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Ecology and Energetics of Encephalization in Hominid Evolution [and Discussion]

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Phil. Trans. R. Soc. Lond. B 1991 **334**, 223-232
doi: 10.1098/rstb.1991.0111

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Ecology and energetics of encephalization in hominid evolution

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SUMMARY

Hominid evolution is marked by very significant increase in relative brain size. Because relative brain size has been linked to energetic requirements it is possible to look at the pattern of encephalization as a factor in the evolution of human foraging and dietary strategies. Major expansion of the brain is associated with *Homo* rather than the Hominidae as a whole, and the energetic costs are likely to have forced a prolongation of growth rates and secondary altriciality. It is calculated here that modern human infants have energetic requirements approximately 9% greater than similar size apes due to their large brains. Consideration of energetic costs of brain allow the prediction of growth rates in hominid taxa and an examination of the implications for life-history strategy and foraging behaviour.

1. INTRODUCTION

Human evolution is characterized by two main systematic changes: the adoption of upright, bipedal locomotion and the enlargement and elaboration of the brain. Whereas the first of these has long been thought of as directly related to foraging behaviour, brain expansion has largely been treated outside an ecological framework. The flexible and sophisticated cognition and behaviour resulting from a large brain have been sufficient for explaining the marked rate of increase since the appearance of the hominid clade. From an ecological perspective, however, it is perhaps more interesting to ask what the costs of encephalization are and how they can be afforded. This question is prompted by the simple observation that given the obvious advantages of high encephalization, its occurrence in the living world is relatively rare (Parker 1990). In considering, for example, the development of human foraging strategies, increased returns for foraging effort and food processing may be an important pre-requisite for encephalization, and in turn a large brain is necessary to organize human foraging behaviour.

Two reasons may be put forward to justify the view that the costs of brain growth and maintenance are essential to understanding the conditions under which encephalization may occur. The first derives from allometric studies. Martin (1981, 1983) has shown that mammalian brain size scales allometrically with body size, and that the relation can be described by the regression equation:

$$E = 1.77W^{0.76},$$

where E = brain mass in grams and W = body mass in grams. Several phylogenetically specific equations have also been derived, especially for primates (Martin 1989), and are used where appropriate.

Allometric studies allow brain size to be studied comparatively across species independent of body size (Jerison 1973; Martin 1981, 1983). Encephalization quotients (EQ) represent the positive or negative residual value of brain mass, calculated by:

$$EQ = BM^{o}/BM^{e},$$

where BM^{o} = actual brain mass and BM^{e} = predicted brain mass for body size.

The coefficient of the allometric equation is close to 0.75, similar to the relationship between body size and basal metabolic rate (BMR) (Kleiber 1961). This implies that brain size and BMR are isometrically related, from which the further inference may be drawn that the size of an individual's brain is closely linked to the amount of energy available to sustain it (Milton 1988; Parker 1990). This suggests that whatever selective pressures there may be driving the size of the brain up, these are satisfied only in the context of there being sufficient energy.

The second point proposed by Martin is that the costs of brain growth are borne by the mother. Most brain growth occurs *in utero* and during the post-natal period before weaning (Martin 1983). Brains are metabolically expensive tissue (Passmore & Durnin 1955), and any increase in the size of the brain will act as a considerable drain on maternal energetics. Sustaining high levels of encephalization must therefore be compatible with female, particularly maternal, energetics which acts as a necessary condition for brain enlargement.

The task of this paper, therefore, is to consider the energetic and foraging implications of encephalization in hominid evolution. In particular we shall attempt to quantify the additional energetic costs of larger brains than those of other primate species and to specify where in the course of hominid evolution these may have become significant and therefore required

Phil. Trans. R. Soc. Lond. B (1991) **334**, 223–232
Printed in Great Britain

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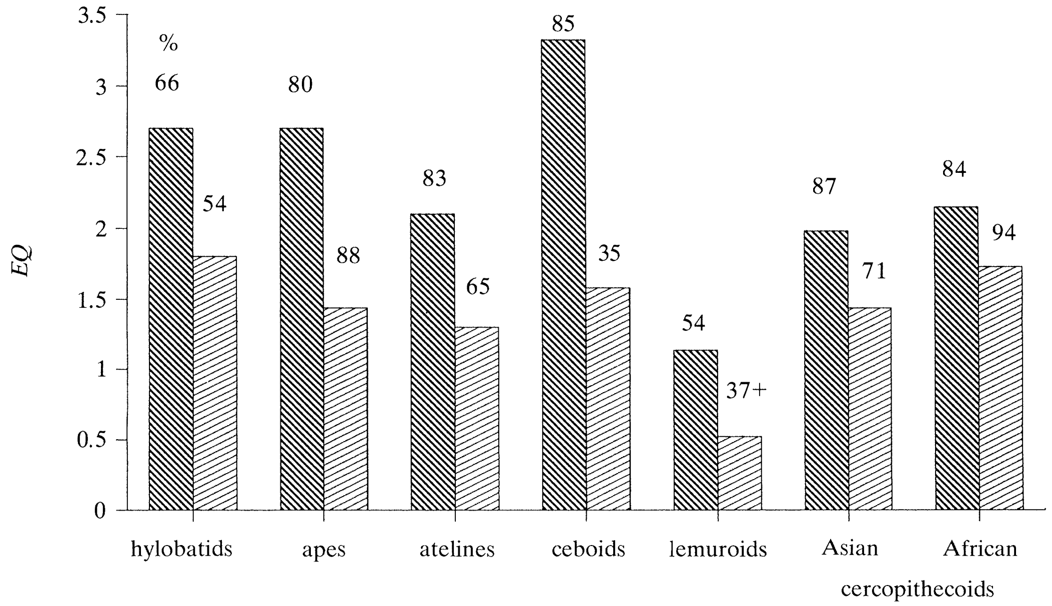

