



Being fat and smart: A comparative analysis of the fat-brain trade-off in mammals



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ABSTRACT

Humans stand out among non-aquatic mammals by having both an extremely large brain and a relatively large amount of body fat. To understand the evolution of this human peculiarity we report a phylogenetic comparative study of 120 mammalian species, including 30 primates, using seasonal variation in adult body mass as a proxy of the tendency to store fat. Species that rely on storing fat to survive lean periods are expected to be less active because of higher costs of locomotion and have increased predation risk due to reduced agility. Because a fat-storage strategy reduces the net cognitive benefit of a large brain without reducing its cost, such species should be less likely to evolve a larger brain than non-fat-storing species. We therefore predict that the two strategies to buffer food shortages (storing body fat and cognitive flexibility) are compensatory, and therefore predict negative co-evolution between relative brain size and seasonal variation in body mass. This trade-off is expected to be stronger in predominantly arboreal species than in more terrestrial ones, as the cost of transporting additional adipose depots is higher for climbing than for horizontal locomotion. We did, indeed, find a significant negative correlation between brain size and coefficient of variation (CV) in body mass in both sexes for the subsample of arboreal species, both in all mammals and within primates. In predominantly terrestrial species, in contrast, this correlation was not significant. We therefore suggest that the adoption of habitually terrestrial locomotor habits, accompanied by a reduced reliance on climbing, has allowed for a primate of our body size the unique human combination of unusually large brains and unusually large adipose depots.

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1. Introduction

Brain size varies considerably among mammalian species of any given body size (e.g., [Striedter, 2005](#)), and humans are arguably the most encephalized species. Similarly, the relative amount of body fat shows considerable variation among mammals ([Pitts and Bullard, 1968](#); [Pond and Mattacks, 1985, 1986](#); [Tyler and Blix, 1990](#); [Navarrete et al., 2011](#)), and humans have remarkably large fat stores. In healthy humans, the amount of body fat accounts for about 12–23% of total body weight in men and 24–34% in women ([Norgan, 1994](#); [Kyle et al., 2001](#); [McArdle et al., 2014](#); [Montagnese et al., 2014](#); [Prado et al., 2014](#); [Bowen et al., 2015](#)). This high amount of stored fat is not entirely a product of modern, industrial lifestyles, since body fat in women is around 19–24% even in

hunter-gatherers or subsistence cultures inhabiting harsh environments ([Lawrence et al., 1987](#); [Yamauchi et al., 2000](#); [Sherry and Marlowe, 2007](#); [Pontzer et al., 2012](#)). Other anthropoid primates, including our closest-living relatives, chimpanzees and bonobos, have only about 1–10% of body mass as fat ([Pond and Mattacks, 1987](#); [Dittus, 2013](#); [Zihlman and Bolter, 2015](#)). Thus, humans exhibit not only unusually large brains, but also unusually large adipose depots for a primate of our body size.

Because adipose tissue is not preserved in fossils, we need broad phylogenetic comparisons over several lineages to compare extant species and examine evolutionary processes underlying this human peculiarity. Many mammals live in seasonal habitats, in which periods of food scarcity impose severe energetic constraints. To deal with the challenge of lean periods, mammals have evolved physiological and/or cognitive strategies. The first, physiological buffering, generally involves storing fat, and is accompanied by seasonally reduced activity and decreased metabolic rates (in extremis leading to hibernation or torpor) as well as seasonal

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breeding if the reproductive cycle can be completed in less than a year (e.g., Pond, 1998; Heldmaier et al., 2004; McNab, 2008; Schmid and Speakman, 2009). Fat storage also has fitness costs. These arise from the increased energetic costs of locomotion due to larger body weight (Browning et al., 2006; Ghiani et al., 2015; and see discussion in Supplementary Online Material [SOM]), but also from increased predation risk or decreased hunting success due to reduced agility and speed (Gosler et al., 1995; Dietz et al., 2007; Zamora-Camacho et al., 2014). In arboreal species, adaptations for agile locomotion and terminal branch feeding may impose additional constraints on the quantity of fat stores (Dittus, 2013).

The second strategy to survive lean periods is cognitive flexibility. The Cognitive Buffer hypothesis (Allman et al., 1993; Deaner et al., 2003; Sol, 2009) predicts that living in more seasonal habitats favours the evolution of relatively larger brains, because enhanced cognitive abilities and behavioural flexibility to cope with seasonal challenges yield a selective advantage. This hypothesis is supported by a positive correlation between climatic variability and brain size in Neotropical parrots (Schuck-Paim et al., 2008). In addition, migrating bird species have smaller brains than non-migrating bird species (Winkler et al., 2004; Sol et al., 2005), which may reflect a cognitive buffer effect in the resident species (Sol et al., 2005) or a reduced selective advantage of enhanced cognitive performance in migratory species (Sol et al., 2010). In platyrrhine and catarrhine primates, van Woerden et al. (2014) found a positive relationship between relative brain size and the amount of buffering, defined as the difference between environmental (and thus potentially experienced) and (actually) experienced seasonality. This finding suggests that a large brain allows monkeys to keep their energy intake relatively constant, e.g., by finding or accessing hidden or protected food sources, despite environmental fluctuations in food availability.

