Primate energy input and the evolutionary transition to energy-dense diets in humans
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Short title: Primate energy input and human evolution

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Abstract. Humans and other large-brained hominins have been proposed to increase energy turnover during their evolutionary history. Such increased energy turnover is plausible, given the evolution of energy-rich diets, but requires empirical confirmation. Framing human energetics in a phylogenetic context, our meta-analysis of 17 wild non-human primate species shows that daily metabolizable energy input follows an allometric relationship with body mass where the allometric exponent for mass is 0.75 ± 0.04, close to that reported for daily energy expenditure measured with doubly-labelled water in primates. Human populations at subsistence level (N = 6) largely fall within the variation of primate species in the scaling of energy intake, and therefore do not consume significantly more energy than predicted for a non-human primate of equivalent mass. In contrast, humans ingest a conspicuously lower mass of food (-64 ± 6%) compared to primates and maintain their energy intake relatively more constantly across the year. We conclude that our hominin hunter-gatherer ancestors did not increase their energy turnover beyond the allometric relationship characterizing all primate species. The reduction of digestive costs due to consumption of a lower mass of high-quality food as well as stabilization of energy supply may have been important evolutionary steps enabling encephalization in the absence of significantly raised energy intakes.

Key words: allometry – food intake – energy balance – seasonal variation – hominins
1. Background

Humans and other large-brained hominins have been proposed to undergo an increased
energy turnover during their evolutionary history and/or to evolve peculiar energy allocation
trade-offs between growth, maintenance and reproduction relative to other primates (e.g. [1-3]). Comparison of basal metabolic rate between modern humans and chimpanzees, our
closest living relatives, suggests that basal energy requirements increased by ~19% during
hominin evolution, though the available data are very limited [1,2]. Similarly, the available
data on total daily energy expenditure (TEE) in humans and apes have been interpreted as
indicating greater energy turnover in humans compared to non-human primates (e.g. 27%
greater than chimpanzees and bonobos, our closest relatives [2]). At some point of hominin
evolution, a shift towards an energy-rich diet [1,4,5] and later towards cooked foods, with an
increased energy extraction per unit mass compared with raw foods [6,7], could have
sustained the increased energy demand of a larger brain (among other possible sources of
energy [2]).

Nonetheless, our understanding of the extent to which human energy turnover
deviates from that of other primates remains incomplete. The recent comparison of TEE
between humans and great apes [2], is influenced by the very low TEE values of orang-utans,
amongst the lowest observed in any mammal. Furthermore, the TEE data for chimpanzees
and bonobos in this study showed much greater variability and imprecision than that typical
of human studies, with a large difference in the mass-controlled TEE of the two ape species
between two different studies [2,8].

Clearly, additional data are needed to understand the evolution of hominin energetics
and its proposed link [1-3] to the peculiar life history traits that modern humans exhibit
relative to other primates. From an ecological perspective, the functioning of the brain
requires continuous energy fuelling but the majority of non-human primates inhabit, and
evolved, in unpredictable seasonal environments that greatly challenge their energy strategy. Some authors have emphasized relationships between environmental unpredictability and the cognitive skills, brain organization and brain size [9,10], while others suggested that hominins may initially have evolved greater stability of energy metabolism, which subsequently allowed encephalization [11].

In the present study, we use an energy intake-based approach to test the hypothesis of a substantial difference in total energy turnover between humans and non-human primates. Specifically, we address the issue whether human traditional societies living at subsistence level have higher food intake and metabolizable energy intake for their body mass, compared with a representative set of 17 free-living non-human primate species. We also test whether these human populations have more stable energy supply year-round compared with other primates.

2. Material and Methods

(a) Non-human primate data.