Figure 1. Pairwise comparison of phylogenetically comparable species of primate with the most extreme preference for high-quality (dark-shaded bars) and low-quality (light-shaded bars) foods. Species: Hylobatids: *Hylobates lar* (HQ), *H. symphalangus* (LQ) (Davies *et al.* 1984); African apes: *Pan troglodytes* (HQ), *Gorilla gorilla* (LQ) (Wrangham 1986, Smuts *et al.* 1987); Atelines; *Alouatta palliata* (HQ), *Ateles paniscus* (LQ) (Smuts *et al.* 1987); Cebids: *Cebus capucinus* (HQ), *Callicebus moloch* (LQ) (Smuts *et al.* 1987); Lemuroids: *Lemur catta* (HQ), *Indri indri* (LQ) (Richard 1985); Asian cercopithecoids: *Macaca nemistrina* (HQ), *Presbytis johnii* (LQ) (Davies *et al.* 1984); African cercopithecoids: *Cercocebus albigena* (HQ), *Colobus badius* (LQ) (Smuts *et al.* 1987). HQ = high-quality feeder, LQ = low-quality feeder.

changes in foraging behaviour. To this end we will first examine the relation between primate foraging behaviour and encephalization.

As a caveat it should be stated that the question of the ultimate causation of encephalization is not considered here. It has been argued that the selective advantages of large brains derive from both social (Jolly 1966; Humphrey 1976; Byrne & Whiten 1988) and ecological pressures (Parker & Gibson 1979; Clutton-Brock & Harvey 1980; Gibson 1986). Here we suggest that whatever the cause of encephalization may be, it is predicated upon energetic and hence ecological conditions (Martin 1983; Milton 1988; Foley 1990). If this is the case then social and ecological factors are likely to be closely related, as indeed may be indicated by the increasing evidence for a strong relation between social and reproductive strategies and ecological conditions (Standen & Foley 1989).

2. BRAIN SIZE AND PRIMATE FEEDING BEHAVIOUR

Two major aspects of brain size and complexity have been related to foraging behaviour among the non-human primates. The first of these is the statistical observation that folivores tend to have smaller brains for their body masses than do frugivores (Clutton-Brock & Harvey 1980). The second is that a diet of 'embedded foods' – foods that are neither visually obvious nor available without considerable time and energy costs associated with processing, and hence extracted from a secondary source – require complex cognitive skills (Gibson 1986). The relatively small brains of folivores are therefore thought to derive from the ubiquitous distribution of leaf foods and their relative ease in extraction from the canopy. A further factor that is significant from the point of view of encephalization is that leaves constitute a relatively low level of nutritional quality. Leaf foods generally provide less energy than fruits as much of the potential carbohydrate energy is bound up in structural cellulose (Hladik 1978; Milton 1984). Furthermore such foods are often defended with secondary compounds, which are either toxic or digestion inhibitors (Waterman 1984). A leaf diet among the non-human primates requires the ability to digest cellulose and hemicellulose through microbial fermentation as in the colobines, or bulk feeding as in the gorillas and gelada. Ingestion of toxic or low quality foliage correlates with low basal metabolic rates for body size in many arboreal folivores (McNab 1978) and in strepsirhine primates (Rasmussen & Izard 1988). Taken together, leaf foods require less cognitive skills to procure and ingest, more digestion time within the daily activity cycle, and additional costs in terms of time and energy for their detoxification.

Fruit eating poses different problems. In general fruits supply relatively easily digested energy as well as protein and fatty acids. The location of ripe fruits, enhanced by potential colour differences with background vegetation may not be difficult, but does require spatial and temporal memory of fruit tree locations and renewal rates (Waser & Homewood 1979) when they are widely and patchily distributed. Many 'fruits' are consumed as seeds, which require extraction from tough casings (Gibson 1986). These are linked to perceptual abilities (the recognition that the edible component is within an inedible substrate) and the manual dexterity and coordination to remove

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such foods. Among most frugivorous primates, fruits are often consumed in combination with other energy- or protein-rich foods such as invertebrates, honey, tree exudates and vertebrates. All these types of food require extractive or capture skills while producing more consumable energy than do leaves. Although the detoxification of unripe fruits can also be a problem (Waterman 1984), frugivores appear to obtain a greater energy intake per gram consumed, even with the increased costs of location and extraction. More complex brain coordination and integration, and memory skills are associated with fruit diets and large brain for body masses.

