation in faunal isotopic values over time have been published (Richards and Hedges, 2003; Hedges et al., 2004; Stevens and Hedges, 2004). Many more measurements are needed, but they indicate that generally there are not large variations in $\delta^{15}N$ values over time, except at periods of great climate change, such as at the end of the Pleistocene. However, until we have large datasets of Palaeolithic faunal isotope values from all regions of Europe, we need to keep producing isotope data from associated fauna, and confirming the ages of that fauna through direct dating.

Another issue is that in order to build an accurate “food web” we need to know the diets of the faunal species chosen for comparison with the omnivorous humans. In the Holocene, this is relatively straightforward as we have extant species that we can observe. The diets of extinct species, however, must be inferred from morphology and comparison with Holocene analogues. For example, there is a debate over the explanation for the low $\delta^{15}N$ values of cave bears, which are explained as either the result of unusual physiological effects due to hibernation, or else due to a vegetarian diet (Bocherens et al., 1994; Liden and Angerbjorn, 1999).

Another problem with isotopic analysis, in both the Holocene and the Pleistocene, is the confounding effects of the consumption of freshwater resources. In the Mesolithic period in Europe we do see good isotopic evidence for the consumption of freshwater fish in the Iron Gates region of the Danube (Bonsall et al.,

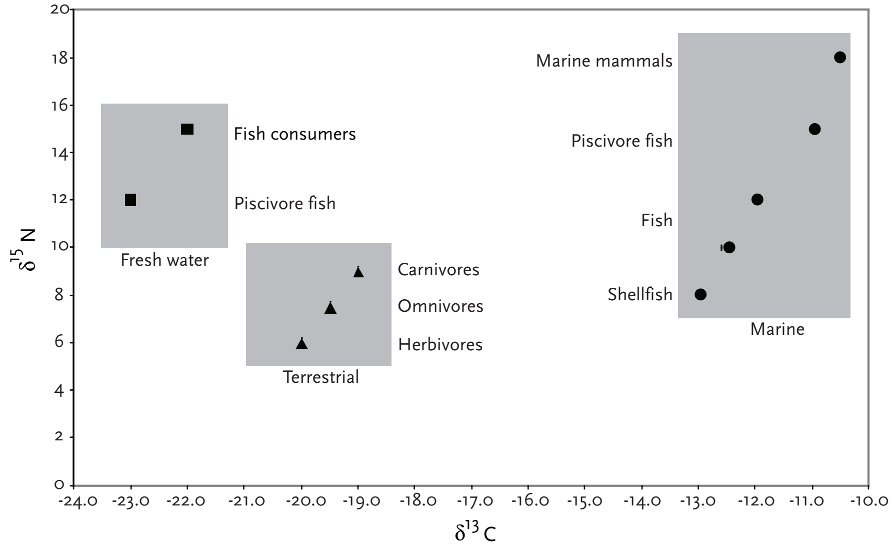

Fig. 1. Typical $\delta^{13}C$ and $\delta^{15}N$ values of fauna from Holocene northwest Europe. After establishing the food web isotopic values of contemporary and local species, hominin isotope values can be compared to determine if the source of dietary protein was more similar to herbivores (e.g. mainly plant protein) or carnivores (e.g. mainly animal protein).

1997; Cook et al., 2001). The significant consumption of freshwater fish there (e.g. close to 100%) was easily recognizable as the humans had very high $\delta^{15}N$ values (e.g. 15 ‰), higher than is possible in terrestrial ecosystems. The effects of freshwater food consumption become more problematic in isotopic studies when the consumption is much less, perhaps 50%. What we then see are very high $\delta^{15}N$ values (e.g. 13 ‰) which are usually higher than in associated carnivores from the same site (e.g. 10 ‰), but not as high as observed for 100% freshwater fish consumption (e.g. 15 ‰). The $\delta^{13}C$ values of freshwater resources are variable and can actually look like a typical terrestrial $\delta^{13}C$ signal, so this is often not useful for identifying the consumption of freshwater fish. Measuring the isotope values of associated fish and aquatic bird remains would be a great help in interpreting the human values, but these are rarely recovered from Palaeolithic sites. In contrast, interpreting the consumption of significant amounts of marine protein is much clearer. This is because $\delta^{13}C$ values of a human that consumes close to 100% marine protein is shifted to approximately -12 ‰ or -13 ‰, compared with terrestrial or freshwater values of ca. -20 ‰, and is also associated with an elevated $\delta^{15}N$ value (e.g. between 15 ‰ and 20 ‰).

Isotope results for Neandertals and early and mid-Upper Palaeolithic humans from Europe

We are unfortunately limited in the number of samples for which we have stable isotope measurements. This is due to both the limited number of specimens available for analyses and the preservation conditions of the material. A number of successful measurements have been made on Neandertals and modern humans in Europe, and these will be discussed here.

Neandertals (c. 120,000 to 28,000 years BP):

To date, there have only been eight Neandertal bone collagen $\delta^{13}C$ and $\delta^{15}N$ isotope results published. Apart from the difficulty in obtaining samples for analysis, a major problem has been extracting well-preserved collagen from the samples. Collagen may survive up to 100,000 years in ideal conditions, but for most situations in Europe, especially in warmer areas, collagen will disappear from bone much earlier. Attempts to extract collagen from older Neandertal samples, such as the lower levels at Vindija, as well as Neandertals from hotter environments, such as Spain, have failed (Richards, unpublished data). Therefore, we are currently limited to analysing more recent Neandertals, and those from relatively temperate environments.

The oldest Neandertal with associated isotopic data is from the site of Scladina in Belgium (Bocherens et al., 1999). Dating of these sites is always problematic, but this Neandertal is believed by Bocherens et al. (1999) to date to between 80 and 120 ka. It is remarkable to be able to extract collagen from sites this old; however, the circumstances of the burial context, a cave in Northern Europe, resulted in the preservation of collagen in the bone. In addition to the older specimen, results from a younger Neandertal (c. 40 ka) have been published from the site of Scladina (Bocherens et al., 2001). Neandertals assumed to date to 35-40 ka have also been measured from the Belgian sites of Spy and Engis (a juvenile) (Bocherens et al., 2001). There are a number of physiological effects on juvenile isotopic values, such as weaning (Herring et al., 1998; Schurr, 1998; Richards et al., 2002), and therefore juvenile data cannot directly be compared with adult values. Therefore, the data from the juvenile from Engis are not discussed further in this paper. Isotopic results have also been published from Neandertals from the site of Marillac, France, estimated to be c. 40-45 ka in age (Fizet et al., 1995). The youngest Neandertals with isotopic data are from the site of Vindija, Croatia, which were directly AMS dated to c. 28,000 years BP (Richards et al., 2000).

The adult Neandertal isotopic data are presented in Table 1. In all studies the Neandertal values were compared with those of herbivores and carnivores from the same sites. A general assumption was made in all studies that the fauna was con-

Table 1. The $\delta^{13}C$ and $\delta^{15}N$ values of bone collagen from European Neandertals. Data sources are: Marillac, Fizet et al. (1995); Scladina 4A-2, Bocherens et al. (1999); Vindija, Richards et al. (2000); Spy and Scladina 1B-4, Bocherens et al. (2001).

Sample no.	Location	$\delta^{13}C$	$\delta^{15}N$	Age (BP)
Marillac 9	France	-20.2	9.3	ca. 40-45 ka
Marillac 10	France	-19.1	11.6	ca. 40-45 ka
Scladina 4A-2	Belgium	-19.9	10.9	ca. 80-130 ka
Vindija 207	Croatia	-19.5	10.1	ca. 28-29 ka
Vindija 208	Croatia	-20.5	10.8	ca. 28-29 ka
Spy OMO 1	Belgium	-19.8	11.0	ca. 35-40 ka
Scladina 1B-4	Belgium	-21.2	11.8	ca. 40 ka

temporary with the Neandertals, which is actually unlikely as these were all from caves, where mixing of fauna often occurs. An exception is the data from Vindija, where it was possible to compare the Neandertal data with that of directly dated contemporaneous fauna. However, all of the other sites are beyond the range of radiocarbon dating, and so it is not currently possible to provide accurate absolute ages for the associated fauna (and indeed the Neandertals).

The isotopic data indicate that in all contexts Neandertals had similar, or slightly higher, $\delta^{15}N$ values than associated carnivores from the same sites. This is interpreted as indicating that Neandertals obtained their protein largely from meat from large herbivores. In no cases were isotopic values observed that indicated the consumption of any measurable amounts of plant foods.

The Neandertal isotope data is remarkably consistent, despite being from geographically and temporally disparate sources, which could indicate that there is a very similar dietary adaptation over the very long time range (potentially 80,000 years) that the isotope data represent. In line with the faunal evidence, it appears that Neandertals were consistently hunting and consuming large herbivores. There is no evidence of any significant contribution of aquatic foods, even though these foods were readily available at a number of the locales studied.

Early modern humans (c. 32,000 to 20,000 years BP):

In contrast to the relatively few Neandertal isotopic values, there are many more modern human early Upper Palaeolithic results available (Richards et al., 2001; Pettitt et al., 2003; Orschiedt, pers. comm.). This is due to both the larger number of samples available for analysis, as well as the greater possibility of collagen survival in more recent material.

