

Supplementary Materials for

Primate energy input and the evolutionary transition to energy-dense diets in humans

Bruno Simmen, Patrick Pasquet, Shelly Masi, Georgius J.A. Koppert,
Jonathan C.K. Wells, Claude Marcel Hladik

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Supplementary note 1. Food intake data in non-human primates and humans

Non human primate taxa. Primate species studied show diverse phylogenetic relatedness (Strepsirhines and Haplorhines), geographic and ecological diversity, and almost span the full range of body size found in living Primates (table S1). They also have diets that require morphological and physiological specializations (hindgut and foregut fermenters among folivorous species) or diets associated with a simple digestive tract as in omnivorous species or species that primarily feed on ripe fruits or a combination of arthropods and fruits.

Food intake. The quantitative method used by field primatologists to estimate food intake is based on direct observation of ingestion and counts of mouthfuls, supplemented with records of feeding rates, usually obtained by following individuals from dawn to dusk. Mouthfuls are converted into wet/dry matter of ingested food, weighing aliquot amounts of each food item [28, 29]. The evaluation of daily food intake in primates living under natural conditions is inherently imperfect, since the weight of foods ingested cannot be directly measured, unlike in closely-controlled human studies. However, previous research has shown that the most reliable and consistent results are obtained with the mouthful method [30,31] ([32] for a comparison with stomach contents). The

prerequisites are: sufficient visibility and full habituation of groups or individuals to human observers allowing tracking of animals at a close distance. We discarded studies that determined the contribution to the diet of food items (a) based on the time the animals were feeding on these items or (b) using the feeding frequency method (as opposed to the estimation of ingested quantities), both of which poorly reflect the amount of food consumed [28-30]. We also discarded studies that involved food provisioning prior to actual measurements of food intake, and some early studies that clearly underestimated energy intake.

In human populations studied, foods or dishes consumed during a meal by individuals or groups of individuals are weighed [32]. In the present paper, we only used data for adult men and women, but field records were obtained from whole families, each surveyed on a weekly basis. In most populations food was consumed in relatively small groups of 1-3 individuals often composed of people of the same gender and age. The food consumption was estimated from common dishes by an iterative process that estimated sharing coefficient within 15 sex and age groups, as defined by the FAO [33]. Sharing coefficient stabilized after 2-3 iterations and did not change anymore after 5 iterations (details in [24,34]). Sharing coefficient allowed to estimate individual consumption in mixed groups. For instance 23,376 dishes were consumed among the Yassa by consumer groups from these 15 sex and age categories (requiring a huge numbers of observers). The first step was to divide each dish equally among its consumers, and average the result for each group. The average consumption of men over 50 years (category 9) is almost 120% of the average of men 20-49, while for group 4 (boys 10-12y) it is about 65%. Using these sharing coefficients (120% and 65%) in a second iteration hardly changes the results, because these two categories eat in homogeneous separate groups. The youngest children usually eat in groups with various other age groups and adults, so that the successive iterations lead later to an equilibrium of the sharing coefficients.

Data on food intake, energy intake and study sites in primate species and human populations tested are summarized in tables S1, S2 and S4.

Supplementary note 2. Energy input models in non-human primates

Models and databases. We focused on studies that aim to estimate ‘metabolizable energy intake’, ie the proportion of ingested energy that is metabolised according to species’ digestive physiology.