Treated comparatively the data on quality of diet and primate brain size per unit of body mass shows a positive correlation (Clutton-Brock & Harvey 1980; Gibson 1986; Milton 1988), but there is considerable variance for at least two reasons. The first is that there are major phylogenetic differences in encephalization quotient among the primate grades (Martin 1989), the second is that whereas species of primate with low quality diets seldom have high *EQ*s, there is no certainty that those with high quality diets will have high *EQ*s as their additional energy may be put to other uses.

The relation between foraging behaviour and *EQ* can best be examined in a sample of primates where there is clear dietary preference for either high or low quality foods. A phylogenetically based pairwise examination of the most extreme folivores and frugivores in each of a number of primate clades (figure 1) shows that the folivore in each case has a substantially lower *EQ*. This is supported statistically. When phylogeny at the family and superfamily level is held constant, a regression of *EQ* on percentage of feeding time on leaves, fruits and animals yields a high level of association ($r^2 = 0.74$, $p < 0.01$ for a negative relationship between folivory and *EQ*; $r^2 = 0.686$, $p < 0.05$ for a positive relationship between frugivory and *EQ*; and $r^2 = 0.709$ $p < 0.02$ for a positive relationship between faunivory and *EQ*; $n = 15$ in all cases). Although high *EQ*s are not invariably associated with high quality diets, low quality diets do not appear to permit or be associated with high *EQ*s. Fruit and animal diets appear to be able to fuel larger primate brains, whereas the low energy and high toxicity of folivorous diets may constrain the available energy and basal metabolic rates.

3. PATTERN OF BRAIN SIZE EVOLUTION IN HOMINIDS

The pattern of brain size increase in hominid evolution has been well established from the cranial and endocranial fossil evidence. Fossil hominid cranial capacity varies from 410 cm^3 (KNM-WT17000 (Walker *et al.* 1986)) to 1750 cm^3 in the Amud 1 Neanderthal (Ogawa *et al.* 1970). The earliest taxon, *Australopithecus afarensis*, at approximately 3.0 Ma has a cranial capacity of 450 cm^3, whereas modern humans, with an origin at about 0.1 Ma have an average of approximately 1350 cm^3. This represents a threefold increase in absolute brain volume, or an increase of about 1 cm^3 per 150–200 generations. The rate of increase is however not constant, with the most rapid rise occurring in the last 1.0 Ma.

EQ for fossil hominids can be calculated where body mass can be estimated from post-cranial dimensions (McHenry 1988; Aiello & Dean 1990). Figure 2 shows the relationship between hominid *EQ* and time. From these data it can be seen that encephalization is primarily a characteristic of the genus *Homo* rather than of the hominids as a whole, and that again the increase occurs relatively late. In particular it should be noted that the *EQ* of the earliest hominids is not significantly greater than the upper range observable in living hominoid apes.

From the ecological perspective paramount here, it may be asked whether there is any link between the increase in encephalization and energetic or foraging parameters, supporting the hypothesis that increases in brain size are constrained by ecological factors. At a speculative level it may be noted that evidence for a significant level of both tool use and meat eating is broadly equated with the date of first appearance of the genus *Homo* (Foley 1987*a*, *b*). Although such an interpretation is contested (Binford 1984), it may be argued that tool use increases extractive efficiency or widens the range of resources available (Torrence 1983, Gibson 1986) and that meat represents a high quality resource, both of which would constitute increases in the net rate of energetic returns necessary for further encephalization.

A more specific expectation, given the proposed relationship between encephalization and maternal energetics, is that increasing brain size should be reflected in growth patterns (Shea 1987). It has long been noted (Schultz 1969) that modern humans are characterized by (secondarily) altricial young and delayed maturation in comparison with other primates. Although the contrast between humans and chimpanzees in life-history patterns may not be as marked as has previously been supposed (Lee 1989), the difference is still significant, especially in terms of cognitive development (see Parker 1990). It may be asked whether this difference is related to brain size. Recent work on dental development patterns (Bromage & Dean 1985; Beynon & Wood 1988; Beynon & Dean 1988) has shown that all hominids display the extended maturation pattern of modern humans. Early

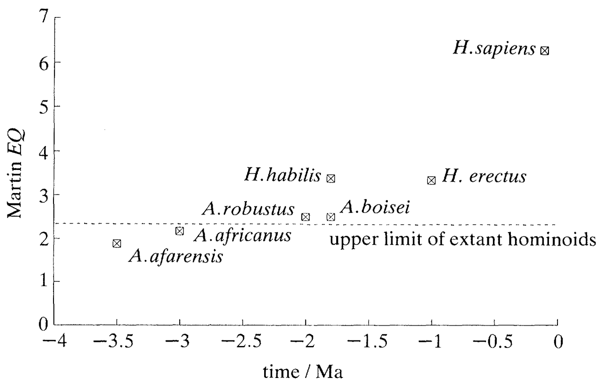

Figure 2. Relation between *EQ* in fossil hominid taxa and time. Data from Aiello & Dean (1990).