However, the advantage of enhanced cognitive abilities provided by increased brain size (Deaner et al., 2007; Reader et al., 2011) comes at the expense of increased energy costs. Brain tissue is among the most metabolically expensive tissues in the body (Rolfe and Brown, 1997; Niven and Laughlin, 2008), and the costs of brain function cannot be reduced temporarily (Lukas and Campbell, 2000; Karasov et al., 2004; Bauchinger et al., 2005). Selection can only favour changes of traits that produce a net fitness benefit, i.e., if benefits exceed costs. The fitness reduction due to the increased energetic costs of brain tissue may outweigh any fitness increase due to cognitive buffering in larger-brained species, especially in extremely seasonal or unpredictable habitats (van Woerden et al., 2010; Weisbecker et al., 2015). In periods of starvation, the brain is sustained by metabolising fat involving ketone bodies (Owen et al., 1967; Hasselbalch et al., 1994; Zhang et al., 2013). This can be a successful strategy to survive seasonally lean periods (Knott, 1998; Harrison et al., 2010), but on balance it is metabolically less efficient. The detour through fat metabolism increases the average amount of energy intake needed per day (Sokoloff, 1973; Hawkins et al., 1986; Mitchell and Fukao, 2001).

The high energy costs of the cognitive flexibility strategy implies that there is a trade-off between buffering seasonally lean periods either passively by storing body fat (“physiological buffering”) or actively by increasing relative brain size, which provides cognitive flexibility to access hidden and highly nutritious food items (“cognitive buffering”). Thus, we expect that selection favours increased brain size only for species which are active throughout the year and hence benefit from using their larger brains continuously. On the other hand, species that rely mainly on body fat and reduced activity to survive lean periods are expected to exhibit relatively small brains. This trade-off should be expressed as negative co-evolution between brain size and fat storage. Navarrete et al. (2011) found a negative correlation between the amount of

adipose deposits and brain size in a broad sample of dissected mammal species. However, for various reasons it is necessary to revisit this issue. First, the negative correlation between dissected fat deposits and brain size was not predicted but found while testing another hypothesis. Second, for some species fat deposits were estimated from single or very few specimens. Third, in primates, Navarrete et al. (2011) could measure only abdominal adipose depots of captive individuals, casting doubt on their finding of an absence of a negative correlation between brain size and adipose depots in primates. For all these reasons, the predicted brain-fat trade-off should be reassessed with an independent sample.

The first aim of this paper is therefore to conduct a broad test of the brain-fat trade-off in mammals. We do so using a novel proxy for the tendency to store body fat: the seasonal variation of body mass within a year, measured as the coefficient of variation (CV) in body mass. The CV body mass is a more precise measure of the tendency to store body fat as it covers the whole year, in contrast to the body fat values obtained from cadavers that can only be assessed at a given point in time, which leaves the seasonal fluctuations unknown (Wells, 2010). Moreover, this measure is available for a larger number of individuals in wild-living mammals.

Our second aim is to investigate the effects of substrate use on the brain-fat trade-off. In many species, locomotor costs are a substantial fraction of total daily energy expenditure (Garland, 1983; Elliott et al., 2013), and transporting adipose depots is costly (Taylor et al., 1982; Garby et al., 1988; Ekelund et al., 2002; Peyrot et al., 2009). Thus, we would expect fewer arboreal or volant species to rely on fat storage than terrestrial or aquatic ones, because flying and climbing involve higher cost of transporting adipose depots than swimming or moving horizontally (Alexander, 2003; Hanna et al., 2008). Accordingly, we predict a stronger trade-off between brain size and the potential to store fat in arboreal or volant species than in terrestrial or aquatic ones. This provides a starting point to investigate whether a bipedal, terrestrial lifestyle allowed humans to evolve the unique combination of unusually large brains and relatively large adipose depots. This combination may have been crucial, because without our extra fat stores we might not have been able to maintain high physical activity alongside our extremely large brains (Pontzer et al., 2016a, 2016b).

2. Material and methods

2.1. CV body mass as a proxy for the tendency to store body fat

In humans, approximately 75% of intra-individual variability in body weight of adult women can be attributed to fat storage in adipose depots (Webster et al., 1984). Similarly, in non-human mammals body fat explained between 41 and 92% of the intraspecific variation in body mass (Artiodactyla: 68–91% [Adamczewski et al., 1987; Adamczewski et al., 1995; Stephenson et al., 1998]; Carnivora: 41–79% [Worthy et al., 1992; Hilderbrand et al., 2000; Beck et al., 2003; Crocker et al., 2012]; Primates: 85–94% [Colman et al., 1999; Power et al., 2001]; Rodentia: 45–70% [Galster and Morrison, 1976; Bintz and Strand, 1983; Lidicker and Ostfeld, 1991; Pulawa and Florant, 2000]). Several studies of mammals and birds found that the amount of body fat was highly correlated with carcass weight for each age and sex and hence that body weight was a good predictor of total body fat (Tribe and Peel, 1963; Bryden, 1969; Morton and Tung, 1971; Schaefer et al., 1976; Reimers et al., 1982; Serie and Sharp, 1989; Lidicker and Ostfeld, 1991; Drew, 1992; Dunbrack and Ramsay, 1993; Power et al., 2001). Although fluctuations in the size of other organs such as liver, kidney or spleen can also affect seasonal changes in body mass, these effects are absolutely and relatively small (Mitchell et al., 1976; Bintz and Strand, 1983;

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