Formally, metabolizable energy content of the diet is the gross energy content adjusted for losses in faeces and urine. Typically, however, most studies of primate energy input assess separately protein, fat, neutral detergent fibres (NDF, i.e. cellulose + hemicellulose + lignin) and soluble sugars or total non-structural (or water soluble) carbohydrates (TNC) content in the diet and use energy conversion factors and species-specific digestibility coefficients to calculate metabolizable energy intake. For instance, the metabolizable energy obtained from fibres depends on fermentation and symbiotic activity from the gut microbiota, and is inferred using digestibility coefficients derived from tests on captive primates (or more rarely, wild individuals temporarily kept in a cage). The standard energy conversion for protein, carbohydrate and fat is 4 kCal.g⁻¹, 4 kCal.g⁻¹, 9 kCal.g⁻¹ but a value of 3 kCal.g⁻¹ is usually preferred for structural carbohydrates to account for the energy used by the intestinal microbiota themselves [44]. TNC is commonly calculated by subtraction as [100- (protein+NDF+fat+ash)]%, following previous application to the determination of human food composition, but this procedure has been regularly questioned, *e.g.* [29, 45-47]. In our primate sample (table S3), TNC determined by subtraction (hereafter referred to as TNC_{sub}) account for 20 to 64% of the dry matter according to primate diets, but such calculation also captures a range of non-carbohydrate components, including organic acids, vitamins, micronutrients, resins and secondary metabolites, some of which may amount to a substantial proportion in primate diets compared with human foods. For instance, condensed tannins reach 20% of the total dry matter of some leaves eaten by mountain gorillas (using internal standards for calibration curves [49]; see also [50]: 7-26% in legume leaves). Therefore, calculating TNC by subtraction may overestimate energy input if other non-caloric substances occur in foods. The concentration of water-soluble sugars has been measured as a substitute for TNC in some studies (*Gorilla beringei beringei*,

Alouatta palliata, *Cebus capucinus*, *Saguinus geofroyi*), but this assay detects only part of the stored soluble sugars beside simple sugars, and does not measure soluble fibres like pectin [29].

Therefore, daily metabolizable energy intake was compared between primate species in our allometric analyses using two databases separately: one set of results corresponding to energy intake calculated according to TNC_{sub} as published in the original papers, which we referred to as the “High-Energy Value of the Diet” (HEVD) database; and a “Low-Energy Value of the Diet” (LEVD) database in which we reduced the energy contribution of TNC_{sub} according to current knowledge of the soluble carbohydrate content of primate foods (table S1; details of calculation below). Since the available information on the spectrum and concentration of the different categories of non-structural carbohydrates in primate diets is fragmentary, we estimated non-structural carbohydrates in the LEVD model by combining information about the concentration of soluble sugar (fructose, glucose and sucrose) with that on starch and soluble fibre in primate diets, supplemented with data from tropical plants.

In the LEVD model, we followed the rule that when the original studies reported the concentration of simple soluble sugars but not of soluble fibre, we calculated total daily energy intake assuming an average concentration of 5% as starch plus 5% as pectin in the total dry matter ingested daily, in addition to the other nutrients assessed. These starch and pectin concentrations are rounded figures derived from our review of primate food chemistry (see ‘*Non-structural carbohydrates in the LEVD model*’). If water-soluble carbohydrates were reported, only a concentration of 5% as pectin was added for calculation of energy input. Finally, when daily energy intake was calculated based on TNC_{sub} determination in the original study (i.e. HEVD), we multiplied reported energy intake by a correction factor of 74%. This factor represents the average difference between energy intake calculated combining the concentrations of individual components of non-structural carbohydrates (soluble sugars, starch and pectin) with other nutrients versus the HEVD mode of calculation (see below the rationale and table S3). In one study, metabolizable energy input was calculated from the gross energy content of foods (kJ.g^{-1}) measured

by bomb calorimetry, supplemented with an assessment of energy loss in faeces (*Leontopithecus rosalia*: [10]). Energy intake reported in this study was assigned to the LEVD model group.

Non-structural carbohydrates in the LEVD model: Simple soluble sugars represent on average 48 ± 13 % of TNC_{sub} in primate diets primarily composed of ripe fruits supplemented with leaves and flowers, and only 15 ± 5 % in diets primarily including vegetative plant parts (weighted intake data; table S3). In the western gorilla's diet, for which we performed a more detailed analysis of food nutrient content [22], the contribution of simple soluble sugars to TNC_{sub} is similar to that of other primates and accounts, together with starch, for only a slightly higher proportion of TNC_{sub} , averaging 52 ± 14 % in fruits and 20 ± 18 % in non-reproductive plant parts. Starch concentration in the gorilla diet is consistent with the few data published for other primates as well as for tropical cultivated plants, with values averaging 3-6% in ripe and unripe fruits and 1-4% in vegetative plant parts overall [8,22,51,52]. Beside simple sugars and starch, other nutrient categories like soluble fibres in the TNC_{sub} fraction provide readily digestible energy. Pectins were found to average 4-6% of the dry matter in fruits and leaves eaten by wild howler monkeys, the only primate species for which data are available [53]. Pectins are widespread in fruit and some tropical leaves [29], but low concentrations have generally been reported in tropical fruits (0.2-1% of the wet weight; e.g. [54]).