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Table 1. *Energetic costs of brain maintenance in humans and chimpanzees for the first five years of life*

	human			chimpanzee		
		average daily energy requirements	cumulative energy requirements		average daily energy requirements	cumulative energy requirements
age/ years	brain size	kJ	kJ × 10^6	brain size	kJ	kJ × 10^6
0	345	364	0.133	172	182	0.066
1	765	807	0.427	277	292	0.173
2	959	1012	0.797	333	351	0.301
3	1058	1116	1.204	362	382	0.441
4	1142	1205	1.644	366	386	0.581
5	1206	1273	2.108	366	386	0.723

(greater than 1.5 Ma) African hominids were dentally more advanced for a given chronological age, based on enamel incremental patterns, than modern humans. Even neanderthals may have matured marginally faster than modern humans (Stringer *et al.* 1990). The pattern of encephalization tracks the slowing down of growth rates in hominids, which in turn indicates changes in female energetics and by implication maternal strategies (Foley 1991).

4. ENERGETIC COSTS OF THE HUMAN BRAIN

Preliminary consideration of the palaeontological evidence for brain enlargement and growth patterns in hominid evolution seems to provide some support for the proposal that the costs of large brains may have been a significant factor in the timing and pattern of encephalization. Before examining in more detail the actual growth patterns of the fossil hominids it is necessary to look at the costs of brain maintenance to determine whether these costs are energetically significant. One reason for doing this is that the data presented so far are equally compatible with an obstetric hypothesis: that is, that because of pelvic constraints on neonate brain size hominids were forced into a more altricial strategy as the adult brain size increased. Although such a hypothesis would not explain why there should be such a prolonged period of post natal growth, it would at least explain why the initial neonate state should be relatively small.

The energetic costs of brain maintenance have been assessed by Passmore & Durnin (1955) as 3.5 ml O_2 per 100 g per minute or 0.07329 kJ per 100 g per minute. This accounts for 20 % of human basal oxygen uptake and energy expenditure. Growth costs are additional to this. These basic estimates can be used to calculate the relative costs of brain maintenance of chimpanzees, used here as a baseline for hominid evolution, and modern humans for the first five years of life.

Chimpanzees and modern humans have different brain growth patterns. Chimpanzees are born with a neonate brain mass that is 47 % of adult brain mass, and adult size is reached by 4 years of age. In contrast modern humans have neonate brain masses that are 25 % of adult mass and by 4 years have reached only 84.1 % (Passingham 1982). Table 1 shows the average daily costs involved in brain maintenance for chimpanzees and humans for the first five years of life. Even in its more atricial state, the cost of the human neonate brain exceeds that of the more precocial chimpanzee, and by the age of five years the costs are three times as great: 1273 kJ day^{-1} compared with 386 kJ day^{-1}. When considered cumulatively it can be seen that the chimpanzee brain will have required 0.723 million kJ, at an average of 350 kJ per day, compared with 2.108 million kJ, at an average of about 1000 kJ per day. Overall the energetic costs of brain maintenance for modern humans are about three times those of a chimpanzee. Growth costs will also be commensurately larger. It should be pointed out that both chimpanzee and some human mothers can lactate for five years, and therefore these costs can be partially borne by the mother. The partitioning of energy between that derived from milk or solid foods during the first five years of brain development is of concern primarily in its effect on future maternal reproduction. From a trophic point of view, the overall costs to the mother are greatest during lactation and less during gestation and after the infant begins to feed independently.

Expansion of the brain incurs considerably higher energetic costs whether or not these costs are spread over a longer period of time, with implications for foraging behaviour. To put this into the context of the overall energetic needs of the infants, Ulijaszek & Strickland (1991) have presented data showing that among Gambian infants the average energy requirement in the first eighteen months of life is 2556 kJ per day. Using the estimates of brain maintenance costs provided above it can be deduced that of this total figure 495 kJ per day are required for the brain. Were those infants to have chimpanzee-sized brains we can calculate their reduced energy requirements. The average daily energy requirements of the chimpanzee brain during the first eighteen months of life are 273 kJ. With this size brain, average daily requirements would be:

2556 (total human costs) − 495 (human brain costs) + 273 (chimp brain costs) = 2334 kJ.

This reduction of 223 kJ per day implies that human

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Table 2. *Estimates of energy costs of brain maintenance for hominid taxa at different growth rates*

(BM = adult brain mass estimated from fossil specimens (Aiello & Dean 1990; calculated from cranial capacity ($BM = 1.06CC^{0.98}$ (Martin 1989))). The brain mass of the hominids from neonate to age 5 calculated as a percentage of adult brain mass assuming (*a*) chimpanzee growth rates; (*b*) chimpanzee growth rate + 25 % shift to human growth rates; (*c*) chimpanzee growth rate + 50 % shift to human growth rates; and (*d*) chimpanzee growth rate + 75 % shift to human growth rates. Energy costs calculated at 105 kJ per 100 g of brain mass per day (Passmore & Durnin 1955). Figures in bold indicate costs exceeding modern humans at the same age; asterisks indicate costs less than chimpanzees at the same age. At human growth rates all figures for fossil hominids are less than or equal to those of modern humans.)