Daily food intake data were selected from field studies undertaken since the 1970’s, updated with new data (electronic supplementary material, note S1). We excluded intake data that have been pooled among adult/subadult individuals and other age classes or lactating/gestating females. We selected studies that provided an estimate of metabolizable energy intake (17 spp.; electronic supplementary material, table S1). These studies commonly assess the proportion of the different macronutrients in primate diets [12]: protein, fat, structural carbohydrates including cellulose and hemicelluloses among cell wall constituents, non-structural carbohydrates including soluble sugars and storage reserve compounds. Fibre digestibility, especially NDF (i.e. neutral detergent fibres which include cellulose, hemicelluloses and lignin) is determined in captivity for the species under investigation, or...
from primate models sharing similar fermenting digestive systems. In many cases, the
calculation of readily digestible sugars or total non-structural carbohydrates (TNC) in the diet
is estimated as the difference between 100% and the sum of all other nutrients (protein, fat,
NDF, ash). We used results obtained with this mode of calculation as a first data set for
analyzing the metabolizable energy input:body mass relationship across primates. We also
used results of a second method for calculating metabolizable energy intake since TNC
determined by subtraction potentially severely overestimates the true proportion of non-
structural carbohydrates (electronic supplementary material, note S2). In the second method,
we assessed the energy contribution of TNC to metabolizable energy intake based on a
review of published data on the concentration of water soluble sugars and soluble fibres in
primate foods and other tropical fruits and leaves. Results from the two ways of calculating
metabolizable energy intake were referred to as the “High Energy Value of the Diet” (HEVD,
involving TNC determined by subtraction in the original papers) and “Low Energy Value of
the Diet” (LEVD, using a correction for TNC; electronic supplementary material, note S2 and
table S1 and S3). Additional information on study sites and feeding ecology of primates
tested is provided in electronic supplementary material, table S2.

(b) Human data.

For consistency of comparisons and to reduce methodological heterogeneity in the evaluation
of food intake, we focused on populations in which direct quantitative methods were applied.
Strict methodological criteria were retained, including procedures in which foods or dishes
consumed during a meal by adult men and women (above 20 years old) were weighed [13]
details in [14]). These criteria were met for five forest and savannah populations from
tropical Africa (Yassa, Mvae, Bakola, Duupa, Koma) and three Nepalese populations from
mid-altitude temperate areas (considered as a single sample in the original study). Depending
on the population, the diet combines farming products, natural plant resources and/or animal
matter from hunting/fishing activities (electronic supplementary material, table S4). They all
live at subsistence level, that is they broadly rely on self-sufficiency modes of food
production/provisioning and have relatively stable energy balance in the long-term (despite
seasonal variations, they do not experience substantial increase in body mass throughout most
of their adult lifespan, as indicated by cross-sectional measurements across wide age ranges
[15]). They do not appear nutritionally deprived according to surveys of their health status
and body mass index [15-17]. We discarded populations under nutritional transition from
their traditional lifestyle, rural populations practicing substantial cash agriculture, or
populations showing excessive body mass index and inadequate energy balance. For
consistency, we also did not retain studies that approximated individual daily food intake by
weighing the mass of foodstuff brought to the village. Food measurements were made at three
distinct seasons, and these data were averaged to avoid potential energy imbalance that may
occur seasonally, often during the peak season of agriculture [18]. Metabolizable energy
intake (electronic supplementary material, table S1) is calculated from classical nutritional
composition tables for raw and cooked foods as well as from complementary analyses made
for specific foods when required.

(c) Data analysis.

We tested which of the HEVD and LEVD models best reflected the actual amount of
metabolizable energy available to primates and hence provided the most accurate set of data
to be contrasted with human energy intake measurements. Specifically, we tested which of
these models best equated total energy expenditure (TEE) measured with doubly labelled
water, the gold-standard method for measuring TEE in free-ranging animals (published data
for primates and analyses in electronic supplementary material, note S3 and table S5). The
basic assumption underlying this comparison was i) that energy fluxes should broadly equate
to a balanced energy budget, and ii) that energy expenditure is maintained within a narrow
physiological range, making it possible to use it as a reference value (as evidenced by a
growing number of mammal studies [8,19,20]).

As for non-human primates, energy input estimates in humans are subject to some
degree of inaccuracy. To assess data consistency, energy input was contrasted with the daily
energy expenditure measured during three seasons alongside with the food intake studies on
four of the populations tested (Douglas bag technique [21] in this case; published data on
these populations and analyses in electronic supplementary material, note S3 and table S5).

A phylogenetically controlled method (PGLS or phylogenetic least squares
regression) was used to assess the effect of phylogenetic relatedness in the allometric analysis
of food and energy intake across species (electronic supplementary material, note S4 and
figure S1).

3. Results

(a) Energy intake in non-human primates and humans

The LEVD model much more closely matched doubly labelled water measurements of TEE
than the HEVD model (electronic supplementary material; Note S3, fig S2), therefore we
only focus on the former model in the subsequent analyses. Energy intake in our human
sample was consistent with energy expenditure measured in parallel using time-activity-
weighted indirect calorimetry, both calculated as the three-season average ([21]; electronic
supplementary material, note S3 and table S5).