Assuming pectin content of the diet of western gorillas and the different primate species of table S4 are similar to that found for howler monkeys, the summed percentage of soluble sugars, starch and pectin would account for 44 ± 9 % of TNC_{sub} in leaf-/unripe fruit-based diets (n=11) versus 68 ± 10 % in ripe fruit-based diets (n=7). However the TNC_{sub} percentage of the total dry matter ingested is lower when leaf /unripe fruits dominate in diets (35 vs 54% on average). Accordingly, the results show that whatever the food categories dominating diets, energy input calculated by summing all different non-structural carbohydrate fractions (i.e. the LEVD model) account for a similar proportion of energy input calculated with the HEVD model, averaging 74 ± 8 % (table S3).

Specific calculations:

Propithecus coronatus, *Propithecus verreauxi* (gallery forest), *Lemur catta*, *Eulemur sp.*, *Eulemur fulvus mayottensis*. Data on protein, lipid, NDF and simple soluble sugars in the seasonal diets of these species were supplemented with chemical assays on ash content (and NDF in *E.f. mayottensis*). This allowed us to assess the contribution of soluble sugars to total non-structural carbohydrates (TNC) determined by subtraction and to build the two different models of energy intake (see ‘Energy input models’ above). When NDF content in the diet of *Eulemur* species studied was < 31%, we used a 41% NDF digestibility coefficient to evaluate the amount of energy derived from microbial fermentation [55]. When fibre content was higher (usually dry season diets) we used 20% fibre digestibility on the basis that cellulose digestibility is only 0 to 21% according to particle size in *Eulemur fulvus* (0 to 30% in *Lemur catta*; [56]) and NDF digestibility in the closely related *Eulemur macaco* is only 12% when fed fibre-rich diets > 31% [57]. The same criteria were used for *Lemur catta*. In captive sifakas fed the same 31% NDF diet as that used for *Eulemur*, NDF digestibility is 60% but is reduced to 41% if the diet contains a higher fibre content (*Propithecus verreauxi*; see also *P. tattersalli*; [55,58]). Since the two wild *Propithecus* populations tested had fibre-rich diets, we used a 41% NDF digestibility coefficient in each case. Body mass data for *P. verreauxi* ($N = 25$) have been collected in 2014 at Berenty Private Reserve by Simmen *et al.* as part of an on-going project on the energetics and reproduction in the sifaka.

Propithecus verreauxi (dry deciduous forest). One population (9-11 focal individuals from 2-3 groups) was studied over a 6-month period (858 hours) in a dry deciduous forest south of Madagascar in the Berenty Private Reserve. Nutrient input was estimated on adult males and females at two different seasons, including part of the lean season during the austral winter (July-September 2007) and during the early wet season when rainfall resumes and young leaves and flowers are abundant (October-December 2009). Since NDF content in the diet varied seasonally

from 30 to 37%, we used 60% and 41% NDF digestibility respectively in our calculations of energy intake (see above). Feeding data were collected by BS, Zoly Sarah and F. Ravahatramananjarasoa. Body mass data have been collected in 2014 at Berenty Private Reserve by Simmen *et al.* (same research project as mentioned above for gallery forest sifakas).

Propithecus diadema. We selected 2007 data corresponding to one sifaka group that contained non-reproductive individuals (group “Cont 2” during austral winter, fig 1 in [7]).

Alouatta pigra. We added NDF (from table IV in [13] in the calculation of total energy input (using 45% NDF digestibility in howler monkeys; [59]).