		age/years					
taxon	*BM*	0	1	2	3	4	5
(*a*)							
A. afarensis	422	208	337	403	439	443	443
A. africanus	454	224	363	434	472	477	477
A. boisei	513	237	383	459	499	504	504
H. habilis (ER 1813)	627	**309**	500	599	952	659	659
H. rudolfensis (ER 1470)	698	**345**	557	667	726	733	733
H. ergaster (ER 3733)	728	**389**	629	753	819	828	828
H. erectus (Sangiran)	857	**423**	**684**	818	891	900	900
H. erectus (Solo)	1057	**522**	**843**	**1010**	**1099**	**1110**	**1110**
H. sapiens (Archaic)	1397	**632**	**1022**	**1223**	**1330**	**1345**	**1345**
Modern humans	1350	290	650	823	905	974	1032
(*b*)							
A. afarensis	422	186	315	381	417	426	430
A. africanus	454	200	339	410	448	458	463
A. boisei	513	212	358	433	474	484	489
H. habilis (ER 1813)	627	277	468	566	619	632	639
H. rudolfensis (ER 1470)	698	308	520	630	689	704	711
H. ergaster (ER 3733)	728	**348**	588	712	778	795	803
H. erectus (Sangiran)	857	**378**	639	774	846	864	873
H. erectus (Solo)	1057	**466**	**788**	**954**	**1043**	**1065**	**1076**
H. sapiens (Archaic)	1397	**565**	**955**	**1157**	**1264**	**1291**	**1304**
Modern humans	1400	290	650	823	905	974	1032
(*c*)							
A. afarensis	422	160*	292	359	390	407	417
A. africanus	454	172*	315	386	419	439	448
A. boisei	513	181	333	408	443	464	474
H. habilis (ER 1813)	627	237	435	533	580	606	619
H. rudolfensis (ER 1470)	698	264	484	594	645	674	689
H. ergaster (ER 3733)	728	**298**	546	670	728	761	778
H. erectus (Sangiran)	857	**324**	594	729	792	828	846
H. erectus (Solo)	1057	**400**	**732**	**977**	**977**	**1021**	**1043**
H. sapiens (Archaic)	1397	**484**	**888**	**1090**	**1184**	**1238**	**1264**
Modern humans	1400	290	650	823	905	974	1032
(*d*)							
A. afarensis	422	137*	275*	337	368	390	408
A. africanus	454	148*	296	363	396	420	439
A. boisei	513	156*	312	383	418	443	464
H. habilis (ER 1813)	627	204	408	500	547	579	606
H. rudolfensis (ER 1470)	698	227	454	557	608	645	674
H. ergaster (ER 3733)	728	257	513	629	687	728	761
H. erectus (Sangiran)	857	279	558	684	747	792	828
H. erectus (Solo)	1057	**344**	**688**	**843**	**921**	**977**	1021
H. sapiens (Archaic)	962	**417**	**834**	**1022**	**1116**	**1184**	**1237**
Modern humans	1350	290	650	823	905	974	1032

infants up to the age of 18 months are approximately 8.7 % more energetically costly than chimpanzees due to their high level of encephalization. The foraging implications are that in some way human mothers (or other helpers) must increase the infant's level of nutritional intake compared to the hominoid baseline used here.

Despite the relative crudity of these estimates they demonstrate the basic proposal that encephalization is predicated upon energetic conditions, and therefore

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that we should expect a close link between expansion of the brain and changes in foraging behaviour and other measures of parental effort, regardless of the precise selective pressures leading to encephalization. As will be discussed below, the energetics of encephalization are a significant factor in human foraging and dietary strategies.

5. ENCEPHALIZATION AND DELAYED MATURATION

It is beyond the scope of this paper to explore the precise foraging behaviour of the early hominids in the context of encephalization. However, because the various hominid taxa of the Pliocene and Pleistocene are characterized by different sized brains it is pertinent to ask where along the continuum from ape sized to human sized brains the costs are likely to become significant. As this is closely tied to the problem of delayed maturation and the switch from an ape to a human pattern of growth (see Shea 1987), this can be best achieved by looking at various growth trajectories for the fossil hominids and the energetic costs that these incur.

The principal question addressed here is whether the increasing energetic costs associated with the expansion of the brain may have pushed hominid growth patterns in the direction of delayed maturation and more altricial neonates, and if so, when is this likely to have occurred? An initial assumption consistent with basic evolutionary principles would be that it is advantageous to the mother to minimize birth interval to maximize lifetime reproductive success. If this holds, then mothers would benefit from rapidly growing young. The fact that hominids have evolved in the opposite direction – towards longer birth intervals and longer periods of infant dependence – suggests that females have been constrained from higher reproductive rates. The hypothesis here is that the energetic requirements of the brain are imposing this constraint. The problem, then, is to quantify these constraints to assess where in hominid evolution secondary altriciality may have evolved.

