Who can afford to be both 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.

Keywords: locomotion costs, bipedalism, terrestriality, body fat, brain size, seasonality

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 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 and colleagues (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 metabolizing 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 and colleagues (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; Pontzer et al., 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 41–92% 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 Jr 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 Jr 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; Adamczewski et al., 1987; Gerhart et al., 1996; Campbell and MacArthur, 1998; Weber and Thompson, 1998) and often out of phase with cycles in body weight (Dauphine Jr, 1975; Mitchell et al., 1976). We therefore used seasonal changes of body mass over a year as a proxy for the tendency to store body fat. We assume that these seasonal changes in body mass match food intake, and hence experienced seasonality, but not necessarily environmental seasonality (van Woerden et al., 2012; van

Woerden et al., 2014). For a given species, we calculated the coefficient of variation (CV = standard deviation/mean) over monthly means of body mass for each sex separately. Data on CV body mass were found for a total of 120 mammalian species, including 111 species in the female dataset and 110 species in the male dataset. The complete datasets are given in the SOM.

Monthly body mass data were compiled from studies that reported adult body mass across the year. If several sources were available for one species, preference was given to studies on large sample sizes conducted in the wild. As captivity might affect body mass variation (under good husbandry conditions most animals gain weight in captivity; Leigh, 1994), we added provenience (wild/captivity) as a covariate in all analyses. Ideally, we would have preferred to use only studies from the wild that report mean body mass for 12 consecutive months. However, in contrast to studies in captivity, most body mass data of wild living mammals have been recorded less frequently. To consider potential effects of unequal sampling we included the number of months sampled as a covariate in all analyses, and did not include studies with less than four months sampled. If body mass data were given for four seasons, pooled across several months (e.g., spring, summer, autumn and winter), we set the number of months sampled to four (15 studies). In most species, monthly mean body mass data was distributed evenly across the year, except for *Antechinus stuartii*, *Myotis lucifugus*, *Rattus fuscipes*, *Zapus hudsonicus* and *Spermophilus franklinii*. We found no differences in the results when controlling for these potentially confounding variables (results shown in the SOM Tables S1–S3).

We also controlled for another possible confounding variable, pregnancy and lactation. Some studies include data from pregnant and lactating females in mean female body mass, which may artificially increase body mass variation in seasonal breeders. Obviously, pregnancy affects a female's weight due to the added weight of the offspring and associated tissues and fluids. Moreover, several studies also showed that females accumulate adipose depots before or during pregnancy and lactation (Randolph et al., 1977; Weiner, 1987; Hickling, 1991; Dufour and Sauther, 2002; Lassek and Gaulin, 2006). To control for this effect, we added the presence or absence of pregnant and/or lactating females in the study species as a covariate in all analyses. Furthermore, we analysed the subsample of studies including only non-pregnant and non-lactating females separately.

In some species, males store body fat for other purposes than to buffer lean periods, e.g., to have an advantage in male-male competition (Boinski, 1988; Lidgard et al., 2005; Crocker et al., 2012). However, it is usually impossible to disentangle the various reasons for body fat storage, as reproductive seasons and experienced seasonality in food intake are generally interrelated (Batzli and Pitelka, 1971; Bronson, 1989; Tyler and Blix, 1990; Réale et al., 2003). Whatever the specific purpose of fat storage, we would always expect a brain-fat trade-off due to the energetic costs of both brains and adipose deposits. To validate the use of CV body mass as a proxy for variation in body fat, we tested whether monthly body mass correlated with percentage body fat in a subsample of studies that measured both for at least five months in the same specimens ($n = 8$ species for females and $n = 4$ species for males, see SOM).

2.2 Brain size

For 105 of the 120 species of the CV body mass dataset, sex-specific data on endocranial volume (ECV) was either compiled from the literature or measured from museum specimens. The ECVs of 330 complete adult crania (third molar present) from three American museums (American Museum of Natural History, New York; National Museum of Natural History, Washington, D.C.; Field Museum of Natural History, Chicago) were measured using glass beads. To control for allometric effects of size, sex-specific mean body mass was included as a covariate in the analyses, taking the overall mean from the same specimens for which CV body mass was determined.

