Evolution of the Human Profile of Fatness

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INTRODUCTION

The tendency to human obesity is the combined effect of relatively high fatness and the ready capacity to store energy to increase fat stores. These characteristics are often attributed to the selective pressure exerted by cycles of "feast and famine" in our past (Hoyenga and Hoyenga, 1982; Prentice et al., 1992; Chakravarthy and Booth, 2004). Such cycles are not described in greater detail, and it remains unclear why other animal species inhabiting similar environmental niches, which might also be supposed to have experienced regular energy stress, have not adapted in a similar manner. This article attempts to provide a more comprehensive review of the factors that may have favoured an enhanced role for energy stores during human evolution.

Adipose tissue, unique to vertebrates, has been proposed to have evolved in response to selection for the ability to increase control over the uptake and storage of energy, and its rapid allocation by the brain to competing specialised tissues (Pond, 1998). Given the role of fatness in buffering energy demand from fluctuations in supply, it is not surprising that adipose tissue varies to a greater extent between species than any other organ (Pond, 1998). In many species, seasonal factors periodically exacerbate imbalances between energy supply and demand, for example aspects of reproduction that may temporarily super-sede feeding in importance. The storing of energy as fat is therefore proposed to have evolved to accommodate such effects, in contrast to species inhabiting more stable environments where energy may be converted directly into more offspring (Pond, 1998). Humans therefore follow other vertebrates in accumulating fat stores in order to buffer energy supply fluctuations, and they are relatively consistent with other primate species in the regional distribution of fat depots (Pond, 1998). What requires explanation is (1) the considerably greater readiness of our species to accumulate fat, when compared to other species of animal inhabiting the tropical savannah habitat where we evolved, and (2) the human ontogenetic profile of body fat content.

Over the last 5 million years hominids showed a trend towards increased body size (McHenry, 1992). There was a modest secular increase in size amongst the australopithecines, but a sharper increase with the emergence of the Homo genus. Such changes in body size are not necessarily consistent with changes in body composition, and the trend suggests only that total energy requirements of hominids likewise increased during this period. While it is plausible that an increase in body size would be accompanied by an equivalent increase in absolute energy stores, an enhanced *readiness* to store fat, or *relatively* greater fat stores, are not inevitable consequences of increasing size. For example, the increased total energy requirements of Homo appear to have been obtained by a range of adaptations, including a reduction in expensive gut tissue (Aiello and Wheeler, 1995), an increase in the energetic efficiency of locomotion (Foley and Elton, 1998), and shifts in the energetics of reproduction (Aiello and Key, 2002) and growth (Wells, 2003). Body fat stores are therefore merely one among a wide variety of adaptive strategies in hominid energetics.

During the adaptive radiation that occurred during the mid to late miocene, hominids appear to have been increasingly exposed to seasonal environments (Foley, 1993). This partly reflects a general climatic trend characteristic of this period, in which tropical forest was replaced by more open and arid environments, making the availability of resources more seasonal (Foley, 1993). However, hominids appear also to have occupied more challenging environments within this broader trend. The habitats occupied by hominids are proposed to have had an increased number of dry months each year, compared to the habitats occupied by ancestral chimpanzee and gorilla populations, following the divergence of these three species from their common ancestor (Foley, 1993). Energy availability would have been reduced in dry months, hence the duration of the dry season represented a significant ecological challenge as is the case today.

Hominids may have used more than one strategy to accommodate this seasonality, for example scavenging for animal food, or utilising a more diverse array of plant foods. This latter adaptation may account for the heavier dentition of robust australopithecines (Foley, 1993). However, it can be assumed that increased levels of body fat would have been highly beneficial in

this scenario, as found in many other species of mammal where seasonal or shorter-term fluctuations in energy supply are similarly problematic (Pond, 1998). It is therefore likely that the human capacity for ready fat deposition began to emerge during this period, becoming a universal characteristic of ancestral hominid populations.