The isotopic data for the eleven humans for which there are measurements are presented in Table 2. As is immediately clear, the modern human data are much more diverse than the Neandertal data, and while many individuals have $\delta^{13}C$

Table 2. The $\delta^{13}C$ and $\delta^{15}N$ values of bone collagen from early modern humans from Eurasia. The majority of the data are taken from Richards et al. (2001), with additional data for Arene Candide from Pettitt et al. (2003) and La Rochette from Orscheidt (pers. comm.).

Sample no.	Location	$\delta^{13}C$	$\delta^{15}N$	^{14}C Age BP
Brno-Francouzská 2	Czech Rep.	-19.0	12.3	23,680 ± 200 (OxA-8293)
Dolni Věstonice 35	Czech Rep.	-18.8	12.3	22,840 ± 200 (OxA-8292)
Kostenki 1	Russia	-18.2	15.3	32,600 ± 1100 (OxA-7073)
Kostenki 18	Russia	-19.1	13.1	21,020 ± 180 (OxA-7128)
Mal'ta 1	Russia	-18.4	12.2	19,880 ± 160 (OxA-7129)
Paviland 1	UK	-18.4	9.3	25,840 ± 280 (OxA-8025)
Sunghir 1	Russia	-19.2	11.3	22,930 ± 200 (OxA-9036)
Sunghir 2	Russia	-19.0	11.2	23,830 ± 220 (OxA-9037)
Sunghir 3	Russia	-18.9	11.3	24,100 ± 240 (OxA-9038)
Arene Candide	Italy	-17.6	12.4	23,440 ± 190 BP (OxA-1070)
La Rochette	France	-17.1	11.2	Ca. 25,000 BP

and $\delta^{15}N$ values similar to Neandertals, there are others with quite different $\delta^{13}C$, and especially $\delta^{15}N$, values. This is illustrated in Figure 2, where the $\delta^{13}C$ and $\delta^{15}N$ values of Neandertals and early modern humans are plotted.

As can be seen, there are a number of individuals with markedly higher $\delta^{15}N$

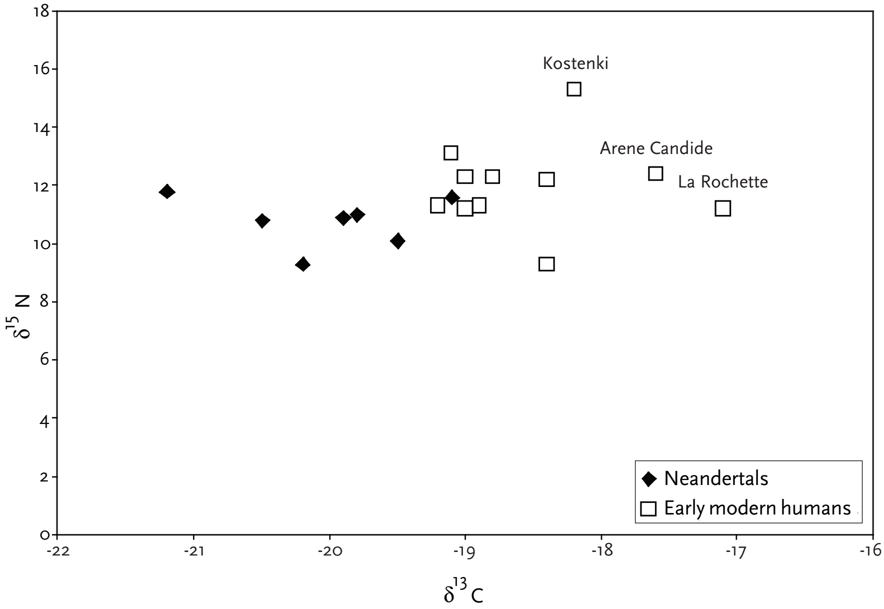

Fig. 2. Neandertal and early modern human $\delta^{13}C$ and $\delta^{15}N$ values.

values than other modern humans and all of the Neandertals, especially Kostenki 1. Additionally, there are a number of modern humans with quite different $\delta^{13}C$ values than the other modern humans and the Neandertals, especially Arene Candide and La Rochette.

It was difficult to obtain associated and directly dated faunal material for isotopic analysis from many of the sites, making it difficult to definitively interpret the human isotopic data. However, there are studies of the faunal isotopic baseline values from this region and time period. The isotopic values of directly radiocarbon-dated herbivores from Northwestern Europe (Richards and Hedges, 2003) showed that there was not an unusual climatic shift in $\delta^{15}N$ values between 32,000 and 20,000 BP. Similar findings were observed by Stevens and Hedges (2004) for directly AMS-dated horses from Europe from this period. Drucker et al. (2003) also attempted to undertake similar studies of long-term variation in herbivore $\delta^{13}C$ and $\delta^{15}N$ values. However, they only assumed the ages of much of the fauna they measured, and did not have direct dates on their samples from the time period of interest here. This is a significant flaw in their studies, as fauna from caves cannot confidently be assigned ages based simply on context. Therefore, for studies of this kind, direct AMS dates are essential, such as those obtained by Richards and Hedges (2003) and Stevens and Hedges (2004). However, in spite of this flaw, the data from fauna assumed to date to this time period again do not show any significant increase in $\delta^{15}N$ values.

The best explanation for the isotopic values of the individuals from the site of Sunghir, using the few faunal isotopic data available, is that they indicate a diet of mainly animal protein, with little contribution from plants or from aquatic resources, freshwater or marine. The isotope data from these individuals, then, indicates a dietary adaptation similar to that observed for the Neandertals.

However, the isotope data are quite different for the specimens from the sites of Kostenki, Arene Candide and La Rochette, and here the data cannot be interpreted as indicating a diet where dietary protein came exclusively from the terrestrial ecosystem. These $\delta^{13}C$ and $\delta^{15}N$ values can best be explained by the inclusion of significant amounts of dietary protein from another ecosystem. As discussed earlier, organisms in aquatic systems have higher $\delta^{15}N$ values than those from terrestrial systems. Therefore, the isotopic values of humans from these sites can be explained by the consumption of freshwater resources, in the case of Kostenki 1, and marine resources, in the case of Arene Candide and La Rochette. The value from the oldest modern human in this study, from Kostenki 1, is remarkably high. This value is also observed for Mesolithic humans from the Danube Gorge region, where freshwater fish was the main source of dietary protein.

For the individuals from the sites of Brno-Francouzská, Dolni Věstonice and Mal'ta, the data fall somewhere in between. Their $\delta^{15}N$ values are higher than 12 ‰, which is higher than the Neandertals; however they are not as high as the two individuals from Kostenki. These data may best be interpreted as a diet mainly consisting of dietary protein from animal sources, likely herbivores, with supplementation by freshwater foods, although these were not a major part of the diet.

The interpretation offered to explain the elevated $\delta^{15}N$ values of some modern humans has been questioned in a useful critique by Drucker and Bocherens (2004). They argue that instead of invoking the consumption of freshwater foods to explain the elevated $\delta^{15}N$ values, there is an increase in the background $\delta^{15}N$ values at this time period, linked to climate. This would, they argue, result in higher human $\delta^{15}N$ values as the herbivore $\delta^{15}N$ values would be elevated, and therefore the humans, having a largely carnivorous diet of herbivore meat, would also have higher $\delta^{15}N$ values. They do not, however, provide well-dated and spatially contemporary comparative faunal material that actually show these elevated herbivore $\delta^{15}N$ values. And indeed, as discussed above, this hypothesized shift was not observed by Richards and Hedges (2003) and Stevens and Hedges (2004), who measured the $\delta^{15}N$ values of European fauna that were directly AMS radiocarbon dated to this time period.

Therefore, until their argument can be supported by data showing this supposed enrichment in background $\delta^{15}N$ at this time, the most parsimonious explanation remains the inclusion of freshwater fish in the diets of these humans. Clearly, this interpretation would also benefit from supportive faunal isotopic data. However, the isotopic values for the humans from the two coastal sites, Arene Candide and La Rochette, are clearly indicative of marine food consumption. Therefore, the consumption of aquatic foods certainly occurs in this period, and this lends support to the interpretation of the inland modern humans also consuming aquatic foods, though from freshwater ecosystems, not marine.

In summary, the modern human isotopic values are more varied than observed for the Neandertals. Often, the isotopic data are similar to those of the Neandertals, and indicate that animal protein was the primary source of dietary protein, again likely large herbivores. However, many of the individuals sampled also have significant amounts of freshwater or marine foods in their diets. This shows that when this resource base was available, modern humans were able to successfully exploit them in large enough quantities to register in their bone isotope values. The interpretation of a broadening of dietary resources by Gravettian peoples is supported by the faunal evidence produced by Stiner (1999, 2001, 2002), who finds increased evidence for aquatic foods (fish and birds) at early modern human European sites, compared with Neandertal sites. Additional support is provided by newer isotopic data from coastal contexts, where Gravettian humans also have elevated $\delta^{15}N$ values, but have linked increases in $\delta^{13}C$ values indicating consumption of marine protein.

Does the isotopic evidence help explain the replacement of Neandertals by modern humans in Europe?