Ateles chamek. We added 36% NDF (table II in [48]) in the calculation of total energy input using 23% NDF digestibility for a monogastric fruit-specialist primate (average from [55,57,60]).

Gorilla gorilla. Daily food intake data for the silverback male were collected and calculated by SM from one habituated group of Western gorillas in Bai Hokou Central African Republic (December 2004-December 2005). Energy intake, as published in [22], is derived from these measures.

Supplementary note 3. Intake-based estimates of energy expenditure vs doubly labelled water measurements (non-human primates) or calorimetry (humans)

- *Primate studies*. Since two modes of calculation (HEVD, LEVD) were used to investigate metabolizable energy intake of wild primates, we tested whether results derived from these models can be equated with total energy expenditure (TEE) measured with doubly labelled water, the gold standard method for measuring TEE. We follow here [61,62] who, based on the isotopic method, emphasize the lack of substantial variation in energy expenditure between seasons across a range of homeothermic mammal species, or between captive and wild subjects of the same species

(including primates), or between hunter-gatherers and sedentary urban populations after correcting for body mass differences. One explanation why TEE is maintained within a narrow physiological range, though there are exceptions, seems to be that the body is able to compensate for the increased physical activity by modifying the energetic allocation to the other functions (e.g. through changes of BMR or reproductive investment; [61,63,64]).

As a first approach, we tested whether HEVD and LEVD results can be equated with TEE in the same species. Paired-data available for use in this analysis are limited to 8 species. We minimized the risk of including long periods of negative and positive energy balance in species showing large seasonal changes in energy intake (*L. catta*, *E. fulvus*, *P. pygmaeus*, *P. diadema*) by selecting periods intermediate between lean and high-food supply seasons. Energy intake estimated with the HEVD model was significantly higher than TEE (Wilcoxon signed rank test for non-normal distribution; mean difference = $1,770 \pm 2,208 \text{ kJ.day}^{-1}$, $W = 28$, $P < 0.02$, $df = 6$; Table S5). In contrast, there was no significant difference between the LEVD data and TEE data (paired-sample *t*-test, controlling for normality of the data: mean difference = $144 \pm 606 \text{ kJ.day}^{-1}$, $t = 0.492$, $P < 0.7$, $df = 7$; table S5) suggesting that this model more closely reflects the amount of metabolizable energy available to primates than the HEVD model. Since the non-human primate data used in the allometric comparisons with humans were averaged between different periods of the year (figure 1), we re-ran the comparison of intake-based estimates vs TEE using the averaged data (table S1). Again, energy intake estimated with the HEVD model provided overestimated values (mean difference = $1,897 \pm 2,311 \text{ kJ.day}^{-1}$, $W = 28$, $P < 0.02$, $df = 6$) whereas no significant difference was detected between LEVD and TEE (mean difference = $245 \pm 764 \text{ kJ.day}^{-1}$, $t = 0.737$, $P < 0.5$, $df = 7$).

As a complementary approach, we contrasted the slope and intercept of the allometric relationships found using HEVD or LEVD with those derived from the TEE:mass relationship published in [65] excluding the torpid lesser mouse lemurs: $\log(\text{daily energy expenditure, in kJ.day}^{-1}) = 0.449 + 0.734 \log \text{BM}$, where BM is body mass in g, with energy expenditure values measured

with doubly labelled water and converted in $\text{kJ}\cdot\text{day}^{-1}$ (using a 4.18 multiplication factor). In this comparison based on the whole set of primate species contributing to the databases on energy input and energy output, the LEVD model was also the most consistent (figure S2). The allometric coefficient was close to 0.75, indicating that the larger the primates the less energy they consumed per gram body mass, as expected. The intercept of the regression line for LEVD data was almost identical to that for TEE, with a mean deviation of only $108 \pm 27\%$ above the TEE:mass slope (versus $131 \pm 25\%$ for the HEVD model).