Plotting the non-human primate LEVD energy intake data (electronic supplementary
material, table S1) against species body mass yields the following phylogenetically-controlled
equation:
log(daily energy intake, in kJ.day\(^{-1}\)) = 0.41 + 0.75 \log\text{BM} (N = 17 \text{ spp}), where \text{BM} is body mass. A disproportionate part (96%) of the variation of energy input was explained by body mass variation (table 1; figure 1).

The data show that humans do not consume significantly more energy than other primates with similar mass. The averaged observed value for humans is 10% above the expected LEVD value (electronic supplementary material, table S5), but it clearly falls within the confidence interval of the slope (figure 1). Calculation of the 95% prediction limits of the LEVD regression for an additional datum (20, 22), energy intake of humans should be > 79% above the predicted value to produce a significant difference (two-tailed t test; > 62% with a one-tailed t-test). Similarly, with a 18% positive deviation from the TEE expected from the TEE:body mass regression published for primate species using doubly labelled water [8], mean energy intake of the humans studied remains largely below the upper limit at 54% of the 95% prediction interval (two-tailed test) calculated for this regression line (43% with a one-tailed test).

Seasonal data available show that human populations exhibit minor variations of energy intake (median 7%, range 2–18%) relative to the nine primate species for which data are available (electronic supplementary material, table S1). Non-human primates show large seasonal variation regardless of their dietary adaptations, body size and phylogenetical relatedness (median 118%, range 0–547%). Exceptions (no variation observed) are the folivorous mountain gorillas that inhabit a relatively stable montane forest environment.

(b) Food intake in humans versus other primates

Food intake in primates including humans (averaged from six populations) follows an allometric relationship in which the equation is:

\[
\log(\text{wet matter input, g.day}^{-1}) = 0.11 + 0.73 \log(\text{body mass, g}).
\]
according to phylogenetic least square regression (table 1). An allometric exponent of 0.74 ± 0.16 is found using dry matter intake (database only available for non human primates in this case; electronic supplementary material, figure S3). Each human population falls as a low outlier in the regression analysis using wet matter (with Homo residual > -3 standard deviations). Figure 2 shows, besides the phylogenetically controlled regression for non-human primates alone, daily food intakes measured in the various human populations studied. All human groups studied consistently ingest remarkably less food than predicted from their body mass, with a conspicuously low mean value of only 36 ± 6% (i.e. 2600 g less, on average) that expected in a non-human primate of the same body size. Only Propithecus coronatus consume very little food relative to its body mass but periods of observations were biased towards the long dry season when animals exhibited a thrifty energy strategy (reference in electronic supplementary material, table S1).

The average energy density of the human diets (population mean ± sd: 6.8 ± 1.6 kJ.g\(^{-1}\) of wet diet including raw and cooked foods) was 178% greater than that of wild non-human primates (species mean ± sd: 2.4 ± 0.6 kJ.g\(^{-1}\) of wet matter).

4. Discussion

Our key finding is that, with a far more rich and energy-dense diet compared to other primates, humans consume much less food to obtain the amount of calories expected relative to their mass. At first glance, these results contradict the hypothesis that the costs of brain enlargement could be compensated by extra energy input. A recent study [2] stated that humans have 27% greater total energy expenditure relative to chimpanzees and bonobos but, as shown in figure 1, the greater energy expenditure of humans relative to apes [2] emerges in part because the three ape species have similar (Pan) or lower TEE (Gorilla, Pongo) than predicted for their body mass. Other relatively large-brain monkeys show only moderate
increase of TEE relative to the expected value (e.g. Sapajus apella; [23]), and their TEE
adjusted for body mass is much smaller than that observed in several primates with a smaller
brain — e.g. some small-brain species fall above the 95% confidence limits of the slope, with
a deviation of 22 to 36% above expectations (see the grey symbols and solid black line in
figure 1).