Did the ability (or perhaps choice?) of modern humans to supplement their diet with small game, and especially aquatic foods, give them an adaptive advantage over Neandertals? Specifically, were herbivore populations under pressure due to hunting by two competing hominin groups, which then led to a decline in the herbivore populations? And if so, were modern humans able to diversify through supplementing their diets with, and in some cases heavily relying on, aquatic resources? And finally, did this phenomenon contribute in some way to Neandertal extinction/replacement?

The dataset is still too small to provide clear answers. A significant problem is that most of the modern human samples are Gravettian (or equivalent), and therefore, date to a time when Neandertals were no longer found in Europe. The assumption here is that the modern humans we have sampled followed a dietary pattern already established by the first modern humans in Europe which did overlap with the Neandertals. One of our samples is from this earlier time period and did coexist with Neandertal populations, and this individual, Kostenki 1, has isotopic results that indicate an almost 100% reliance on freshwater foods.

Despite these limitations, the isotope data here do tell us new information about the dietary adaptations of modern humans and Neandertals in Palaeolithic Europe. Presented with the same geographical region and available resources, Neandertals relied on large herbivores for their dietary protein, and only rarely, if at all, used aquatic resources. The first modern humans in Europe used a broader dietary base than the Neandertals, in some cases supplementing their diet of herbivore protein with substantial amounts of aquatic foods. We are still in the early stages of this analysis, but it is possible that this adaptation of modern humans to use a broader range of foods, especially those not used by Neandertals, gave modern humans a competitive advantage over the successful, but more economically conservative, Neandertals.

Conclusions

Clearly, this is an interesting and fruitful area of analysis, but is in many ways still in its early stages. We understand a great deal about isotopic analysis for reconstructing past diets, but there are still many unclear areas, especially when it comes to interpreting $\delta^{15}N$ values. What is needed now is a great deal of new data, especially on Palaeolithic fauna, to establish baseline values for different areas of Europe and for different periods of the Palaeolithic. New areas of research, such as the measurement of oxygen, hydrogen and sulphur, hold some promise of providing clearer information on past diets, especially in terms of the consumption of freshwater fish, or in identifying specific foods that were consumed. There is a great deal to be done, but it is an exciting time for this area of research, and holds great promise for providing clear, direct evidence for the diets of hominins in Middle and Upper Palaeolithic Europe.

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The Evolution of the Human Niche: Integrating Models with the Fossil Record

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Introduction

One of the most striking characteristics of modern humans is our large and metabolically expensive brain. Hominins are the most encephalized species, a position obtained only recently: until the beginning of the Pleistocene, dolphins were the largest brained creatures on the planet, exceeding all primates, including the hominins (Marino, 1998). Only with the emergence of the *Homo ergaster/erectus* lineage, i.e. an approximate 4 to 5 million years after the split from the chimpanzee lineage (Stauffer et al., 2001; Cela-Conde and Ayala, 2003), did hominins take the place of the largest brained animal. This 1.8 million years of hominin brainy prominence pales in comparison to the approximately 20 to 30 million years that some marine mammals have been maintaining their large brains. The trigger for brain expansion in marine mammals was probably environmental, specifically the cooling of the southern ocean (Fordyce, 1980). These environmental changes may have offered specific challenges, selectively favouring larger brains (Conway-Morris, 2003). The persistence of these large brains for many millions of years requires additional explanations, possibly related to the evolution of complex forms of social strategies and communication (e.g. Connor and Krützen, 2003; Whitehead, 2003).

Because of their high costs, large brains are rare (or as Richerson and Boyd (2005) have proposed, animals are under strong selection to be as stupid as they can be…). Most mammals have brain sizes that match an appropriate body size, but some have larger or smaller ones than would be predicted by body size. For instance, elephants have larger brains than expected, as do some marine mammals such as toothed whales and dolphins. However, humans provide the strongest exception. Our large brain is one of the most striking features that make us stand out amongst other mammals, including our nearest relatives, the primates. At the genetic level we are very similar to chimpanzees (Li and Saunders, 2005), but our gene expression differs (i.e. the frequency and amount of proteins made), particularly so for brain genes (Enard et al., 2002), which may have an impact at various levels, e.g. hormones, life history and behaviour. We clearly differ from other primates in many aspects of morphology and behaviour as well as life history: we take even longer to grow and have considerably longer lifespans; we are born with large amounts of fat under our skin and appear more or less hairless compared with our closest relatives. We devote much time and energy to raising our offspring and have an almost global distribution. We also differ in the way information and skills are transmitted culturally in different societies, in the role of different social learning processes and teaching, and in the inferred hallmark of modern humans, our linguistic capacities.

Many workers, including some of the contributors to this volume, consider these peculiarities as being ultimately related to changes in diet within the hominin lineage, more specifically as the result of natural selection favouring individuals who gathered high-quality, nutrient- and calorie-rich food in an efficient and productive manner. As the papers in this volume show, differences of opinion exist over the specifics of these developments. For instance, Aiello (this volume; cf. Aiello and Wheeler, 1995) sees changes in diet as removing a constraint on brain growth, whereas Kaplan and colleagues (this volume, cf. Kaplan et al., 2000, 2003) see the shift to valuable but hard to acquire food resources as the driving force behind the evolution of a larger brain and other human peculiarities such as the modern human life history.

A wide range of disciplines studies the issues related to the development of these human peculiarities and the development of the human niche. A series of important hypotheses has been put forward to explain the origins of such features and the interrelationships between variables such as life history and dietary adaptation, between brain size and longevity, between the knowledge-intensive character of our dietary strategies and brain size, and so on. Many of these models are based on comparative studies of a wide range of extant species, including primates, and most of them show that dietary adaptations play a central role.

Another important source of information for studies of the development of the human niche is the fossil and archaeological record, consisting of fossil remains of earlier hominins and evidence of a wide range of human activities, from broken-up and cut-marked bones with associated stone artefacts appearing in Africa as early as 2.6 Ma to the well-known art objects dating to the final part of the European Pleistocene.

One of the biggest challenges for palaeoanthropological studies concerns the integration of these two datasets, i.e. to use these models to develop constraints on interpretation of the fossil record and at the same time put some meat on its bare bones. Likewise, other disciplines should use the fossil record to test their hypotheses. Diet is important in this broad field of research, because it offers the opportunity to integrate the theoretical models with such data. Many aspects of the diet of earlier hominins are visible in the archaeological and hominin fossil record, which contains abundant evidence for changes over time. Comparison of the diets of human foragers and those of other primates, especially apes (Kaplan et al., this volume), constitutes another entry into these changes.

In this paper we will review the main current theories and data in this domain. We shall start with a short summary of the main developments in hominin biological and cultural evolution. This will be followed by a longer section dealing with various features that make humans such peculiar mammals and how these may relate to aspects of our diet. Finally, we will present an example of an integrative approach to the Neandertal record, focusing on one particular aspect, the use of space.

The fossil and archaeological record

The first possible hominins appear around 6 to 7 million years ago in the fossil record (Haile-Selassie, 2001; Brunet et al., 2002). Though the hominin status of these specimens is not uncontroversial, their appearance date almost tallies with assumptions based on genetic studies of the chimp-human divergence (e.g. Ruvolo, 1997; Stauffer et al., 2001). The earliest unambiguous fossil hominins, such as *Australopithecus anamensis* and *A. afarensis*, were bipedal creatures but still retained some form of arboreal lifestyles, as demonstrated by a combination of long forelimbs, curving phalanges and barrel-shaped thorax (Wood, 2002). The evolution of bipedalism has traditionally been related to changes in the environment, including increasingly dry conditions and the expansion of open habitats (new palaeoenvironmental studies suggest a more wooded and humid context, cf. Reed, 1997). One prominent theory is that changes in the environment presented new problems to arboreal apes, some of which started to forage the more scattered resources of the mosaic landscape at ground level (e.g. Foley, 1995). This new foraging behaviour selected for a more upright gait that was energetically more efficient than being on all fours (Rodman and McHenry, 1980), at the same time being advantageous in terms of thermoregulation (Wheeler, 1991). Importantly, this shift in foraging strategy and diet is also documented with changes in dental morphology leading to larger teeth, presumably required for the processing of coarser vegetation.

To a first approximation, the size of the brain scales to body mass in mammals and primates, so that as body size increases, so does the brain. From this relationship we can see in the fossil record when hominin brains came to exceed the predicted values, i.e. show increases in “relative” brain size. With the appearance of the first australopithecines (i.e. *A. afarensis,* from ~4 Ma), brain size is not markedly different to other apes. However, we do see increases in brain size over time, both in relative and absolute terms, with the appearance of the robust australopithecines at 3 Ma (Elton et al., 2001). These species developed extreme megadonty, with even bigger teeth and jaws that required huge muscle attachments to operate them, giving rise to the robust characteristics in the skull, hence the name "robust" australopithecines. It is thought that these developments were directly related to changes in diet, from soft fruits to harder, more fibrous vegetal foods (Grine, 1986).