- *Human studies.* As for non-human primates, energy input estimates in humans are subject to some degree of inaccuracy. For instance, nutritional composition tables used classically to assess energy input from raw and cooked foods may not correctly account for the net effect of cooking and non-thermal processes on energy input. For example, cooking increases the digestibility of resistant starch but can also reduce the amount of energy available according to the mode of preparation of a dish (e.g. potential loss of nutrients through amylose and amylopectin solubilization in boiled starchy foods, or fat loss due to dripping in roasted meat [66]). Accordingly, as for non-human primates, we assessed whether estimated daily energy input equates daily energy expenditure. Together with the food intake studies carried out during three seasons to cover an annual cycle, daily energy expenditure was investigated by one of us (PP) in men and women in 4 of the populations tested using repeated short-term respirometry measurements (Douglas bag technique). These physiological measurements were made during major daily activities, including resting at wakening (supplemented with estimates of the costs of minor activities and sleep), and were weighted according to individual time budgets, allowing total daily energy expenditure to be estimated [67,68] (table S5). Daily metabolizable energy intake did not differ significantly from daily energy expenditure in these populations (two-tailed paired-sample t test after controlling for normality with Shapiro-Wilk test and considering men and women as separate samples in each of the four populations, mean difference = $-220 \pm 747 \text{ kJ}\cdot\text{day}^{-1}$, $t = -0.833$, $P < 0.5$, $df = 7$). Therefore,

energy intake estimates are sufficiently reliable when they are averaged across the human sample studied (with the same protocol) for an interspecific comparative purpose.

In these human populations, the mean deviation of energy expenditure relative to the primate TEE:mass relationship was $119 \pm 12\%$. They had lower TEE and physical activity level (average PAL: 1.75, range: 1.65-1.81; table S5) than some other farming populations, for instance Massa or Gambian farmers, but the latter practice cash agriculture and were measured during the peak of agricultural season [69-71].

Supplementary note 4. Statistical analyses of food and energy intake

We used phylogenetic least squares regressions (PGLS) to control for phylogenetic effects in allometric analyses [72]. We first reconstructed a phylogenetic tree (figure S1) from the published database of Bininda-Emonds *et al.* [73] on mammal phylogenetic relationships with branch length specified. When relevant, Perelman *et al.*'s [74] and Zinner *et al.*'s [75] primate phylogenies were used to specify relationships unresolved in the Bininda-Emonds *et al.* database. The strength of the phylogenetic signal (λ) in regression analyses was determined according to maximum likelihood in BayesTraits v2 (on-line version of July 2013; [76, 77]). Best-fit models were assessed from log-likelihood (Lh) scores [78]. Differences are considered significant at $\alpha < 0.05$.

Supplementary note 5. Costs of digestion and diet

As both body mass and meal size can be used to predict the cost of specific dynamic action in humans ($SDA = 1.83 \text{body mass (in kg)} + 0.26 \text{meal mass (in g)} + 123.6$; [79]), we calculated that an individual would save $\sim 600 \text{ kJ.d}^{-1}$ by reducing the quantity of food ingested to as low as 36% that of a primate with similar mass, as we report in this study (figure 2). The volume of food, raw or combined with cooked foods, that our hunter-gatherer ancestors have been consuming is unknown, nonetheless one study [80] documents the foraging effort and yield of Baka familial groups engaged for several months in expeditions dedicated to hunting and gathering. These activities yield

about $2 \text{ kg}\cdot\text{d}^{-1}$ per individual of edible fresh food, mainly yam and meat as a complement (versus $1.5 \text{ kg}\cdot\text{d}^{-1}$ on average in subsistence populations tested). These forest foods represent only 40% of the mass of food consumed daily by a primate with similar mass (36% in our populations, as mentioned above), which would then result in a $\sim 500 \text{ kJ}\cdot\text{d}^{-1}$ SDA reduction based on the same predictive equations.