In the contemporary world, the role of fat stores in buffering seasonal fluctuations in energy supply is well established. The most extreme seasonal weight changes, averaging over 4-5 kg, are found in western African populations, but significant fluctuations have also been observed in various populations from southern and eastern Africa, Asia, New Guinea and Latin America (Ferro-Luzzi and Branca, 1993). More detailed studies have suggested that the majority of this weight change occurs in fat mass (Lawrence et al., 1987). Recent seasonal food shortages that have been recorded in many human societies over the last century (Whiting, 1958) may exceed the stress experienced by ancestral hominids who practiced hunter-gathering rather than agriculture (see below), but the role of fat in addressing this stress can be assumed to be generic, and it is therefore likely that the stress of seasonality initiated evolution of the unique human profile of fatness.

The greater fatness of adult females compared to that of males, found in all contemporary populations (Norgan, 1994) suggests that reproductive energetics was a second factor of particular importance in the evolution of the human fatness. This sex difference can be further linked to the unusually high fat content of the neonate at birth, given the role of maternal nutrition in regulating offspring growth in early life. Elucidation of the factors that may account for these aspects of human fatness may aid identify the likely time period during which the traits evolved.

Later hominid evolution was characterised by a marked increase in encephalisation, and the relatively high cost of brain tissue, particularly in early life when the contribution of brain metabolism to whole-body metabolism is at its highest, has been proposed to have been a critical factor in hominid energetics (Foley and Lee, 1991). Current interpretation of the fossil record suggests that encephalisation in the Australopithecines was similar to that of other apes, whereas there were marked and consistent increases during the evolution of the genus Homo (Lewin, 1998). Though such increases are generally calculated for adults, it can be assumed that the increased brain size was also evident at birth, considerably increasing energy requirements in early life in comparison with the chimpanzee (Foley and Lee, 1991). Unlike some tissues, the brain cannot respond to inadequate energy supply by reducing its size, and its energy requirements are therefore not only high but obligatory (Kuzawa, 1998).

The additional energy costs of offspring encephalisation are passed on to the mother during the periods of gestation and lactation, with the latter generally accepted to be the more expensive period (Clutton-Brock et al., 1989). Increasing encephalisation of the infant has been calculated to have increased the energy costs for Homo erectus females by 40% compared to the Australopithecines, assuming lactation to be continued for proportional time periods (Aiello and Key, 2002). Paradoxically, the period during which offspring nutrition is directly funded by maternal lactation appears to have fallen in comparison with other living ape species, such that the inter birth interval is reduced compared to that of chimpanzees and gorillas (Aiello and Key, 2002). This effect has been proposed to represent a maternal adaptation to accommodate the high offspring brain costs (Aiello and Key, 2002). Growth rates in primates in general are lower than in other mammal species (Lee et al., 1991), and this is particularly the case after infancy in humans (Bogin and Smith, 1996), when the mother continues to provision the child indirectly rather than through lactation. Thus, the larger brain appears to be traded off against slower growth to prevent excessive energy demands on the mother.

The high costs of the brain, and the early age of weaning when the quality of the diet is assumed to worsen, have been proposed to account for the relatively high fatness of human neonates at birth and the subsequent increase in fatness during infancy (Kuzawa, 1998). The immediate period after birth, when lactation is being established, is a particularly vulnerable time for the offspring, and breast-milk provides little energy in the first week compared to subsequent weeks (Evans et al., 2003). Weaning, when nutritious breast-milk begins to be replaced by low energy-density foods, likewise increases the risk of uncertainty in energy supply, with this effect exacerbated by the increased possibility of infection, and adverse effects on appetite (Kuzawa, 1998). Fat stores buffer this uncertainty, and the principle organ benefiting from this protection is the large and vulnerable brain.

Just as fat stores are valuable to the infant at this stage of life, so they are valuable to the female in adolescence and during the years of fertility,

to support the energy costs of pregnancy and, of greater cost, lactation. A recent study of mothers in New Guinea illustrated how successive pregnancies steadily depleted maternal fat stores (Tracer, 2002). Reflecting the importance of fat stores in reproduction, nutritional status appears to play a role in the regulation of female reproductive maturity (Frisch and McArthur, 1974). This mechanism remains controversial, but the average weight at menarche has remained roughly the same over the last century, such that secular trends in weight are associated with earlier age at menarche (Frisch and Revelle, 1971).