The next important evolutionary event is an increase in brain size, with the appearance of the genus *Homo*. Though the taxonomic status of *Homo habilis* and *H. rudolfensis* is still unclear, many workers agree with Wood and Collard's (1999) suggestion that these hominins should rather be classified as australopithecines. Their brain size varies between 500 and 800 cubic centimetres (cc), and their 650 cc average is larger than that of other australopithecines. With the emergence of "real" *Homo* (*ergaster/erectus*) sensu Wood and Collard (1999), a further increase in cranial capacity (to 900 cc) accompanies a marked increase in body size, mainly in females, who almost double in size compared with australopithecine females (Aiello and Key, 2002). Thus, it is around this time that sexual dimorphism becomes reduced to almost modern values. Another noticeable change in trajectory from earlier hominins with the advent of *Homo* was a reduction in tooth and jaw size, probably relating to differences in dietary strategy or the way in which food was being processed.

The timing of these events is important for assessing how they relate to major landmarks in hominin culture, sociality, and biogeography. Stone tools appear before *Homo,* at 2.58 Ma at Gona (Afar, Ethiopia), where they are associated with cutmarked bones (Domínguez-Rodrigo et al., 2005). A study of these assemblages suggests "...that hunting and/or aggressive scavenging of large ungulate carcasses may have been part of the behavioral repertoire of hominins by c. 2.5 Ma" (Domínguez-Rodrigo et al., 2005). This early date is not surprising, as comparative primate studies have revealed that chimps (McGrew, 1992) and capuchins (Phillips, 1998; Moura and Lee, 2004) make and use tools to help them forage in the wild. The taxonomic status of the producers of these assemblages is unknown, and at least three hominin species were present at that time. As discussed below, some have intimately tied the archaeological evidence for meat consumption to the increase in brain size (Aiello and Wheeler, 1995).

From about 1.8 Ma, we have hominin fossils from areas outside of Africa, e.g. from Dmanisi (Gabunia et al., 2000; Vekua et al., 2002) and from Java (Swisher et al., 1994). Most workers (e.g. Antón et al., 2002; Mithen and Reed, 2002) implicitly assume that the *Homo* lineage emerged where the earliest fossils are found, i.e. in East Africa, but this has to be considered a working hypothesis rather than an established fact, as Robin Dennell has pointed out at various times (2003, 2004). It is clear that hominins were present in Asia (e.g. at the well-dated site of Dmanisi) a few hundred thousand years before the first Acheulean handaxes appear in the East African record. Who these toolmakers were, in taxonomic terms, is largely unclear. Many workers lump the *Homo* specimens around this time under the label *Homo erectus*. They see *Homo erectus* s.l. as a very widely distributed (from East Africa to Java) polytypic species (e.g. Rightmire, 1984, 1990; Antón, 2003), incorporating WT-15000 (Nariokotome boy) from West Turkana (*Homo ergaster*), the Dmanisi hominins (Rightmire et al., 2006) and the Java material (*Homo erectus*). However, Schwartz and Tattersall's recent interpretation of the Dmanisi assemblage illustrates an important competing view: "... In short, none of the Dmanisi fossils can be regarded as belonging either to Asian *Homo erectus* or to the species containing its supposed African relatives" (2005: 500).

Around one million years ago the first hominins leave their traces in Mediterranean Europe, and it is only during a temporary northward expansion of their familiar habitat at around 700 ka that they make it up north, to southern England, probably for a very short period only (Parfitt et al., 2005). A substantial occupation of the northern temperate latitudes of Europe becomes visible in the archaeological record only around 500 ka (Roebroeks, 2001). At roughly the same time period, hominins move north in Asia (Dennell, 2003), and the southern parts of Europe see a more substantial hominin presence, e.g. in Italy (Mussi, this volume). From this time onward hominins are present in both interglacial and significantly colder climatic conditions all over Eurasia.

At about 600 ka, a new hominin appears, *H. heidelbergensis*, with a similar body size to *H. erectus/ergaster*, but with a larger brain (averaging 1200 cc). This development is well documented in Africa (e.g. Bodo 600 ka, Ethiopia; Kabwe 200 ka, Zambia; Elandsfontein 300 ka, Florisbad 260 ka, Singa ~160 ka, South Africa; Jebel Iroud ~190 ka, North Africa). However, the most exceptional increase in brain size occurs with the independent evolution of *Homo sapiens* and Neandertals, in Africa and Europe. According to the fossil record the first *H. sapiens* appear in Africa, and this almost tallies with the predictions based on intra-population genetic studies (Cann et al., 1987; Ingman et al., 2000). Either way, humans are estimated to have originated about 250 ka in Africa, with the first fossils (those with unequivocal human attributes) at Omo Kibish (190 ka) and Herto (160 ka) in Ethiopia and at Klasies River Mouth (120 ka), South Africa. Their first appearance outside Africa is in Israel at 90 ka, then Australia at around 60-40 ka. They enter Europe at around 35,000 ^{14}C years BP (Trinkaus et al., 2003) and by 30 ka they have replaced all other living hominins throughout the world (save one newly discovered isolated island species in South East Asia that may have lived till 18 ka, cf.

Morwood et al., 2004; Brown et al., 2004). It is only with the appearance of humans and Neandertals (but humans in particular) that we see signatures of more complex behaviour and culture. We can trace the beginnings of these to the Middle Stone Age in Africa (McBrearty and Brooks, 2000) and the Middle Palaeolithic of western Eurasia, but the changes in the European record coinciding with the appearance of modern humans (Mellars, 2004) are beyond any comparison with the 2.5 million years of hominin cultural evolution that preceded the Upper Palaeolithic.

Model review

Diet and brains

Brains are metabolically expensive organs, contributing a relatively large portion of the body's basal metabolic rate, the rate at which an animal expends energy to maintain life when at rest (Aiello and Wheeler, 1995; Leonard and Robertson, 1996; Milton, 2003). Costs are even greater in gestation and infancy in humans, with our brains consuming about 80% of the total energy intake as newborns, compared with 20% for adults. Measuring the high energetic costs of the human brain highlights the importance of strong selective benefits to having a larger brain and enhanced cognitive abilities in human evolution. In addition, it suggests that diet may have been an important factor in providing the nutritional basis for the selection of larger brains.

Surprisingly, the human basal metabolic rate is no higher than that of primates with smaller brains (Aiello and Wheeler, 1995). Aiello and Wheeler (1995) have suggested that the metabolic costs of a large brain were off-set by a decrease in the size of the similarly expensive gut in the course of human evolution, associated with a change in diet. Such a reduction in gut size would only be compatible with high-quality, easy-to-digest food. Milton (1999) provides an alternative scenario. Changing environmental conditions in Plio-Pleistocene Africa, involving a decline in plant productivity and an increase in secondary biomass (Leonard and Robertson, 2000), would favour a shift in diet in hominin species, either to specialization on lower quality plant foods or routine access to meat. Meat is a very useful source of protein, many minerals and vitamins that humans require, and also essential fatty acids (Milton, 1999). It is not as useful as an energy source – the metabolic costs of protein conversion greatly exceed those of converting carbohydrates or fat, and the amount of fat available for consumption in prey species varies. However, Milton (1999) has pointed out that if humans could satisfy these other dietary requirements with meat, this would free up gut space for energy-rich vegetable foods, and meat can also aid the digestion of poor-quality plant foods. This departure from the diet of other apes was subsequently important in supporting the evolution of a larger brain in *Homo*, and the reduction in gut size, but the two were independent.

Subsequent phases of brain expansion, notably increases between 600 and 150 ky ago (Ruff et al., 1997), would also have involved increases in energy costs. Other authors have highlighted the high concentration of long-chain fatty acids in an easy-to-exploit form in a shore-based diet (Broadhurst et al., 2002). They suggest that marine foods could have been important in the dramatic increase in brain size in our own species. However, this seems less likely for another encephalized species, the Neandertals. Cooking could have been important in later human evolution, reducing the toxins in food and increasing digestibility (Aiello and Wheeler, 1995).

In addition to the energetic costs of running an adult human brain, there are nutritional and biochemical costs for growing one (Robson, 2004). In humans, the most dramatic brain growth occurs post-natally in the first year of life, providing a uniquely longer and more rapid phase of growth compared with all other mammals, leading some to believe that a dietary impact on human brain size should occur during this period, i.e. through maternal milk (Martin, 1983). However, studies show that unless the mother is undergoing extreme nutritional distress, diet does not appear to affect maternal milk, with the components of specific biochemical building blocks needed for brain growth remaining more or less stable across human populations consuming a variety of diets (Robson, 2004). Furthermore, primate and human milk also appears to be essentially the same in terms of the nutritional components (Robson, 2004). However, human babies are unusual in being born with large quantities of body fat, which Cunnane and Crawford (2003) argue provides insurance for the biochemical requirements of brain growth.

Brain growth, albeit at a slower rate, is also an important feature of childhood, a unique human life history stage after weaning (Bogin and Smith, 1996). Humans wean children early relative to their dental development, but provision them with suitable foods throughout their childhood (Bogin and Smith, 1996; Kennedy, 2005). They are therefore able to offer more energy and nutrients than would be available just from maternal milk. The immaturity of children's dentition and digestive tracts and continued growth of the brain means that they require a diet low in total volume but dense in energy, lipids and proteins, and are dependent on adults for care and to provide food (Bogin, 1997, 1999). Thus, a change in diet could have been important in providing suitable food for weaned children, and early weaning may have been important for the continued pattern of brain growth in childhood (Milton, 1999; Kennedy, 2005). Again, a dietary shift could have provided nutritional support for the initial expansion of the brain, in conditions where there was selection for enhanced cognitive capacities in adults.