Dealing with seasonality is an ecological challenge, and we have no a priori prediction on how sociality might affect the brain-fat relationship. Nevertheless, differences in sociality may act as a confounding variable that independently influences both brain size evolution and fat storage, yielding spurious results. We therefore integrated group size as a covariate in our models. However, group size never exerted a significant effect, and the akaike information criterion (AIC) of the models that included group size was always higher than in those excluding it (results not shown).

2.3 Substrate use

Data from published sources were used to assign each species to one of two substrate use categories, terrestrial (0) or arboreal (1), based on their main habit. Species were classified as terrestrial when they spend more than 50% of observation time on the ground. Data on substrate use were taken from the published literature (Meier, 1983; Gittleman, 1986; Myers et al., 2006; Rowe and Myers, 2011; see SOM). Volant and aquatic taxa (Chiroptera, Cetacea and Pinnipedia) were not analysed, since too few species were available to test them separately. Instead, we graphically examined whether aquatic species fit into the pattern observed in terrestrial clades (and volant into arboreal ones), since volant and aquatic mammals can be regarded as the most extreme cases with respect to the locomotor costs of adipose depots.

2.4 Statistical analyses

All statistical analyses were performed using JMP^{TM} 10.0 (SAS Institute Inc, 1989) and R3.1.3 (R Core Team, 2015). All continuous variables were log-transformed before analysis in order to yield normally distributed residuals. To test for an intraspecific relationship between CV body mass and percentage of body fat, non-parametric Spearman correlations were used. To assess the overall significance of the correlation between CV body mass and percentage body fat across species for males and females, we used a weighted z-transform test to combine all *p*-values across species using the “combine.test” function from the “survcomp” package (Haibe-Kains et al., 2008) in R3.1.3 as recommended in Whitlock (2005). For this test, we assigned a weighting value based on the number of months available for each species.

In the interspecific models, a strong phylogenetic signal in the data, i.e., lambda estimated to be close to one in all models, warranted the use of methods to control for phylogenetic non-independence (Pagel, 1999). Phylogenetic analyses were performed in R, using phylogenetic generalized least-squares regression (PGLS; Martins and Hansen, 1997) in the “caper” package (Orme, 2013). The phylogenetic tree was based on a composite supertree (Fritz et al., 2009) and is given in SOM Figure S1. The outcome of PGLS can be strongly influenced by outliers or data points with a high leverage (Jones and Purvis, 1997). We therefore repeated all analyses after removing one data point with an absolute

studentised residual larger than three (*Meles meles* in the female dataset). However, results were qualitatively very similar, and thus we only report results from analyses including all species. The CV body mass was treated as an independent variable and brain size as a dependent variable in the PGLS models, while mean body mass was included as a covariate. We also tested for an interaction effect between mean body mass and CV body mass, and potentially confounding variables as described above (SOM Table S4). All models were run for each sex-specific dataset separately and additionally in a subsample of non-pregnant and non-lactating females. Primates were also analysed separately, specifically to examine the questions raised by Navarrete et al.'s (Navarrete et al., 2011) results for this order. To test the influence of locomotor costs on the brain-fat trade-off, the category of substrate use was included as an independent variable in the models. Furthermore, the influence of substrate use on CV body mass was also tested separately. To illustrate our findings, species or suborder mean values and residuals from non-phylogenetic least-square regressions are shown in all figures (Figs. 1–2 and SOM Figs. S3–S4), following common practice (Symonds and Blomberg, 2014).

3. Results

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

First, we validated the use of CV body mass as a proxy for the tendency to store body fat in a sample of species for which both measures were collected on the same individuals. In females, we found strong positive correlations between CV monthly body mass and percentage body fat in five out of eight species, and a positive trend for two additional species (SOM Fig. S2). Only one species (*Macaca fuscata*) did not exhibit any positive relationship. However, the body fat values of *Macaca fuscata* were based on only dissected mesenteric and omental fat (Muroyama et al., 2006). The Fisher's combined probability test revealed a significant overall positive correlation between CV body mass and percentage body fat ($p < 0.001$). In females, CV body mass may therefore be a reasonably good proxy for the tendency to store body fat.

In males, only one out of four species showed a significant relationship between CV monthly body mass and percentage body fat (SOM Fig. S2). Although the Fisher's combined probability test revealed a significant positive correlation between CV body mass and percentage body fat ($p = 0.018$), this test is asymmetrically sensitive to small p -values compared to large ones (Rice, 1990). We therefore include the analyses of the male dataset in the remainder of this paper, but placed stronger confidence in the interpretation of the results on females.