Linking variability within and between individuals in fat stores to the influence of the large human brain is therefore a hypothesis that is already supported by various sources of evidence, though further investigations are recommended. Such an association would suggest that the relatively high fat content of humans at birth, and the tendency of the sexes to differ increasingly in body composition during adolescence, may have characterized the evolution of the genus Homo, rather than earlier ancestral hominid species with encephalisation levels similar to those of other contemporary ape species (Lewin, 1998).

Humans have not only been exposed to ecological stresses characteristic of global climate change, they have also, though their active role in the construction of ecological niches, manufactured more specific selective stresses. Such local stresses may reflect the regional climate, ecological factors such as the range of other plant and animal species, and more recently, agricultural practices. Such adaptations to local ecological conditions have been proposed to have favoured a variety of "thrifty" genes (Neel, 1999). Whereas such genes may have aided adaptation to local energy stress in past generations, they are now linked to the susceptibility to obesity as the environment changes again under the influence of westernization (Kagawa et al., 2002).

The active role of niche construction would explain why these genes appear to have a localised distribution within the human gene pool. Kagawa et al. (2002) have attributed variability in single nucleotide polymorphisms to a variety of local stresses including migratory patterns, dietary ecology, agricultural patterns and climatic patterns. Thus, while it is logical to suggest for example that all human populations practicing agriculture may have been exposed to famines over recent millenia, the traits that may have proved beneficial to survival can be assumed to have varied between local environments. Thus, all contemporary humans may have thrifty genes, but we may differ in terms of the traits that those genes affect.

Many populations characterised by particular thrifty genes have been exposed to extreme and rapid changes in dietary intake and lifestyle within recent decades, resulting in marked changes in body composition (Ulijaszek, 2001). As glucose intolerance, induced by the interaction of thrifty genes with the western lifestyle, is associated with both increased mortality and decreased fertility, the prevalence of these genes may decrease in frequency in these populations as the western lifestyle spreads (Dowse et al., 1991). Thus, the reverse process to that proposed by Neel may now operate, with thrifty genes in contemporary niches being costly rather than beneficial.

Any gene that influences energetics might be considered a thrifty gene. Those genes that underlie the more general capacity to adapt to seasonality discussed above may be considered thrifty genes, following the same process of selection that has acted on other animals with relatively high fat content. What is important about the specific thrifty genes highlighted by Kagawa and colleagues is that their origin can be attributed to relatively recent adaptation to local environmental conditions. Thus, these thrifty genes can be assumed to have emerged since the evolution of anatomically modern humans approximately 40,000 years ago, and hence to comprise an independent and relatively recent component in the evolution of human energetics and fatness.

Agriculture, which is likely to have been a particularly important selective pressure acting on modern humans, emerged only recently. Around 12,000 years ago, human began to shift from foraging to farming, and at the present time only a tiny minority of human populations continue to practice foraging. The emergence of agriculture in the archaeological record is not associated with apparent improvements in health, rather with increased rates of certain infectious diseases, and increased nutritional stress, reflected in a downward trend in body size that has only recently been reversed (Cohen, 1998). Thus, the idea that farming was initially adopted because of improved returns on subsistence activity is not well supported. Compared to that of foragers, the diet of farmers is nutritionally poorer due to the reduced varieties of food and the detrimental effects of long-term storage (Cohen, 1998).

However, potentially of greater significance

for human health in the long term were the ecological and social implications of storing surplus per se. Differential access to food stores allows the development of power imbalances, and the relationship between food stores and power bases, rather than any genuine subsistence advantages of agriculture, may therefore have encouraged its rapid spread across populations (Cohen, 1998). Small social groups not only have a modest buffer against famine, but are also vulnerable to plunder by larger social groups.

Farming appears to have enabled the emergence of marked inequality in social status, which continues to underlie differential exposure to nutritional stress today as it did in previous generations. Social inequality is well known in the animal kingdom, where many social species are characterised by dominance ranking that is maintained through physical force. For example, high-ranking primate females monopolise the best resources and have significantly higher reproductive success as a consequence (Packer et al., 1995; Johnson, 2003). In humans, the development of farming appears to have enabled inequality to be maximised, as shown by the various large-scale "civilisations" that emerged in several parts of the world around 5000 years ago (Cohen, 1998). In turn, an increasing number of individuals in large-scale complex societies no longer work directly in subsistence, and have an increased vulnerability to fluctuations in food supply.