Diet, morphology and life history

Modern life history theory is used to study the relative timing of skeletal and dental development that may be related not only to extrinsic factors such as environment and diet, but to biological factors governing the key phases of life cycles. Body and brain size are intimately tied to diet and life history patterns in mammals as a whole, and the primates have evolved particular morphological and biological traits, such as larger brains, a slower growth rate, a reduction in litter size and producing larger offspring that live longer compared with other mammals.

Within primate genera these key differences can be related to diet and lifestyles directly. For instance, masticating fibrous foods such as leaves makes higher demands on teeth, so it makes sense for leaf-eating primates (folivores) to have rapid dental development compared with fruit-eating primates (frugivores). Fruits are more ephemeral and patchy in their distribution, and often contained in a protective casing, which may make the foraging niche of frugivores relatively complex (Parker and Gibson, 1977; Clutton-Brock and Harvey, 1980; Gibson, 1986; Harvey and Krebs, 1990). As folivores have a relatively easy foraging strategy that requires little in the way of learning, primates eating leaves could potentially start foraging fairly early on in life. In fact, it has been shown that folivores tend to wean at an earlier age (Godfrey et al., 2001) compared with frugivores. Dietary quality has been shown to be correlated with brain size, in that folivorous (leaf-eating) primates have smaller brains, whilst primates who eat fruit and animal foods (insects, meat) generally have larger brains (Foley and Lee, 1991). Species with larger brains need a longer period of post-natal brain growth and, since this is generally completed at weaning, a later age at weaning, which has implications for development, the dependency of offspring, birth spacing, and hence population growth. In addition, a number of authors have pointed out that a longer juvenile period could be particularly useful for organisms that need to learn complex foraging skills (Milton, 2000; Kaplan et al., 2000). This pattern of delayed weaning, extension of the juvenile period, and delay of the age at first reproduction is seen amongst the apes.

Humans have fine-tuned this pattern of slow growth and development even further. We combine a long juvenile period and lifespan, with caring and providing food for inefficient weanlings, thereby increasing not only the period of growth and time available for learning, but also the reproductive rate. All of these factors can be related to diet. Having large, slow-growing babies is energetically costly for mothers during gestation and lactation. Shortening the inter-birth interval, by weaning children earlier, increases the female reproductive rate, and allows some of the costs of caring for dependent weanlings to be shared among others (Aiello and Key, 2002). Providing such care could increase the fitness of grandparents, leading to selection for longer lifespans, and an extension of life history phases generally (O'Connell et al., 1999). According to Aiello and Key (2002), earlier weaning is likely to have occurred in *H. erectus,* in response to a major increase in reproductive costs associated with increasing female body size. Kaplan and colleagues (2000, this volume) present a model of human life history evolution in which a large brain, longer juvenile period and longer lifespan co-evolve in the context of a complex foraging niche. They argue that human foraging is relatively complex and skill intensive. Complex skills take a relatively long time to learn, and an individual only becomes more productive later in life, so that the benefits are highest if an individual is relatively long-lived. These delayed returns interact with the mortality risks associated with particular skills, and investment in ways of protecting against mortality, to produce selection for a longer lifespan and juvenile period.

Humans have a relatively long period of accelerated post-natal brain growth and are born with excess fat compared with all other living apes (Cunnane and Crawford, 2003). According to Bogin (2003), humans have a unique period, childhood, in their life cycle, in which body growth is very slow but brain growth continues. The childhood phase is particularly important for learning, because children have few responsibilities to take up their time, because of cognitive abilities that help efficient learning of particular skills (e.g. language) and because environmental complexity during childhood can have a positive and direct effect on brain structure (Kennedy, 2005). Brain growth to adult size is almost complete by the age of 7 (Cabana et al., 1993), when childhood ends. After this period, body size starts to increase steadily. However, there is another uniquely human life history phase, adolescence, characterized by a spurt in skeletal growth, culminating in sexual and behavioural maturity (Bogin and Smith, 1996). In addition to explaining the length of human growth and development, theories of human life history evolution need to explain the distinctive pattern, in terms of the length and rates of growth of particular phases of development, which underlies this trend.

An important consideration explaining the evolution of these unique human life history phases is the constraints set by parameters such as brain and body size and life history variables, and their implications for the evolutionary trajectory of the species. For instance, although humans have the largest relative brain sizes of all animals, they are born with brains that are approximately 12% of their body size, similar to other apes. Why not just have larger brained newborns? The constraints of our bipedal gait, requiring a narrow pelvis, and large brain requiring slow growth, did not permit this as a solution. Instead, human babies are born with skulls not fully formed, so that the skull can pass through the pelvic canal, and must then grow their brains rapidly in order to attain larger adult brains. It is during this period that having extra fat pays off, as it acts as a fuel to help the brain grow (Cunnane and Crawford, 2003). So increasing the window for accelerated growth and the laying down of fat in-utero may have been important evolutionary events in the hominin lineage. As discussed above, these events are intimately tied to diet and, in particular, to the consumption of high-quality, nutrient-rich foods.

Whilst we can see what is special about humans by comparison with our closest living relative, the chimpanzee, we need other information to tell us when these changes came about in the hominin lineage, and test the hypotheses described above. Genetic studies will help us to identify when certain human-specific genes evolved, especially those that could be related to morphology, while fossil evidence for changes in dentition, body and brain size and comparative data from primates provide the basis for predicting hominin life history parameters. Interestingly, such studies show that certain intermediate patterns emerge for hominins between chimps and humans.

Diet and social organization

In attempting to reconstruct social organization, palaeoanthropologists have focused on the evolution of life history in the hominins. Encephalization has implications for maternal energetic costs in child-rearing, and thus for parenting strategy. A key question is the timing of the evolution of cultural strategies for the extension of provisioning effort to others than the biological mother (Buckley and Steele, 2002). Aiello and Key (2002) highlight the increased reproductive costs associated with larger body size in *H. erectus* females, and suggest a range of reproductive and social solutions that could have met those costs as discussed above. Continued encephalization and occupation of high latitudes probably increased the energetic load on both males and females while also increasing dietary dependence on meat (Mussi, this volume). Reduced body size and sexual dimorphism in *H. erectus* and subsequent hominins is consistent with a pattern of reduced male-male competition (Steele, 1996: 114) that might suggest more affiliative social interaction in this species. Some workers suggest that pair-bonding associated with male parental care can be traced as far back as *Australopithecus* (Reno et al., 2003). Men and women in contemporary hunter-gatherer societies often forage for different resources in different ways. Sometimes, this involves men going after resources that are variable, larger, and have a greater protein and fat content. One explanation of this pattern is that males and females are cooperatively acquiring food for their dependent children (Lee and DeVore, 1968; Isaac, 1978; Hill and Hawkes, 1983; Kelly, 1995). However, a number of authors suggest that mating investment and male status competition may be important mechanisms for male hunting in modern hunter-gatherers, particularly where variable, valuable resources are available (Hawkes et al., 1991; Bliege Bird, 1999; Smith and Bliege Bird, 2000). Thus differences between men and women's foraging are based on different reproductive priorities (Bliege Bird, 1999). It is important to note that any of these mechanisms could result in more high-quality food for children. Based on a prisoner's dilemma model, Key and Aiello (2000) argue that men will cooperate with women when women's reproductive costs are relatively high, even when women do not reciprocate: this would suggest that such male foraging strategies might have been favoured in *H. erectus*. These models also have implications for sharing and social relations in the wider group.

Among primates, the prevalence of non-maternal care varies greatly from none at all to occasional grooming and play to feeding and holding infants (Ross and MacLarnon, 2000). Where we have data for hunter-gatherer societies, children are held or carried by someone other than the mother for 20-50% of the time (Hewlett, 1991). Differences in longevity between males and females in primate species are related to provision of care for infants (Allman and Hasenstaub, 1999): the human pattern suggests that females are the primary caregivers but that paternal care is also important. Childcare, provisioning or even education by grandparents may affect the survival of their grandchildren or reproductive rate of their children, with implications for the evolution of slower or later maturation (O'Connell et al., 1999; Lee, 2003). Interestingly, a gene associated with slower aging (apoE3) apparently spread after 175-600 ka (Finch and Sapolsky, 1999; Fullerton et al., 2000).

Contemporary hunter-gatherers also engage in a wide range of group-based subsistence efforts. The exploitation of large "packet" food resources that can be divided provides incentives for food sharing (Winterhalder, 1996). A large number of mechanisms explain patterns of human food sharing in different contexts, including scrounging, sharing, and costly signalling (Winterhalder and Smith, 2000). As the authors comment, it seems probable that a similar range of mechanisms was relevant in the past. A number of contexts in human evolution could have favoured cooperative behaviour relatively early, for instance, group defence (Guthrie, this volume) and hunting large mammals at close quarters. Unfortunately, it is hard to make a strong link between archaeological evidence for activities favouring cooperation and the quality of interaction involved. Humans are unusual in showing altruistic behaviour in large groups, and in their predisposition to altruistic punishment and rewarding for cooperative behaviours (Fehr and Fischbacher, 2003). It is possible that some form of cultural group selection, involving cultural transmission of cooperative norms, is necessary to explain the forms of cooperation seen in humans (Fehr and Fischbacher, 2003).