Of course, food reduction has occurred over a much longer time scale during human evolution and its impact on the evolution of the energy budget cannot simply be extrapolated from short-term food restriction studies. Overall, however, these calculations converge to indicate that with reliance on easier-to-digest diets and the “relaxation” of digestion costs, a substantial portion of total energy expenditure likely has been saved. There are no data available on digestion costs in non-human primates but experimental studies indicate that domestic pigs of the size of normal-weight humans, with whom they share an omnivorous tendency and a functionally similar digestive system, show a $\sim 1600 \text{ kJ}\cdot\text{d}^{-1}$ reduction of the thermal effect of feeding when submitted to a 40 % decrease in the size of a $\sim 2.4\text{-kg}$ readily digestible meal [81]. Therefore, there has been a potential for significant net energy gain since early humans changed their diet by ingesting a lower amount of less fibrous food, with both quantitative and qualitative factors resulting in reduced digestion costs [82]. A substantial reduction in energy expenditure through this mechanism could offset both the increased energetic cost of the brain ($815 \text{ kJ}\cdot\text{d}^{-1}$ relative to this ape species, assuming a similar metabolic rate per unit of brain mass [61]) and the greater locomotion costs of hunter-gatherers relative to chimpanzees ($< 700 \text{ kJ}\cdot\text{d}^{-1}$). Indeed, the average daily energy cost of ranging is 31% greater in the Hadza (ie, $297 \text{ kJ}\cdot\text{d}^{-1}$; [64], and up to 66% greater in Ache (ie, $700 \text{ kJ}\cdot\text{d}^{-1}$), another hunter-gatherer society that travels almost 4 times more kilometres each day than chimpanzees (chimpanzees: $4 \text{ km}\cdot\text{d}^{-1}$ [64], Hadza: $11.8 \text{ km}\cdot\text{d}^{-1}$ [64], Ache: $14.2 \text{ km}\cdot\text{d}^{-1}$ [83]; data combined for both sexes). In this comparison with apes, the daily locomotor cost of the Ache was first calculated for each sex by multiplying the daily walking distance (M: $19.2 \text{ km}\cdot\text{d}^{-1}$, F: $9.9 \text{ km}\cdot\text{d}^{-1}$ [83]) by the metabolic cost of walking ($2.05 \text{ kJ}\cdot\text{kg}^{-1}\cdot\text{km}^{-1}$ [64]) and body mass (M: 59.6 kg , F: 51.8 kg [83]).

Supplementary tables

Table S1. Body size, food and energy intake in free-ranging non-human primates and human populations at subsistence level