However, whereas in previous generations the poor within complex societies served to insulate the rich from famine (Brown and Konner, 1982), in contemporary western populations the poor lack access to the healthier diet and lifestyle that protect against obesity in the modern energy-rich environment, and hence have higher rates of overweight.

Regular famine, as opposed to seasonal energy shortages, may likewise have been a relatively recent factor in human evolution, linked to the development of agriculture. Whereas hunter-gatherers typically exploit a wide variety of food sources, and can migrate in order to avoid severe energy stress, sedentary farmers specialising in a few crops are much more exposed to environmental deterioration. Keys and colleagues (1950) demonstrated that over 400 famines have been documented in the historical literature, which though inevitably biased towards western populations also covers regions such as China extensively (Prentice, 2001). Because of its predisposition to famine, agriculture is therefore likely to have imposed the strongest selective pressure favouring thrifty genes in recent times.

SUMMARY

Soft tissue is not preserved in the fossil record, and in order to reconstruct the evolutionary history of human body fatness it is necessary to review indirect evidence. The present article has sought to identify both the environmental changes that occurred in the last 5 million years, and the relevant physical changes that characterised our ancestors during hominid evolution. This approach has highlighted seasonality and entry into localised agricultural environments as factors that have increased the selective pressure of fluctuations in energy supply. As with other relatively fat mammals, humans are likely to have evolved increased fat stores to buffer such predictable fluctuations in energy availability. Over and above these general adaptations, the marked encephalisation that emerged in the genus Homo increased vulnerability to uncertainty in energy supply. Fat stores therefore acquired increased value to the young offspring and the reproducing female, enabling protection of the large brain with its obligatory energy requirements.

Contemporary humans are therefore characterised first by relatively high fatness for a species that evolved primarily in the tropics, and second by a ready capacity to acquire fat stores. Many researchers have attempted to consider whether the current obesity epidemic can be attributed to excess energy intake or low energy expenditure. From an experimental perspective, this debate is fruitless, as the degree of energy imbalance is too small to be attributed with confidence to one or other of the two factors (Wells, 1998). However, it is possible to adopt a broader perspective. Given current low levels of physical activity, it could be argued that contemporary individuals simply consume energy in excess of requirements, and should modify their diet. However, the evidence reviewed in this article favours a different argument. The tendency to store energy as fat may itself be considered a natural and unproblematic aspect of human biology. Contemporary individuals tend to be fatter because we no longer balance this tendency with the expenditure of substantial energy on subsistence, and no longer experience regular periods of energy insufficiency. This approach implies that obesity is likely to be prevented more successfully if we attempt to modify our obesogenic environment, rather than relying on indivi-

duals voluntarily altering their dietary and activity behaviours.

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ABSTRACT The readiness with which humans acquire fat, the basis of the contemporary obesity epidemic, is often attributed to the value of energy stores in accommodating cycles of feast and famine. However, other species inhabiting similar niches have experienced the same stress without adapting similarly. This article reviews the factors that may have favoured high fat levels, and the capacity to acquire them, in human evolution. First, early hominids inhabited increasingly seasonal environments during which fat stores are likely to have helped buffer regular uncertainty in energy supply. Second, the trend towards increased brain size in the genus Homo must have increased vulnerability to such uncertainty, favouring increased fat stores in the young offspring and the reproducing female. Third, the evolution of agriculture increased the stress of uncertainty, with sedentary populations, consuming a narrow diet, less capable of preserving energy supply. The human tendency to construct localised ecological niches may also have favoured the evolution of a range of "thrifty genes" that now underlie regional differences in obesity susceptibility. Thus, the interaction of environmental uncertainty and the large human brain may best explain our unique profile of fatness. Given the stability of these ecological stresses over time, the enhanced role of fat stores in human biology may be considered natural, and only problematic when uncertainty in energy supply is reduced. This argument suggests that obesity may be prevented more successfully by addressing the modern obesogenic environment, rather than relying on individuals voluntarily altering their diet and physical activity patterns.

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