Large primate groups may form because of the benefits in reducing the risk of predation (Isbell, 1994). This determines overall group size in some primates, and the quality of social relationships between females in the group is influenced by competition for resources within and between groups (Sterck et al., 1997). Where predation pressure is less important, foraging group size may reflect the distribution of resources, while larger groups form based on other benefits to sociality such as obtaining a mate, learning, or reducing variance in resources through sharing (Milton, 2000; Winterhalder and Smith, 2000). Aiello and Dunbar (1993) suggest based on a primate trend with brain size that the hominin group size increased over time (Steele, 1996, has criticized the predictive value of this model). However, larger body size and tool use may have increased the hominins' ability to defend themselves. In addition, increased body size, a dietary shift and living in northern latitudes would have had major implications for hominin population density and home range size (Gamble and Steele, 1999; Leonard and Robertson, 2000). As discussed below, some authors argue that relatively complex social interactions occur in larger primate groups. The fragmentation of groups could add an additional element of social complexity as individuals have to recognize other people over longer intervals in time and space, and may use different forms of communication (Milton, 1999; Dunbar et al., 2003). Contemporary and historic hunter-gatherers form social networks on a larger scale, such as clans or tribes, while people sharing a language could also be described as a population group. The formation (and limitation) of such networks may be based on linguistic communication and on symbolically mediated exchange, another unique feature of humans.

Selective pressures for larger brains

It is often taken for granted that the benefit of a larger brain is an increase in "intelligence". Aspects of intelligence might include "learning an unrestricted range of information; applying this knowledge to other and perhaps novel situations; profiting from the skills of others; and thinking, reasoning or planning novel tactics" (Byrne, 1995: 38). That brain size has a role in cognition is confirmed by evidence that primate species with larger brains tend to innovate, learn from each other and use tools more frequently than others (Reader and Laland, 2002). These intellectual abilities are likely to be useful for extreme generalists, species adapted to exploit continually changing environments. Mathematical models show that learners have an advantage in environments that are variable but do not change so fast that prediction becomes impossible (e.g. Boyd and Richerson, 1985).

A number of hypotheses have been proposed to explain large primate brains, which highlight ecological and social contexts. As Reader and Laland (2002) point out, these explanations all feature environmental variability: an animal's environment includes factors such as climate, vegetation, predators, and also its conspecifics. Primates are generally gregarious, and conspecifics may change their behaviour rapidly and employ similar levels of intelligence, producing a highly variable social context. A number of authors have argued that the social world is the principal challenge shaping primate intelligence: individuals are favoured who can use and exploit others in their social group, in both cooperative and competitive situations (Jolly, 1966; Humphrey, 1976; Byrne and Whiten, 1988; Whiten and Byrne, 1997). By contrast, ecological hypotheses focus on the difficulty of tracking variable food resources, particularly across larger home ranges, and the learning requirements and tool use involved in extracting food from a protective matrix (Parker and Gibson, 1977; Clutton-Brock and Harvey, 1980; Gibson, 1986; Harvey and Krebs, 1990; Milton, 2000). Species that focus on large, high-quality items of food may have to deal with several of these problems (Kaplan et al., 2000; Milton, 2000). As Deaner et al. (2000) have pointed out, these hypotheses are not exclusive. A number of authors have suggested that niche breadth and behavioural flexibility might be favoured in periods of increased climatic variability (Vrba, 1985; Potts, 1998; Richerson and Boyd, 2000).

Another interesting suggestion is that brainier species may expose themselves to more novel situations, thus speeding up the rate of evolution (Wilson, 1985). The number of species in bird taxa does correlate with behavioural flexibility (Nicolakakis et al., 2003). Finally, life history parameters and brain size may co-evolve if there is selection on the length of the juvenile period related to time available for learning (Kaplan et al., 2000).

There is strong empirical support for the social brain hypothesis. Neocortex volume correlates with a number of measures of social complexity including group size and the frequency of social play (Dunbar, 1992; Barton and Dunbar, 1997). The relationship with group size is also present in bats, carnivores, insectivores, and odontocete cetaceans (Gittleman, 1986; Marino, 1996; Barton and Dunbar, 1997; Dunbar and Bever, 1998). Deaner et al. (2000) have shown that results of tests of ecological and social hypotheses vary depending on how brain size is scaled and the regression methods used. Some analyses show a correlation between brain size and measures of ecological complexity such as home range size (Deaner et al., 2000; Kaplan et al., this volume), while other analyses produce negative results (Dunbar, 1998). Strong correlations between key variables (group size and home range size) present a problem for distinguishing which variable is more important in a multiple regression analysis. In general, less attention has been focused on establishing suitable measurements of ecological complexity relevant to a range of species, and to determining the relevant measurements of brain size, and a role for ecology cannot be ruled out.

Further insight into these questions comes from comparative psychology. According to Tomasello (1999), primates have the ability to understand something of relational categories. While this ability can be demonstrated in an experimental context involving objects, it takes training; by contrast, individuals seem to understand something of third-party relationships and employ that knowledge readily in the wild. This would seem to support an argument for selection on these particular cognitive abilities in a social context. However, interpreting primate psychology is complex: other authors argue that apes but not monkeys have a theory of mind (Byrne, 1995; Dunbar, 2003).

Chimpanzees, the brainiest non-human primates, live complex social lives, use tools frequently in the wild, have regionally distinct traditions, and hunt colobus monkeys. Social learning, innovation and tool use frequencies correlate with each other and with brain size in the primates (Reader and Laland, 2002). Reader and Laland (2002) suggest that social and ecological hypotheses should not necessarily be considered as alternatives: the ability to generate solutions by innovation or by learning a useful response from someone else could be advantageous in the same circumstances. By contrast, Dunbar (2003) suggests that environmental changes will lead to selection for specifically social cognitive abilities, as primates solve ecological problems together. Another possibility is that socio-ecological demands might often evolve in tandem. For example, species that forage for high-quality resources also tend to have fission-fusion social organization. This could be more complex because in these contexts primates use different forms of long-distance communication, and because maintaining social relations may be more demanding in terms of memory and cognitive representation of individuals who are absent (Milton, 2000; Dunbar et al., 2003).

The role of social solutions is particularly clear in human foraging strategies. Co-operative acquisition, sharing food and information, and educating young people are all key elements of foraging as practised by contemporary hunter-gatherers. Kaplan and Robson (2002) suggest that human ecological and social intelligence evolved in the context of a distinctive foraging strategy, with strong benefits to co-operation selecting for greater social intelligence and subsequently language skills. The cognitive demands of these adaptations – for instance, language, or an extended form of altruism – may be different from those in large primate groups (Steele and Shennan, 1996).

Humans are unique in their capacity for language and elaborate culture, as well as specific forms of social learning. How do these features relate to the large human brain? Boyd and Richerson (1985) argue that the human brain and culture co-evolved. Cultural learning saves some of the costs of complex cognition, by allowing people to learn elaborate skills and factual knowledge without individual experience or invention. They argue that human cognition and culture are rare phenomena because some of the benefits of cultural learning are only available once there is a pool of learners. Language is cognitively extremely demanding and involves intensive learning over an extended period of childhood. It seems probable that these factors could be relevant in the dramatic increase in human brain size after 250 ka or even more so after 100 ka, and it is possible that such adaptations could cause a major increase in evolutionary rates. Human brain size is part of a general hominin trend involving a number of radiations, and different explanations are probably important at different periods. In addition, the increase in human brain size is matched by that in Neandertals.

An integrative approach to the Neandertal record

How can we integrate these models of the evolution of the human niche with data from the archaeological and fossil record, for instance, the Neandertal record? Here, we present an overview of the current knowledge of Neandertal evolution, the environments they occupied and diet. The Neandertals provide an interesting challenge to models of the evolution of the human niche. As close relatives, they share many biological characteristics with modern humans, including a large brain for their body size. At the same time, there are some striking differences in the archaeological record for the two species in Europe. Explanations for these differences often highlight supposed cognitive differences. However, we suggest that it would be worth exploring an alternative explanation, beginning with the observation that a number of studies have identified differences in energy requirements and use between Neandertals and modern humans (Churchill, 2005; Sorensen and Leonard, 2001). Here, we present an example of the application of an energetics perspective to the archaeological record, focusing on the use of space. This is based on a model developed by Verpoorte (2006).

What are Neandertals?

Ever since their first discovery, in 1856 in the Neander Valley, Germany, the Neandertal story has been rife with controversy over who they were, where they came from, who their ancestors were, and one of the most important questions in paleoanthropology: why did they go extinct? Decades later, with a mass of data from the fossil and archaeological record, along with ancient DNA extracted from Neandertal specimens for genetic studies, we still have no concise answers, as the data are always open to interpretation. One of the main points of contention is whether or not they contributed genetically to modern man, or whether they should be considered a completely separate species. Popular models used to describe these relationships include the 1) “single origin model” (or “Out of Africa”), which supports the view that all modern humans arose from a single African ancestral population in a relatively short time frame and that these modern humans replaced all other archaic hominins as they migrated out of Africa into Europe and Asia; 2) the “multi-regional model”, which stipulates that all living humans arose in situ in all regions independently from archaic stock with a long chronology, with the possibility of gene flow between populations, i.e. Neandertals in Europe contributed to the evolution of modern Europeans; 3) and finally, with the recent developments in genetics, the "assimilation model" (also known as "mostly out of Africa"), which lies somewhere between the aforementioned models (Smith et al., 2005). Here the scenario is described as modern humans originating in Africa, and thence migrating into Western Asia and later into Europe, but instead of seeing the whole replacement of Neandertals, in this instance genetic exchange between the two species occurs. Thus, Neandertals may have contributed to modern human DNA in Europe initially, but ultimately if modern humans had higher effective population sizes, they would have swamped out the Neandertal genes.