3.2 Influence of substrate use on the relationship between brain size and CV body mass

We had predicted that a brain-fat trade-off, and thus the negative correlation between brain size and CV body mass, would be more pronounced in predominantly arboreal species than in species with a largely terrestrial substrate use. Including substrate use as an effect in multiple regressions, we found a significant interaction effect between CV body mass and substrate use in females and a strong trend in males (Table 1 and Fig. 1) in the predicted direction. For the subsample of predominantly arboreal species, we found a significant negative correlation between brain size and CV body mass in both sexes, both in mammals in general and within primates (Table 2 and SOM Fig. S3). For the subsample of mostly terrestrial species, the correlation between brain size and CV body mass was not significant in either sex (Table 3). An analysis of the brain-fat relationship within terrestrial primates was not possible because our study comprised only two predominantly terrestrial primate species. In all subsamples, the brain-fat trade-off was always stronger in females compared to males and even stronger in the subsamples comprising only non-pregnant and non-lactating females (Tables 1–3). Overall, arboreal mammals exhibited less seasonal variation in body mass than did terrestrial species (Fig. 2 and SOM Table S5). The same difference was also observed within primates (Fig. 2 and SOM Table S5). The few data points available for aquatic species fit into the pattern observed for terrestrial clades, and the volants into that observed for arboreals, consistent with the prediction of a trade-off between brain size and the tendency to store body fat in volant clades, but not in aquatic ones (SOM Fig. S4).

4. Discussion

4.1 *Testing the brain-fat trade-off*

Using seasonal body mass variation as a proxy for the tendency to store body fat, we found that brain size and the tendency to store body fat are negatively correlated in predominantly arboreal mammals. This result adds to other studies showing that seasonality plays a role in brain size evolution (Schuck-Paim et al., 2008; Sol, 2009; van Woerden et al., 2010; van Woerden et al., 2012; 2014; Weisbecker et al., 2015). It also lends support to our prediction that encephalization (cognitive buffering, active strategy of survival) and fat storage (physiological buffering, passive strategy of survival) are compensatory strategies to buffer against seasonal starvation, unless the reduced cost of transport of additional body fat, as in terrestrial species, alleviates this trade-off and thus allows organisms to combine both strategies.

We attempted to assess the validity of using CV body mass as a proxy for the variation in adipose depots. While significant positive correlations between body mass and percentage body fat were found for females in most species, for males a significant correlation was found in only one out of four species. Taking these results from the rather small samples at face value, this suggests that there is a sex-specific difference in body mass variation over the year, perhaps partly due to sexual selection. Female reproductive success relies more on the ability to store body fat, as it enables the female body to bear the energy costs of pregnancy and lactation (e.g., Bercovitch, 1987; Richard et al., 2000; Ellison, 2001; Dufour and Sauter, 2002; Zenuto et al., 2002; Martin, 2007). These studies and our finding that the brain-fat trade-off was more pronounced in females than in males make it reasonable to conclude that in females energetic constraints on reproduction aggravate the trade-off between brain size and body fat. Males, on the other hand, may rely less on body fat to achieve increased reproductive success (Leader-Williams and Ricketts, 1982; Setchell and Dixon, 2001), but rather on muscle mass, as robust musculature would aid in mate searching and be advantageous during male–male fights. This

sex difference can explain the relatively lower strength of the correlation of body mass with body fat over the year in males (Bonnet et al., 1998; Schulte-Hostedde et al., 2001; Boos et al., 2002).

These conclusions must remain somewhat preliminary, especially for males, in the absence of a more thorough validation study of CV body mass as a proxy of variation in body fat. In any case, the use of dissected body fat is also far from ideal, as body fat values obtained only from cadavers reflect the values at the time of death, and seasonal fluctuations therefore remain unknown (Wells, 2010). It would evidently be very useful if not only body mass variation but also a more direct measure of body fat content could be assessed in a large number of wild animals. Although the published literature contains a variety of measures of adipose depots in living subjects such as palpation, skinfold thickness, perirenal adiposity, the number of adipocytes in bone marrow, and adipocyte volumes from tissue samples (Ellis, 2000), these measures have not yet been compared to each other or across species. This assessment would therefore require targeted studies.