The simple assumption employed in the analyses set out below is that the absolute brain costs of the human growth curve represent a ceiling for hominids. Table 2 shows the energy requirements for brain maintenance of various hominid taxa during the first five years of life. The energy costs are calculated from the adult brain mass assuming various growth rates. The first set of assumptions is that growth is similar to that of chimpanzees (i.e. 47 % neonate brain mass, 75.7 % at year 1, and so on). As can be seen, the energy requirements for all species lie below those of the modern human, and for the neonate, even the largest brained australopithecine – *A. boisei* – has costs that are only 65 % of that of modern humans. Although these costs are greater than those of chimpanzees, it may be argued that there is little by way of selective pressures for the evolution of altriciality in this genus. It may perhaps be inferred that at this stage of hominid evolution there had been no significant shift in growth patterns; an inference broadly consistent with other lines of evidence (Bromage & Dean 1985; Bromage 1987). For the genus *Homo*, on the other hand, costs begin to exceed those of modern humans. The neonate requirements of all species are greater than those of modern humans with their slower rates of growth, and for later hominids this effect spreads through to the older age groups. It thus may be argued that with the larger brains associated with the genus *Homo* – that is above 600 cm^3 – some shift towards altriciality should occur if energy is a significant constraint.

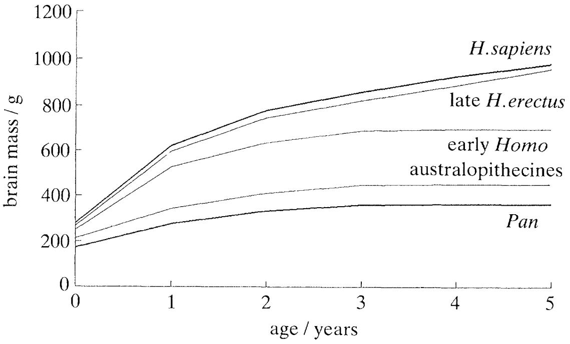

Figure 3. Predicted pattern of brain growth for fossil hominids compared with chimpanzees and modern humans. See text for discussion of methods.

This approach can be extended to model the effects on energy requirements of changing growth rates. For example, Table 2*b* shows the energy requirements for brain maintenance if growth rates are shifted 25 % of the way from chimpanzee to modern human patterns. As can be seen, as the growth rates become more retarded the brain costs of various hominid taxa drop below that of modern humans. Table 2*c*, *d* shows the effects of further shifts – 50 % and 75 % – towards modern humans.

From these simulations it is possible to construct some expectations for the growth patterns of specific hominid taxa. First, it can be argued that none of the non-*Homo* species would have departed significantly from the ancestral ape pattern in their growth rates. Second, the shift from an ape to a human growth pattern would have occurred initially in the earliest phase of infancy, with only a gradual effect on later phases. In other words, hominid growth shifted first among neonates and then successively through the later phases of infancy. Third, the appearance of genus *Homo* is likely to coincide with the first shift in growth rates towards a human pattern. And fourth, the fully modern human growth patterns are likely to have become established during the course of *Homo erectus*. The predicted growth curves of the hominid taxa are shown in figure 3, based on an assumption of minimum change from chimpanzees compatible with an energetic cost below that sustained by modern humans.

Putting these models into a more specific historical context, it can be argued that the critical threshold for a change in neonate brain size from the ape baseline is 590 g adult brain mass; for a change in first year growth rate the threshold is 820 g adult brain mass; and for years 2, 3, 4 and 5 it is 860, 870, 980 and 980 g respectively. In evolutionary terms these values co-

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incide with *H. habilis* for the neonate, and various temporal successive stages of *H. erectus* (*sensu lato*) for the later ages. By the time of *H. sapiens sensu lato* it would be expected that fully modern growth rates would occur. This is consistent with growth patterns inferred from dental development in neanderthals (Stringer *et al.* 1990; Trinkaus & Tompkins 1990).

6. HOMINID FORAGING AND LIFE-HISTORY STRATEGIES IN THE CONTEXT OF ENCEPHALIZATION

The conclusion to be drawn from the analyses and data presented above is that there is an ecological dimension to encephalization. The precise implications for hominid foraging behaviour should therefore be considered.

(*a*) *Timing of dietary shifts*

A number of foraging and dietary changes have been proposed for hominids during the course of their evolution: meat eating, increased extractive efficiency through technology, use of underground resources, food sharing, central place foraging. If the higher costs of encephalization are the primary causes of these shifts then there is no reason to expect these to occur before the appearance and evolution of the genus *Homo*. Andrews & Martin (this symposium) have shown that there is very little evidence for major changes in diet among the hominoids before 2.0 Ma. The appearance of stone tools, evidence for large mammal bone processing (Blumenschine, this symposium), and the change in hominid dentition around this date, coincident with the origins of genus *Homo*, may indicate that encephalization is closely related to changes in ecology.

(*b*) *Additional energetic requirements*

The central point here is that having a large brain imposes additional energetic costs on both the infant and the mother. As discussed above, brain costs are only a proportion of overall energy requirements, but using the same methodology we can suggest the extent to which various hominid taxa will have required greater energy inputs for offspring. Figure 4 shows the percentage of additional energy requirements above those of a chimpanzee, by using modern human infant energetics data (Ulijaszek & Strickland 1991) less the brain costs, plus the estimated brain costs for a series of modelled levels of encephalization. Again it can be seen that australopithecines (basal hominids) have costs only about 1% higher than chimpanzees, but that for *Homo* the additional costs vary from 5 to 17%, depending upon brain size and age. It could be argued that these models indicate the extent to which different hominids require different levels of energy intake.