All data available therefore suggest that humans do not stand out as a major outlier
in the primate data. We acknowledge that measurements of food intake have shortcomings
that challenge comparisons of daily energy intake across human groups or primate species.
For instance, part of the variance observed in the energy intake:body mass relationship for
primates likely reflects measurement errors. In food intake surveys of humans associated with
food weighing, there are inter-observer errors, and some study subjects may omit to declare
the food they consumed outside their regular meals. There is also some uncertainty in the
energy value of some cooked foods, and potentially large day-to-day variation in energy
balance through variation in food intake and physical activity. However, this latter effect is
reduced in the case of weekly monitoring [24], the method we used here. On the positive side,
low costs of the method allow energy intake to be measured in larger sample sizes than usual
in isotope studies and in different seasons, which collectively improves accuracy of habitual
energy turnover at the population level. Of note, our analysis of seasonal data averaged for
the year showed that energy intake estimates did not differ significantly from energy
expenditure measurements in the subsample we analysed (electronic supplementary material,
ote note S3 and table S5). This suggests that any inaccuracy in our method should not markedly
affect our conclusions.

In the same way, the variability around the allometric regression line drawn for
energy intake does not necessarily result mainly from methodological inaccuracy but may
also reflect species or population biological characteristics. We note for example the
important variance in the scaling of primate TEE data with body mass (see § above) despite
the use of a rigorous method (doubly labelled water). Clearly, greater accuracy in future
energy intake studies and standardization of these methods relative to isotopic studies should
increase the robustness of comparative analyses.

Keeping in mind these methodological issues, our meta-analysis of primate energy
intake suggests that ‘reorganization’ of the energy budget, rather than substantially increasing
its total value, was probably an important step in brain evolution in the genus *Homo* [1,3].

There are several different ways in which such reorganization could have been achieved.
First, the classic ‘expensive tissue hypothesis’ proposed that energy was diverted to the brain
through reducing size of the gut [25] but this hypothesis has not been supported across
mammals in general, and across primates in particular [3,26]. However, other tissues that may
have traded off against the brain include muscle or liver [1,27]. The decreased cost of
digestion due to the remarkable diminution of food intake (see below) may also have
contributed to the assignment of the released energy to maintaining a larger brain. Second,
humans have thrifty life histories, with slow growth profiles, reducing energy demands of
both juveniles and parents supporting them [28]. Third, humans may distribute energy costs
socially, both overall and through cooperative breeding [29-31]. Social capital can provide
‘energy insurance’ protecting individuals from foraging failure [11]. Finally, humans may
also benefit from somatic insurance, in the form of body fat stores. In contrast to social
capital, body fat ring-fences energy for individual use [32]. Each of social and somatic capital
can smooth over fluctuations in energy supply, reducing the need for routinely high energy
intakes [33]. This generic strategy may initially have been favoured to resolve the stress of
seasonality, potentially permitting the onset of encephalization in the absence of raised energy
intakes [11]. Whereas subsistence human populations are able to maintain energy intake
relatively stable across the year, the great seasonal variability in energy intake observed in
nonhuman primates — possibly implying periods of negative energy balance [34-36]
(electronic supplementary material, table S1) — is a telling example of the constraints
imposed by natural food resources on the expansion of energy budgets.

The reduction of the quantity of food ingested to as low as 36% that of a primate
with similar mass, the second main result of our study (Figure 2, see also [37]), suggests that
humans may have targeting foraging at energy-dense foods which in turn may have reduced
the energy costs of digestion. An extensive analysis of the activity budget among primates is
beyond the scope of this paper, nonetheless the total time devoted to subsistence activities in
the humans tested (5h30 ± 1h00, calculated from [21, 38, personal observation]) is not
markedly different from that spent feeding/foraging by chimpanzees, i.e. 5h ± 1h30 in various
habitats (and is less than that in orang-utans and lowland gorillas; [39]). In contrast, the
specific duration of harvesting and processing food relative to feeding time is considerable in
humans. In some hunter-gatherer societies, the cost of ranging is estimated to be 31% greater
than in chimpanzees due to longer distances travelled daily and larger body mass [2,8,40].