4.2 Effects of substrate use

Adipose depots contribute both to body mass, which increases the total energy requirement for physical activity, and to body volume, which may impact locomotor traits such as speed and agility. Several lines of evidence in our study suggest that substrate use affects these costs of body fat through the latter's effects on locomotion efficiency (see SOM for an extensive discussion). First, we found a stronger trade-off between brain size and the potential to store body fat (as proxied by CV body mass) in arboreal clades compared to terrestrial ones. Several studies showed that climbing and other locomotor types used in arboreal niches, such as vertical clinging and leaping, involve much higher costs of transporting additional weight than moving horizontally (Warren and Crompton, 1998; Hanna et al., 2008). Thus, if locomotion costs are higher, less energy can then be allocated to the brain, as postulated by the expensive brain framework (Isler and van Schaik, 2009), resulting in a stronger brain-fat trade-off in arboreal species compared to terrestrial ones.

Second, we showed that arboreal species exhibited less seasonal variation in body mass than terrestrial mammals, potentially suggesting that arboreal species face constraints on the amount of body fat they can store. However, our sample of arboreal mammals is heavily biased towards primates, as body mass data of more arboreal non-primate mammals are presently lacking. Future studies testing the relationship between body fat and substrate use are therefore needed to substantiate this finding.

Third, in fully aquatic species, large body size and volume do not increase cost of transport if geometric similarity of the body form is maintained (Marino, 1998; Pond, 1998; Alexander, 2003). Indeed, rather than hamper, fat stores enhance locomotor efficiency, which has been demonstrated in several seal species (Beck et al., 2003; Adachi et al., 2014; Richard et al., 2014). It seems likely, therefore, that an aquatic lifestyle does not entail a brain-fat trade-off, allowing the combination of both strategies of fat storage and brain enlargement to buffer seasonally lean periods. Indeed, several marine or semi-aquatic mammals, such as whales and dolphins, seals, sea lions and beavers, exhibit both a relatively large brain and large adipose depots compared to other mammals (Marino, 1998; Pond, 1998), perhaps also due to thermoregulatory needs (Mclellan et al., 2002; Montie et al., 2008; Zeng et al., 2015). Due to the small number of aquatic species in our sample (three pinniped species and the bottle-nosed dolphin *Tursiops truncatus*), our data are inconclusive in this respect. Moreover, CV body mass may not be an adequate proxy of the tendency to store body fat in fully aquatic species, as they probably maintain a high level of body fat throughout the year.

Fourth, we predicted (but could not test) that flying species experience an even stronger trade-off between brain size and body fat than other animals. Flying mammals, such as bats, are expected to have even higher costs of transporting adipose depots compared to terrestrial and arboreal clades. It is difficult to test this hypothesis using a comparative approach, as there is only one phylogenetic group of volant mammals, but, not surprisingly, the proportion of body fat in bats indeed tends to be

relatively low, regardless of their size (Wells, 2010). For birds, we would expect that the relationships between brain size and fat storage also depend on their mode of flight or their locomotor habits. Migrating birds or lineages that depend on flapping flight are expected to show a stronger trade-off than non-migrating birds or lineages that evolved energy-efficient forms of flight such as soaring. In sum, our study confirms the hypothesis that the trade-off between brain size and the potential to store fat is stronger in arboreal clades compared to terrestrial ones. Whether it can be expanded to volant and aquatic animals requires further testing.

4.3 Implications for hominin evolution

Humans stand out among non-aquatic mammals by having both an extremely large brain and a high amount of body fat (Wells, 2010). Our comparative results therefore provide support for the notion that, among species with a more terrestrial lifestyle, the brain-fat trade-off is relaxed relative to arboreal ones because of the lower costs of transporting additional adipose tissue. We admit that extending the conclusions from such a comparative study to explain the evolutionary trajectory of a single lineage is risky, especially in the light of the small number of predominantly terrestrial primate species in our study (*Pan troglodytes* and *Macaca fuscata*). Nevertheless, in our dataset these two species were among the primates with the highest CV body mass values. A recent study reporting estimates of body fat percentage using the doubly-labelled water method (Pontzer et al., 2016a) found similar relationships within hominoids. The genus *Pan*, which most frequently engages in vertical climbing and has the longest daily travel distances amongst great apes, exhibited a lower proportion of body fat than both *Gorilla* and *Pongo*, which showed similar values. Gorillas are relatively terrestrial and their daily travel distances are very short, suggesting that low locomotion costs relax the constraints on the quantity of fat stores. As wild orangutans are largely arboreal (Ashbury et al., 2015), it remains unclear whether the high percentage of body fat noted in the Pontzer et al. (2016a) study is due to a captivity effect or whether the capacity of fat storage is strongly selected for in this genus, which suffers from severe and unpredictable starvation periods due to El Niño effects (Knott, 1998). Preliminary data on brain size support the notion that female *Pongo pygmaeus morio*, the subspecies