(*c*) *Meat eating*

These estimates suggest that for all *Homo* species there is a significant additional energetic requirement, but perhaps the most interesting point is that they are not higher. The recent debate over the importance of meat-eating in human evolution has focussed closely on the problem of the means of acquirement (see Blumenschine, this symposium), but rather less on the quantities involved. The implications of the data presented here is that a small increase in the level of energy and protein available through meat eating may have major consequences for the nutritional status of the populations concerned. Given that other plant foods, especially underground resources, may also be incorporated into the diet, then a small increase in the amount of scavenging and hunting over the levels observed in chimpanzees may be sufficient. In considering the evolution of human carnivory it may be that a level of 10–20% of nutritional intake may be sufficient to have major evolutionary consequences, and that the conditions under which protein starvation (Speth, this symposium) may result will seldom occur.

(*d*) *Costs and benefits of resource exploitation*

Hawkes (this symposium) has argued that selection of resources is not merely a function of availability and nutritional quality, but of these in relation to the costs of exploitation and processing. Meat eating, it may be argued, represents an expansion of resource breadth beyond that found in non-human primates. What may be equally significant is that hominids, through technology or some other aspect of their behaviour such as cooperative foraging, may have increased returns in foraging by reducing costs. This may also be the case with bipedalism (Foley 1991). In other words, some early hominids had greater amounts of energy available to them because they were able to exploit resources more efficiently and at lower energetic costs. This in turn provided the energetic basis for high rates of encephalization.

(*e*) *Palaeoecology*

Hominids at the time of the appearance of *Homo* were occupying the savanna environments that had expanded in the late Tertiary (Foley 1987*a*). Although these to some extent are resource depleted compared to tropical forests for a frugivore, and are highly seasonal, they do offer a different resource structure in terms of patch distribution and the abundance of large mammals that may have provided the preconditions for a change in foraging behaviour that enhanced the availability of high quality foods at critical times of the year. *Homo*, with its associated encephalization, may have been the product of the selection for individuals capable of exploiting these energy- and protein-rich resources as the habitats themselves expanded (Foley 1987*a*).

(*f*) *Maternal strategies*

Mothers from a variety of primate (and other mammalian species) have a goal of weaning infants at an optimal mass, ensuring those infants' survival, and themselves producing again (Lee *et al.* 1991). What is variable between the species are the ecological constraints on what the rate of growth to weaning can be.

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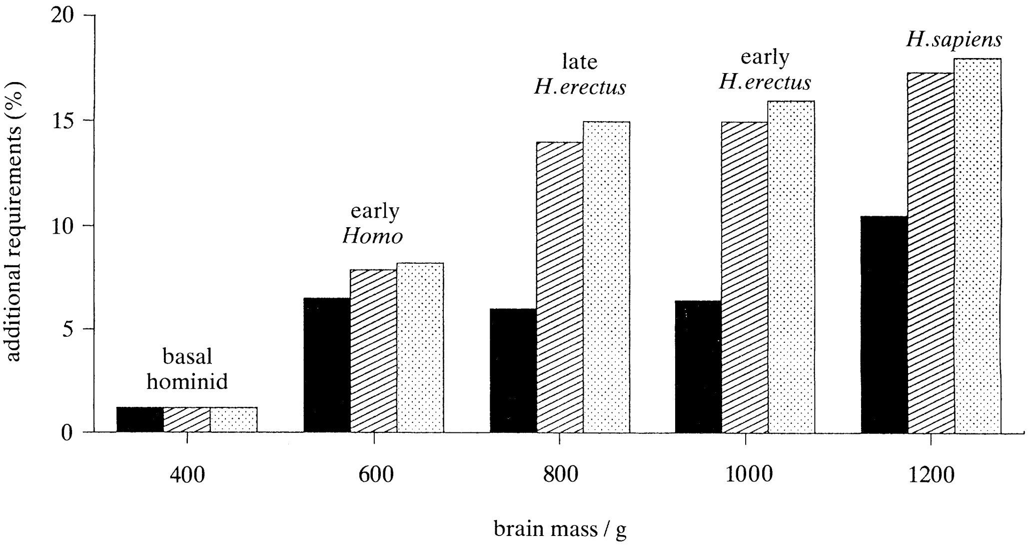

Figure 4. Estimates of the percentage increase in energy requirements of different brain sizes above those of chimpanzees for hominid infants from birth to 18 months. See text for method. Solid bars, neonate; dashed bars, 12 months; stippled bars, 18 months.

The energy available to the mother for offspring growth can either derive from the incorporation of higher quality food, from feeding for longer each day, or from maintaining lactation over a longer period. The strategy pursued by the mother results from the constraints on energy available through the diet, the time and energy costs of processing that diet, and the time budget limitations on the mother.