The genetic studies certainly indicate a recent African origin for all modern humans and furthermore show that Neandertal DNA lies outside the known human variation. Numerous studies based on the fossil evidence show that Neandertals exhibit unique morphological traits in the crania and skeleton (Stringer, 1974; Lahr, 1994; Harvati et al., 2004) and show different patterns of growth and development giving rise to such traits (Ponce de Leon and Zollikofer, 2001). One of the most compelling sources of information comes from the chronology, which shows that humans appear in Africa (160 ka) long before they appear in Europe (~35 ka), and Neandertals independently appear in Europe around 130 ka (disappearing ~30 ka), which makes them contemporaneous with humans, whilst the process of Neandertalization, some have argued, starts in Europe considerably earlier, from ~500 ka (Hublin, 1998; Arsuaga et al., 2000). The common ancestor of Neandertals and humans is thought to have come from an archaic African hominin stock. A group of these archaics made their way to Europe prior to 500 ka, where they gave rise to Neandertals, whilst those remaining in Africa gave rise to *Homo sapiens*.

As for their origins, theories of their disappearance continue to be highly debated, with models of replacement due to competition with technological and cognitive advances of the incoming modern humans, or ecologically derived models based on changing habitats postulating the high adaptability of modern humans at the expense of the less adaptable and unique specializations of Neandertals.

In what kind of environments were they present, and what do we know about diet?

Neandertals are by far the best-studied extinct hominins, with a rich fossil record sampling hundreds of individuals. This record is heavily biased towards the western part of their range, western Europe, with the northern, eastern and southern limits to their distribution poorly documented because of imbalances in research intensity (Dennell and Roebroeks, 2005). The juvenile from Teshik-Tash, Uzbekistan, is the easternmost one known, at roughly 1300 miles from its nearest fossil neighbours, Shanidar in Iraq and 2000 miles from Kiik-Koba in the Black Sea area. The southern limit of their distribution is unknown, and may have extended over the whole of Arabia and the Indian subcontinent – until these regions produce the necessary fossil evidence, we simply cannot be certain.

The question of Neandertal biotopes has been the subject of a great deal of study in recent years (e.g. Gamble, 1987; Roebroeks et al., 1992; Gamble and Roebroeks, 1999; Van Andel and Davies, 2003). From these, we now know that for much of the Neandertal time range, western Eurasia was dominated by a biotope that has become known as the Mammoth steppe (Guthrie, 1990). This was a highly productive habitat which supported a very diverse grazing community with the mammoth as its characteristic species. This Mammoth steppe stretched from Cantabria to Alaska, and it is clear that within this monolithic concept one can uncover a great deal of chronological and spatial variation. Ice core studies suggest that apart from the Holocene, climate instability has dominated the North Atlantic climate over the last 230,000 years, i.e. a major part of the Neandertal period (Dansgaard and Johnson, 1993).

During glacial maxima animal populations contracted into refugia, expanding into previously abandoned territory again during climatic ameliorations. Turq (1999) has suggested that the Aquitaine basin may have functioned as one of the Neandertal refugia in western Europe, predicting that cold periods should see an increase in both the number of sites and very rich assemblages there. While most workers seem to agree on an “ebb-and-flow” model for Neandertal occupation patterns at a regional and a continental scale (Gamble, 1986), the question is where their limits were. Turning their known distribution patterns into inferences on environmental limits has led to considerable debate, for example over their ability to cope with climax-interglacial forested environments (Gamble, 1986, vs. Roebroeks et al., 1992). Current evidence strongly suggests that Neandertals were indeed able to cope with such interglacial environments (Roebroeks and Speleers, 2002). In fact, recent data retrieved from early Middle Pleistocene exposures in East Anglia indicates that this was already the case about 700,000 years ago (Parfitt et al., 2005). In sum, Neandertals were present in a wide range of environments, and only the most extreme phases of the glacial-interglacial cycles seem to have led to range shifts and retreat into refugia, whose locations are not easy to identify (but see: Gamble and Roebroeks, 1999).

The evidence from archaeozoological studies of faunal remains uncovered at Neandertal sites as well as stable isotope studies of their skeletal remains indicate that animal products formed an important part of their diet. Archaeozoological data tell us that they were hunting and which species were at stake (Jaubert et al., 1990; Gaudzinski and Roebroeks, 2000; Stiner, 2002; Binford, this volume), the isotope studies tell us that they were top level carnivores (Richards et al., 2001). In line with the wide variety of habitats documented for Neandertals, prey species varied from reindeer at Salzgitter-Lebenstedt (Germany: Gaudzinski and Roebroeks, 2000) to aurochs at La Borde (France: Jaubert et al., 1990) and forest rhino at the last interglacial site of Taubach (Germany: Bratlund, 1999; see also Binford, this volume). A focus on prime-aged individuals has been documented at various locations, including Salzgitter-Lebenstedt and La Borde. Such a specialization is unknown in other carnivores and has been interpreted as a good sign of niche separation (Stiner, 2002). In the Levant, archaeozoological studies indicate that Neandertal hunting activities may even have led to a decline of red deer and aurochs populations.

Middle Palaeolithic exploitation of small prey has been documented at lower latitudes, largely confined to "gatherable" food items (marine molluscs, tortoises, legless lizards and ostrich eggs, cf. Stiner 2002). The limited evidence for the use of relatively fast-moving small game (such as rabbits or game birds) has been interpreted as indicating lower Neandertal dietary breadth compared with later humans in this region.

An energetics perspective on Neandertal use of space

In his book *The Foraging Spectrum* Robert Kelly (1995) took an ecological perspective on the variation in hunter-gatherer subsistence, mobility, and trade, among other areas of behaviour. This work provides a starting point from which we can explore the implications of a difference in energy requirements for populations occupying similar environments (this is of course a simplifying assumption). Here, we present an example of the application of an energetics perspective to the archaeological record, focusing on the use of space. This is based on a model developed by Verpoorte (2006). First, we will discuss the archaeological evidence for Neandertal use of space, then the case for high Neandertal energy requirements, and finally we will discuss the implications of high energy requirements for spatial behaviour (effective foraging radius, staying time and site structure).

Neandertal use of space

The European Lower and Middle Palaeolithic record contains a large number of open as well as rock-shelter locales with sometimes excellent preservation of the original spatial layout of find scatters. Though some archaeologists have seen the remnants of "hut structures" or "dwellings" in the distribution maps of Lower and Middle Palaeolithic sites, the interpretation of such *structures latentes* is extremely problematic. All claimed traces of Lower and Middle Palaeolithic dwellings have been criticized, and all fail to pass close scrutiny of taphonomic processes (e.g. Terra Amata, Bilzingsleben, Rheindahlen, etc., see Kolen, 1999, for a review). Even the presence of unambiguous wind shields is rare. The same applies to the use of fire. While traces of the former presence of fires are surprisingly rare before the beginning of the Middle Palaeolithic, at about 300,000 years ago, we do know remains of fireplaces from Middle Palaeolithic sites. On open air sites these are usually in the form of some patches of burnt flints and/or burnt bones, occasionally associated with some evidence for burned sediments [for example, the fireplaces at Beauvais in northern France (Locht, 2004)]. Likewise, fireplaces in caves usually consist of little more than a shallow pit with a lens of charcoal and ashes, e.g. the ones excavated at Roc de Marsal, France (Sandgathe et al., 2005), or the sequence documented at Kebara (Bar-Yosef et al., 1992; Speth, 2006).

Neandertals and earlier hominins simply seem not to have made structural investments in the spatial layout of "camp life", even though this does not mean that camp life was not "organized": Speth (2006) has, for instance, convincingly shown that Neandertals used Kebara cave, Israel (Bar-Yosef et al., 1992), over long periods of time in a manner consistent with the way modern hunter-gatherers might use such a cave. Unambiguous remains of dwellings or stone-lined hearths are not a common phenomenon in every Upper Palaeolithic site in Europe, on the contrary, but the complete absence of such features in Middle Palaeolithic contexts is one of the many striking differences between the European Middle and Upper Palaeolithic record, from the Aurignacian onward.

The Neandertal energy budget

A number of recent studies have concluded that Neandertals had a higher basal metabolic rate (BMR) than Anatomically Modern Humans (AMH) due to a higher body mass and different shape (Sorensen and Leonard, 2001; Steegman et al., 2002; Aiello and Wheeler, 2003; Churchill, 2006). According to Churchill (in: Culotta 2005), Neandertal BMR was about 25% greater than that of modern humans. Based on this high BMR, estimates of total energy expenditure (TEE) of Neandertals are proportionally high. Churchill (2006) estimates that it took on average between 3500-5000 kcal per day to feed an adult Neandertal. These estimates are comparable with those from other studies, falling at the lower end of the range of male and the higher end of female values reported by Sorensen and Leonard (2001), and slightly above those of Steegman et al. (2002). This can be compared with mean daily energy expenditure of 3000-4000 kcal per day for males pursuing traditional foraging practices in the circumpolar regions (Steegman et al., 2002).