| Species | Sex | Body weight (g) | Food intake wet weight (g.day ⁻¹) | Daily energy intake | | Seasonal change energy (%) | Refs. |
|----------------------------------|-----|--------------------|---|---|--|----------------------------------|----------------------|
| | | | | HEVD high value (kJ.day ⁻¹) | LEVD low value (kJ.day ⁻¹) | | |
| Non-human primates | | | | | | | |
| <i>Lemur catta</i> | M+F | 2280 | 447 | 1207 | 910 | 133 | [1, 2], this study |
| <i>Eulemur sp</i> | M+F | 1840 | 452 | 1093 | 761 | 39 | [1, 2], this study |
| <i>Eulemur f. mayottensis</i> | F | 1840* | 258 | 773 | 597 | na | [3, 4], this study |
| <i>Propithecus coronatus</i> | M+F | 3600 | 238 | 1069 | 715 | 46 | [5], this study |
| <i>Propithecus diadema</i> | M+F | 5140 | na | 2250 | 1665 | - | [6, 7] |
| <i>Propithecus verreauxi</i> | M | 3100 | 343 | 1310 | 1020 | 116 | [1], this study |
| <i>Propithecus verreauxi</i> | M+F | 2800 | 362 | 1182 | 929 | 119 | this study |
| <i>Saguinus geoffroyi</i> | M+F | 515* | 125 | na | 381 | na | [8, 9] |
| <i>Leontopithecus rosalia</i> | F | 650 | na | na | 259 [†] | 165 | [10] |
| <i>Cebus capucinus</i> | M+F | 3000* | 400 | na | 1324 | na | [8, 11] |
| <i>Alouatta palliata</i> | M+F | 7000* | 1200 | na | 2292 | na | [8, 12] |
| <i>Alouatta pigra</i> | M+F | 6640* | 1096 | 3202 | 2369 | na | [13, 14] |
| <i>Ateles chamek</i> | M+F | 8250 | 1000 | na | 2446 | na | [15] |
| <i>Papio cynocephalus</i> | M | 23120* | 1361 | 6383 | 4723 | na | [9, 16] |
| <i>Papio ursinus</i> | F | 15500 | 1900 | 3929 | 2908 | na | [17] |
| <i>Pongo pygmaeus</i> | M+F | 62500* | na | 14789 | 10944 | 391 | [18, 19] |
| <i>Pongo pygmaeus</i> | M+F | 56700* | na | 7038 | 5208 | 547 | [19, 20] |
| <i>Gorilla beringei beringei</i> | M | 200000 | 18800 | na | 38530 | none | [21] |
| <i>Gorilla gorilla gorilla</i> | M | 169000* | 6852 | 21059 | 15584 | 65 | [22, 23], this study |
| <hr/> | | | | | | | |
| Humans | Sex | Body weight (g) | Food intake wet weight (g.day ⁻¹) | Energy intake (kJ.day ⁻¹) | | Seasonal change energy (%) | Refs. |
| Yassa | M+F | 56800 | 1678 | 10246 | | 2 | [24, 25] |
| Mvae | M+F | 57100 | 1560 | 9527 | | 3 | [24, 25] |
| (Ba)Kola | M+F | 46600 | 1598 | 9315 | | 18 | [24, 25] |
| Duupa | M+F | 49350 | 1390 | 9227 | | 2 | [25, 26] |
| Koma | M+F | 50800 | 1591 | 9677 | | 10 | [25, 26] |
| Tamang, Ghale, Kami | M+F | 47250 | 934 | 9246 | | 15 | [27] |

Models for High Energy Value of the Diet (HEVD) and Low Energy Value of the Diet (LEVD) differ in the mode of calculation for total soluble carbohydrate content in the diet (note S2). “Seasonal change” is expressed as the % increase or decrease between the two most different seasons (or, for humans, crop periods, ritual and celebration periods versus lean periods). na: not available; Body mass data in non-human primates are taken from the original studies that estimated daily energy input (references indicated) or from other sources (*). [†]: gross energy corrected for dry matter digestibility. Energy intake data presented for humans >20 years old were selected from the larger datasets used in the published studies indicated. See tables S2 and S4 for study sites and additional references.

Table S2. Study site, ecology and food intake (as dry matter) in non-human primates