affected most by habitat unpredictability, exhibit smaller brains than the other subspecies or *Pongo abelii* (Taylor and van Schaik, 2007). However, reliable conclusions about the interrelations between fat storage, brain size, and locomotor mode within hominoids require more detailed data on these traits in several wild ape species and subspecies.

Humans have adopted a fully terrestrial lifestyle and almost completely abandoned climbing, which is energetically very expensive (Pontzer and Wrangham, 2004; Hanna et al., 2008). In addition, early *Homo* also evolved an energetically more efficient striding gait compared to the probably less efficient australopith-like form of bipedalism (Bramble and Lieberman, 2004; Nagano et al., 2005; Pontzer et al., 2009; Pontzer et al., 2010). It is therefore likely that lowering the energy costs of locomotion early on in the evolution of *Homo* may have allowed for selection to favour 'diversion' of this energy to the brain. Besides this reallocation, the human lineage also evolved an acceleration in metabolic rate, i.e., a higher energy throughput and thus more energy for larger brains or increased production (Pontzer et al., 2016a). The combination of efficient walking, metabolic acceleration and several other factors (Aiello and Wheeler, 1995; Burkart et al., 2009; Wrangham, 2009; Isler and Van Schaik, 2014) may therefore have enabled the extraordinary brain enlargement evident in our lineage. Moreover, abandoning climbing and adopting more efficient bipedalism may have reduced the load effect of adipose depots on the energy costs of locomotion. Navarrete et al. (2011) estimated that 10% additional fat stores would increase the percentage of energy used for locomotion by about 2–3% in chimpanzees, but by only 1% in extant human foragers. They assumed that the costs of locomotion increase less steeply with additional body mass in bipedal locomotion compared to quadrupedal locomotion, or in efficient bipedalism compared to australopith bipedalism; however, this remains to be tested.

Seasonality in diet composition or food availability accounts for much of the variability among mammalian species in brain size (van Woerden et al., 2014; Weisbecker et al., 2015) and average fatness (Pond, 1998). Habitat seasonality is also often suggested as a major selective factor in the hominin radiation (Foley, 1993; Burkart et al., 2009; Wrangham, 2009). Acceleration in metabolic rate in larger-brained early humans is likely to have aggravated the impact of seasonal fluctuations in

energy intake, because increased energy throughput exposes humans to a greater likelihood of energy shortfalls (Pontzer et al., 2016a). As 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 temporarily reduced (Lukas and Campbell, 2000; Karasov et al., 2004; Bauchinger et al., 2005), we propose that increased body fat deposits may have been essential in providing an energy buffer against temporal fluctuations in energy intake in early *Homo*. It seems likely, therefore, that the almost unique human strategy of combining cognitive buffering during lean periods (for example, by extractive foraging and tool use) with the increased potential to store fat in adipose depots (physiological buffering), was driven by pronounced seasonal variation in food sources, which was a characteristic of the African tropical savannah mosaic during the late Pliocene. This strategy in humans also enabled early *Homo* species to survive the unpredictability of new environments, as they greatly expanded their geographic range (Wells and Stock, 2007; Potts, 2012; Wells, 2012). Under these conditions, freedom from arboreal constraints on the amount of body fat, and the development of large brains, may have helped the first terrestrial hominins to maintain an approximately constant energy supply despite the environmental uncertainty of resource availability in unfamiliar terrestrial habitats (Foley, 1987; Navarrete et al., 2011; Wells, 2012).

Acknowledgements

We gratefully acknowledge the many people and institutions have contributed data to our compilation. In particular, we thank David Camps, Patricia Anne Fleming, Benedikt Gehr, Didier Julien-Laferrière, Tinka Plese, Carsten Schradin, Sofia Silva, Tierpark Hellabrunn München, Dirk Ullrich from the Alpenzoo Innsbruck and Luc Wauters. We thank the American Museum of Natural History, New York, the Field Museum, Chicago and the National Museum of Natural History, Washington, DC for allowing us to collect endocranial volumes, and Sereina M. Graber for her help with this. We also thank Marcus Clauss for fruitful discussions and Caroline Pond for sharing her data on mammalian body fat for

preliminary analyses. Financial support was provided through the Swiss National Science Foundation grant no. 31003A-144210, the A. H. Schultz Foundation and the University of Zurich.