The figures cited above point to a stark contrast in energy requirements between Neandertals and modern humans, and it is this comparison to *extant* modern humans that is often implicitly used when comparing Neandertals and AMH. Middle Upper Palaeolithic (MUP) humans had a larger body size than modern humans by about 10 kg (Ruff et al., 1997). However, because of their body size and shape, estimated Neandertal energy requirements still exceed those of modern humans by 5-10% (MacDonald, Roebroeks and Verpoorte, in press). Other factors contributing to the energy budget, including the effects of living in cold climates, and species-specific characteristics of locomotion, reproduction and life history mean that this is a very conservative estimate.

Effective foraging radius

According to Kelly (1995: 132-135), the distance from a residential camp at which a forager can procure resources at an energetic gain is limited by the return rates for those resources. This relationship is demonstrated with a simple central place foraging model (Kelly, 1990, 1991). In this simple model, the net return from foraging decreases further from camp as the forager spends more time and energy traveling to and from the foraging area relative to the time spent collecting and processing food resources. The effective foraging radius is largely a product of the return rates of the available resources and the degree of dependence on them. The distance at which a forager brings home at least a day's worth of food at an energetic gain becomes shorter as the return rate decreases (for instance, if resources are over-exploited) or as the individual's workload increases (for instance, if a family member falls ill).

This model can help us to understand the implications of higher energy requirements for the effective foraging radius of Neandertals, as illustrated in Figure 1. We assume that Neandertals and AMH foraged from a central place and that resources were homogenously distributed. Under similar environmental conditions, if a forager requires higher daily energy returns, the distance at which he or she can forage from camp at an energetic gain becomes shorter. Thus, if Neandertals had relatively high energy requirements, we would expect them to have a shorter effective foraging radius, shown by the difference between distances d1 and d2 in Figure 1.

Staying time

Kelly (1995: 132-133) highlights a strong relationship between individual foraging and camp movement. A small difference in the effective radius can have dramatic effects on the foraging area (Kelly 1995: 137). The decision to move camp is likely to be influenced by the conditions around the camp. As the effective foraging radius becomes shorter, the forager will probably move camp after a shorter time (as resources diminish in abundance due to exploitation) and for a shorter distance. The decision to move is likely also to be influenced by expected returns from the area around the new camp and transport costs (Kelly 1995: 136-139). A shorter staying time has knock-on effects for mobility patterns over a longer time span, including frequency of moves and the total distance covered in a year.

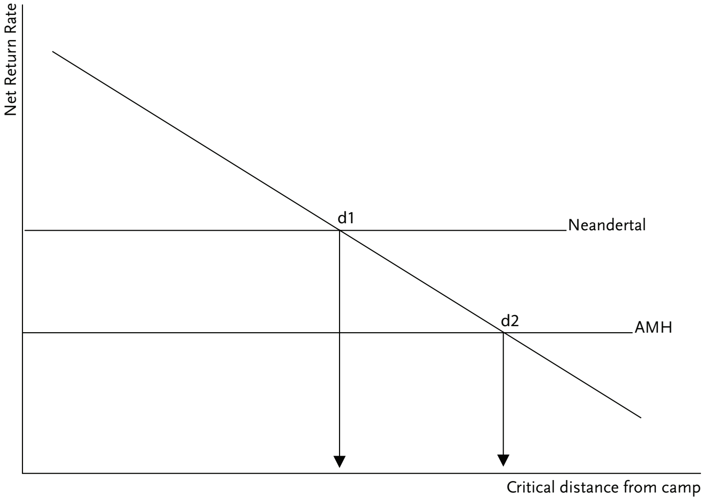

Fig. 1. Consequences of high energy requirements for central-place foraging under similar environmental conditions.

For example, as a thought experiment, we can assume that the effective foraging radius was 3 km for Neandertals and 4 km for modern humans in a similar environment. This 25% difference in foraging radius results in a foraging area 77% larger for modern humans. If we assume that Neandertals stayed in this area for 20 days compared with 35 days for modern humans, this results in Neandertals moving 8 more times per year than modern humans. If both move just far enough to reach a camp in a completely new foraging area, this results in a single movement 2 km further for humans than Neandertals, but also in Neandertals traveling 28 km further in total camp movements in the course of a year (18 x 6 km = 108 km/ year, 10 x 8 km = 80 km/year). However, if we take travel within the foraging radius into account, Neandertals move 2190 km per year, and modern humans move 2920 km per year (365 x 6 km and 365 x 8 km respectively).

The important point as far as Neandertals are concerned is that higher total energy expenditure implies shorter stays and moving camp more frequently, but less total movement over a year. This fits in well with studies suggesting that Neandertals experienced higher locomotion costs than modern humans (Steudel-Numbers and Tilkins, 2004).

Site structure

If the central-place foraging model applies and Neandertals used locations over a shorter time than AMH did, this has implications for investment in site structure or “furniture” (Binford, 1990). A number of authors have suggested that there should be an inverse relationship between staying time and investment in housing (Kent and Vierich, 1989; Binford, 1990; Kent, 1992). Investments in a site (for instance, constructing a shelter, building a hearth structure) have costs in time, energy or materials, and people are more likely to invest heavily in a site if they anticipate staying a longer time. Studies of variation across cultures and also between different settlement types occupied by a particular group of people show that investment in house construction (for instance, use of durable materials and different materials for roof and walls) correlates with length of stay, among other factors (Kent and Vierich, 1989; Binford, 1990; Kent, 1992). Verpoorte (2006) has modelled the costs of investing in site structure in relation to staying time. Many of the costs of investment in a site are highest to start off with. These investments pay back over the use-life of the structure, for instance in providing warmth or shelter. If Neandertals occupied locations for a shorter time than AMH, the payback for investing in a structure would have to outweigh the initial costs over a shorter time period. This implies that we should not necessarily expect Neandertals to have built huts, or in general terms to have invested in site "furniture" in such a way that this left clear archaeological traces. Given the energetic constraints, low investment is better than high investment in locations.

Conclusions

A wide range of disciplines is studying the issues related to the development of the human niche. A series of important hypotheses has been put forward to explain the origins of unusual human features, and the interrelationships between such variables as brain size and diet, longevity and foraging strategy, social organization and the evolution of intelligence. Diet is important in this broad field of research, providing one prospect for an integration of such models with the abundant archaeological and fossil evidence for diet and foraging strategy.

As clearly outlined in Aiello's notes in this volume, energetics has proved an extremely productive line of integrative research into the fossil record. In addition to identifying key questions about the evolution of larger human brains, this approach has highlighted the strong relationship between changes in brain size and changes in diet, and provided a source of deductions about hominin social organization (Aiello, this volume; Leonard et al., this volume; Mussi, this volume). As Aiello concludes, the dietary and energetic implications of the combination of a relatively large brain size and body size can explain some of the physical, life history and social characteristics of humans. It is also clear from these notes that this line of research is connected to models of the evolution of human social intelligence and life history parameters presented by Dunbar and by Kaplan and colleagues in this volume.

We hope that our Neandertal case study shows that an energetics perspective also yields interesting predictions about behaviour that are testable in the archaeological record. In this example, higher total energy expenditure implies shorter stays and moving camp more frequently and less total movement over a year. In addition, it implies lower investment in sites. These predictions accord well with current knowledge of the Neandertal record for the use of space. This is a preliminary attempt, and other aspects of the Neandertal record discussed in this paper or in other papers in this volume could also be addressed in this way. For example, Richards (this volume) provides evidence for a relatively narrow Neandertal dietary niche, and suggests that this had costs in competition with modern humans, raising the question of why Neandertals did not broaden their dietary niche. Possible areas for future research include diet breadth (Kelly 1995, Chapter 3) and lithic technology (Ugan et al., 2003).

Based on several papers in this volume (Aiello, Leonard et al. and Mussi), a number of key biological and behavioural changes shown in the fossil record would have altered the energy budgets of hominin species: these include bipedalism, increasing brain size, increasing body size and the occupation of the middle latitudes. All of these changes in the energy budget would have had implications for behaviour, suggesting numerous applications for an energetics perspective. In addition to explaining differences between the Middle and Upper Palaeolithic record, this approach yields possible explanations for variation within the Middle and Upper Palaeolithic. Not all Upper Palaeolithic humans built archaeologically visible dwellings, on the contrary, and many Upper Palaeolithic groups seem to have neglected aquatic resources (Richards et al., 2001), and in that sense some Upper Palaeolithic humans behaved in many domains in a “Neandertal way”.

In our view, the energetics perspective opens up a major arena of integrative research on the Palaeolithic. An energetics perspective could integrate various approaches covered in this volume including lithic studies, isotope studies, and faunal analyses. It can be applied to hominin social organization as well as subsistence, can explain variation over time and space, and provides explanations of specific archaeological patterns as well as the evolution of aspects of the human niche.

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