We calculate that the increased energy costs of harvesting/processing foods (300-700
kJ.d⁻¹ according to the hunter-gatherer societies considered; electronic supplementary
material, Note S5) could easily be offset by lower costs of digesting smaller food volumes. In
humans, digestion costs represent ~10% of TEE (e.g. [41,42]) and increase basal energy
expenditure by ~25% [43]. Based on predictive equations incorporating meal size and body
mass, a human consuming the reduced amount of food we report here, relative to the primate-
predicted amount (~64%), would experience ~600 kJ.d⁻¹ lower costs of digestion (electronic
supplementary material, Note S5). Experimental studies on animal models with a digestive
physiology similar to humans, such as pigs, indicate that further meal reductions can reduce
digestion costs much more (~1600 kJ.d⁻¹; [44]). We note that this energy saving could
compensate for both the higher cost of foraging for energy-dense foods, and for maintaining a
large brain (the increased energy cost of the human brain compared to a chimpanzee is estimated at ~800 kJ d\(^{-1}\) [2]; electronic supplementary material, Note S5) among other metabolically costly organs. Moreover, on an evolutionary scale, the transition from a relatively fibrous diet toward softer edible foods in the genus *Homo* [4] likely led to an additional decrease in the energy cost of digestion [45].

In conclusion, greater stability of energy use may have been important for human evolution, as others argued, while total energy budget does not seem to have increased to unusual proportions relative to other primates. We hypothesize that the calories saved by using readily digestible foods may have been one of the various means of reallocating energy to energy-demanding organs or costly life history traits specific to human. Future studies should investigate the variation of digestion costs in different nutritional contexts in humans and non-human primates to tackle this evolutionary biology issue in a more appropriate phylogenetic perspective.

Data accessibility. The datasets supporting this article have been uploaded as part of the electronic supplementary material.

Authors’ contributions. B.S. designed the study, analysed data, and drafted the manuscript. B.S. and S.M. contributed to new data collection in the field. All authors interpreted the data and wrote the paper. All authors approved the final version before publication.

Competing interests. We have no competing interests.

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Table legends

Table 1. Results of the phylogenetic generalized least-square models testing the strength of
the phylogenetic signal ($\lambda$) for various $Y$ parameters plotted against body mass ($\log Y = \alpha + \beta$
$logBM$, with $BM$ in g).
Figure legends

Figure 1. Scaling of daily energy intake and total daily energy expenditure (TEE) with species body weight in non-human primates and subsistence-level humans. Main figure: the solid orange regression line, \( y = 0.75(\pm0.04)x + 0.42(\pm0.15) \), refers to the “Low Energy Value of the Diet” (LEVD: filled circles) database for non-human primates (averaged for each species where seasonal data or different population data are available; electronic supplementary material, table S1). The solid black line shows the scaling of TEE (measured using doubly labelled water; diamonds) with body mass in primates, \( y = 0.73(\pm0.03)x + 0.45(\pm0.12) \) (after [8]). Recent additional TEE results for apes [2] include data combined for chimpanzees and bonobos (\( Pan^* \)). The average energy intake of human populations tested in this study (blue circle; \( N = 6 \)) is shown. Regressions using best-fit models are derived from phylogenetically controlled analysis (table 1). The dotted lines show the 95% confidence interval for each of the two regression lines. Box: details of human deviation from the TEE:body mass relationship (populations averaged for men and women; Y: Yassa, M: Mvae, D: Duupa, T: Nepalese, B: Bakola, K: Koma).

Figure 2. Relationship between daily food intake and body weight of primates. The regression line is calculated for free-ranging non-human primate species using the best-fit model derived from the phylogenetically controlled analysis (table 1). Human populations are figured separately. The dotted lines show the 95% confidence interval for the regression line.
Figure 1. Scaling of daily energy intake and total daily energy expenditure (TEE) with species body weight in non-human primates and subsistence-level humans. Main figure: the solid orange regression line, $y = 0.75(\pm0.04)x + 0.42(\pm0.15)$, refers to the "Low Energy Value of the Diet" (LEVD: filled circles) database for non-human primates (averaged for each species where seasonal data or different population data are available; electronic supplementary material, table S1). The solid black line shows the scaling of TEE (measured using doubly labelled water; diamonds) with body mass in primates, $y = 0.73(\pm0.03)x + 0.45(\pm0.12)$ (after [8]). Recent additional TEE results for apes [2] include data combined for chimpanzees and bonobos (Pan*). The average energy intake of human populations tested in this study (blue circle; N = 6) is shown. Regressions using best-fit models are derived from phylogenetically controlled analysis (table 1). The dotted lines show the 95% confidence interval for each of the two regression lines. Box: details of human deviation from the TEE:body mass relationship (populations averaged for men and women; Y: Yassa, M: Mvae, D: Duupa, T: Nepalese, B: Bakola, K: Koma).
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