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Figure captions

Figure 1. Relationship between log(brain size) and CV body mass in (a) males and (b) females, for the two types of substrate use (raw species values, blue = terrestrial, red = arboreal). Phylogenetically controlled statistics summarised in Tables 1, 2 and 3.

Figure 2. Coefficient of variation in body mass in (a) terrestrial and arboreal female mammals and (b) terrestrial versus arboreal female primates. For statistics, see SOM Table S5.

Table 1

Multiple regressions with log(brain size) as the dependent variable and CV body mass, log(mean body mass), substrate use, and the interaction between CV body mass and substrate use as independent variables (*n* = 88 for males, *n* = 89 for females).^a

model ^b	lambda	adj. r ²	predictor variables	estimate	std. error	<i>p</i> -value
All mammals, males	0.899	0.901	CV body mass	-0.003	0.593	0.997
			log(mean body mass)	0.657	0.023	<0.001
			substrate use	0.181	0.190	0.344
			CV body mass*substrate use	-2.301	1.186	0.056
All mammals, all females	0.950	0.899	CV body mass	0.449	0.453	0.325
			log(mean body mass)	0.651	0.023	<0.001
			substrate use	0.174	0.200	0.389
			CV body mass* substrate use	-2.902	1.455	0.049
			inclusion of reproductive	-0.017	0.084	0.836
			females in the study			

^a Pinnipedia, Chiroptera and Cetacea are not included in the analyses.

^bThe *p*-values of both models were <0.001. Significant effects are highlighted in bold.

Table 2

Phylogenetic generalized least squares regression models^a with log (brain size) as the response variable in arboreal mammals.

sample	<i>n</i>	lambda	adj. <i>r</i> ²	predictor variables	estimate	std. error	<i>p</i> -value
Arboreal mammals, males	37	0.918	0.867	CV body mass	-2.726	0.910	0.005
				log(mean body mass)	0.615	0.041	<0.001
Arboreal mammals, all females	36	0.986	0.853	CV body mass	-2.903	1.076	0.011
				log(mean body mass)	0.577	0.041	<0.001
				inclusion of reproductive females in the study	-0.097	0.085	0.262
Arboreal mammals, non-pregnant & non-lactating females	28	0.969	0.890	CV body mass	-3.528	1.126	0.004
				log(mean body mass)	0.592	0.044	<0.001
Arboreal primates, males	28	0.490	0.924	CV body mass	-3.067	1.160	0.014
				log(mean body mass)	0.667	0.042	<0.001
Arboreal primates, all females	28	1.000	0.897	CV body mass	-4.185	1.466	0.009
				log(mean body mass)	0.585	0.046	<0.001
				inclusion of reproductive females in the study	-0.293	0.086	0.002
Arboreal primates, non-pregnant & non-lactating females	25	1.000	0.899	CV body mass	-3.878	1.536	0.019
				log(mean body mass)	0.605	0.050	<0.001

^aThe *p*-values of all models were <0.001. Significant effects are highlighted in bold.

Table 3

Phylogenetic generalized least squares regression models^a with log (brain size) as the response variable in terrestrial mammals.

sample	<i>n</i>	lambda	adj. <i>r</i> ²	predictor variables	estimate	std. error	<i>p</i> -value
Terrestrial mammals, males	51	0.890	0.906	CV body mass	-0.045	0.693	0.948
				log(mean body mass)	0.667	0.030	<0.001
Terrestrial mammals, all females	53	0.925	0.911	CV body mass	-0.445	0.543	0.417
				log(mean body mass)	0.675	0.029	<0.001
				inclusion of reproductive females in the study	0.066	0.136	0.629
Terrestrial mammals, non-pregnant & non- lactating females	5	0	0.993	CV body mass	-0.130	5.435	0.983
				log(mean body mass)	0.808	0.063	0.006

^aThe *p*-values of all models were <0.001. Significant effects are highlighted in bold.

Figure 1

Figure 2