Among the hominoids, the relatively higher costs of growth imposed by the larger brain is met partially by the incorporation of higher energy foods (e.g. termites among female chimpanzees (McGrew 1979)). If food energy is not sufficient to maintain a 'typical' growth rate, then lactation is extended, with consequences for correlated life-history parameters (Lee *et al.* 1991). Even with the incorporation of high quality energy from animal foods, the opportunity and foraging costs associated with animal foods might have limited the mother's ability to sustain high growth rates, leading to selection for an energetically less demanding strategy of increase the duration of growth.

The observation of slower rates of development and an extended period of immaturity among *Homo* suggests that mothers were indeed under energetic and time-budget constraints which could not be compensated for entirely by a shift to a higher quality diet. It also suggests that alternatives such as male provisioning or utilizing female kin caretakers to lessen the mother's energetic burden were unlikely to play a major role in maintaining high growth rates and rapid development, at least in the earlier *Homo*. As a result there was selection for a shift in life-history parameters towards slower development.

7. CONCLUSIONS

Whereas bipedalism has generally been considered in ecological terms, encephalization in hominid evolution has not received the same treatment (Milton 1988). The link between relative brain size and metabolic rate (Martin 1981, 1983; Parker 1990) has provided the theoretical basis for examining how the evolution of larger brain size relates to changes in foraging and dietary behaviour, as well as to changes in life-history parameters. It has been argued here that the increased energy requirements associated with larger-brained offspring imposed additional costs. Simulation of these costs indicates that mothers would have been required to raise the level of energetic maternal effort by between 1 and 17% during the course of hominid evolution. One means of achieving this would be through slower growth rates, which in turn would have constrained the lifetime reproductive success of female hominids. This change in life-history strategy appears to be associated specifically with the genus *Homo*. It is probable that the evolution of larger brains within the genus requires both increased foraging efficiency and the incorporation of higher quality foods in substantial quantities in the diet, in combination with the life-history changes. The conclusion to be drawn is that encephalization among hominids, or indeed among other mammalian lineages, is dependent upon ecological conditions.

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Discussion

E. M. Widdowson (*9 Boot Lane, Barrington, Cambridge, U.K.*). Dr Foley has discussed only the brain as a whole. If he is interested in intelligence it seems as though it should be the forebrain he should be considering. Has he any information about the forebrain of gorillas and chimpanzees compared with that of man?

R. A. Foley. It is certainly the case that certain parts of the forebrain in humans have expanded at a greater rate than the other parts. This is especially true of the neocortex, although it should be noted that the cerebellum has also increased at a higher rate. The neocortex is 3.2 times larger than predicted from non-human primates based on body size alone (Passingham 1982). However, it appears that this allometric pattern of brain part increase is general to the primates and mammals as a whole. In other words, a plot of neocortex volume against brain volume yields a very strong log-linear relationship, showing that species with large brains have larger neocortex. Modern humans fall on the predicted line for size of neocortex for their overall brain volume. This suggests that total brain size is a useful indicator of other neocortex size.

E. M. Widdowson. Does a change to bipedalism involve an increase in the calcium requirement for the longer and wider bones?

R. A. Foley. It is difficult to answer the question about calcium requirements on a *pro rata* basis, but assuming that chimpanzee and gorilla bones require the same levels of calcium as humans, we can ask whether humans have more skeletal mass per unit body mass.

There is an allometric relationship between body mass and skeletal mass (Prange *et al.* 1979), although this has not been calculated in detail for primates. However, the principal parts of the skeleton represent 79% of body mass in chimpanzees, 65% in humans and 51% in gorillas (Steudel 1980). Given this scaling with body mass, there is little reason to expect higher requirements associated with bipedalism.

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C. D. Knight (*Polytechnic of East London, U.K.*) Dr Foley stressed the high energetic costs of large brain size, and the extent to which these costs would have posed problems for mothers having to feed and care for large-brained offspring. He then went on to picture bipedalism as the factor that enabled evolving females to cope with these burdens. How closely is he linking encephalization with what seems to be the much earlier emergence of bipedalism? Dr Foley will be aware that there are other models that make no such connection, linking encephalization instead with the success of females in increasingly harnessing the provisioning energies of males; features such as ovulation-concealment and continuous receptivity being interpreted as functional in this context. How far would he go in arguing that the bipedal female solved her own problems without need for a change in mating strategies?

R. A. Foley. The improvement in the fossil record in recent years has shown us that, chronologically, bipedalism and encephalization are disjoint. It may well be that bipedalism is a necessary (but not sufficient) precondition for major encephalization. The simple point can be made that bipedalism is in some circumstances an energetically efficient adaptation, and therefore this might counterbalance some of the additional requirements of encephalization (Foley 1991). Dr Knight is right to point out that female strategies may evolve independently. What we are less certain about is whether major changes in the parenting behaviour could occur without some shift in the mating strategy, as by and large these two aspects are closely linked.

J. H. P. Jonxis (*Rijksstraatweg 65, 9752 AC Haren, The Netherlands*). In the first months after birth the energy metabolism of the brain is far higher than in a somewhat older baby. In those first months the brain covers about half of the total heat production.

R. A. Foley. This is an illuminating comment and underpins the argument we have put forward that brains impose high costs which will be increased if encephalization occurs.