| Species | Diet | Study site | Habitat | Body weight (g) | Dry matter intake (g.day ⁻¹) | Refs. |
|----------------------------------|----------|--|-----------------------------------|--------------------|---|----------|
| <i>Lemur catta</i> | F/O | Berenty private reserve, Madagascar | gallery forest | 2280 | 103 | - |
| <i>Eulemur sp.</i> | F/O | Berenty private reserve, Madagascar | gallery forest | 1840 | 94 | - |
| <i>Eulemur f. mayottensis</i> | F/O | Saziley, Mayotte | semi-deciduous dry forest | 1840 | 67 | - |
| <i>Lepilemur leucopus</i> | Fol | Berenty private reserve, Madagascar | dry deciduous forest | 609 | 65 | [36] |
| <i>Propithecus coronatus</i> | Fol | Antrema, Madagascar | semi-deciduous dry forest | 3600 | 92 | - |
| <i>Propithecus diadema</i> | Fol (sd) | Ranomafana, Madagascar | mid-mountain evergreen rainforest | 5140 | 210 | - |
| <i>Propithecus verreauxi</i> | Fol | Berenty private reserve, Madagascar | gallery forest | 3100 | 117 | - |
| <i>Propithecus verreauxi</i> | Fol | Berenty private reserve, Madagascar | dry deciduous forest | 2800 | 94 | - |
| <i>Saguinus geoffroyi</i> | F/O | BCI, Panama | evergreen rainforest | 515 | 31 | - |
| <i>Leontopithecus rosalia</i> | F/O | Poco das Antas Biological Reserve, Brazil | Atlantic coastal rainforest | 650 | na | - |
| <i>Cebus capucinus</i> | F/O | BCI, Panama | evergreen rainforest | 3000 | 100 | - |
| <i>Alouatta palliata</i> | Fol | BCI, Panama | evergreen rainforest | 7000 | 300 | - |
| <i>Alouatta pigra</i> | Fol | Palenque National Park, Mexico | evergreen rainforest | 6640 | na | - |
| <i>Alouatta seniculus</i> | Fol | Fica Merenberg, Colombia | high-altitude tropical forest | 7300 | 266 | [37] |
| <i>Ateles chamek</i> | F/O | Bolivia | semi-humid forest | 8250 | 262 | - |
| <i>Macaca fuscata</i> | F/O | Shimokita Peninsula, Honshu, Japan | snow-covered forest area | 12600 | 596 | [38] |
| <i>Macaca fuscata</i> | F/O | Kinkazan island, Japan | cool temperate forest | 8000 | 221 | [39] |
| <i>Papio anubis</i> | F/O | Laikipia plateau, Kenya | grassland, dry woodland | 18700 | 492 | [40] |
| <i>Papio cynocephalus</i> | F/O | Amboseli National Park, Kenya | savannah, woodland | 23120 | na | - |
| <i>Papio ursinus</i> | F/O | Table Mountain National Park, South Africa | shrubland, plantations | 15500 | na | - |
| <i>Theropithecus gelada</i> | Fol | Simen Mountain National Park, Ethiopia | tropical alpine vegetation | 18500 | 898 | [41] |
| <i>Semnopithecus entellus</i> | Fol | Polonnaruwa, Sri Lanka | semi-deciduous dry forest | 8650 | 321 | [35, 42] |
| <i>Semnopithecus vetulus</i> | Fol | Polonnaruwa, Sri Lanka | semi-deciduous dry forest | 6240 | 188 | [35, 43] |
| <i>Pongo pygmaeus</i> | F/O | Sabangau, Central Kalimantan, Indonesia | peat-swamp forest | 56700 | 641 | [20] |
| <i>Gorilla beringei beringei</i> | Fol | Bwindi Park, Uganda | mid- and mountain rainforest | 200000 | 3948 | - |
| <i>Gorilla gorilla gorilla</i> | F/O, Fol | Dzanga-Ndoki Nat. Park, Central African Republic | evergreen rainforest | 169000 | 2059 | - |

F/O : Frugivore/omnivore ; Fol : folivore; sd: seed-eater

References: see table S1; additional references where mentioned

Table S3: High Energy Value of the Diet (HEVD) and Low Energy Value of the Diet (LEVD) in primates feeding on different staple foods

| Staple food/Species | Habitat/season | Soluble sugars | | Daily energy intake | | |
|---|----------------|-----------------|-------------------------|--|---|------------------------------|
| | | % dw | % of TNC _{sub} | High value (HEVD) kJ.day ⁻¹ | Low value (LEVD) kJ.day ⁻¹ | % of HEVD |
| A. Ripe fruit diet | | | | | | |
| <i>Lemur catta</i> | GF/ ws | 38.7 | 60.9 | 1412 | 1159 | 82 |
| <i>Eulemur sp.</i> | GF/ lds | 9.4 | 24.2 | 908 | 610 | 67 |
| " | GF/ ws | 21.8 | 43.2 | 1146 | 870 | 76 |
| <i>Eulemur fulvus mayottensis</i> | DSDF / ds | 18.9 | 42.4 | 773 | 597 | 77 |
| " | DSDF / ws | 35.7 | 57.4 | 1214 | 971 | 80 |
| <i>Eulemur macaco</i> | SHF/ ws | 36.3 | 61.5 | 1774 | 1492 | 84 |
| | <i>mean:</i> | 26.8 ± 10.8 | 47.7 ± 13.4 | | | 78 ± 6 |
| B. Ripe fruit/leaf diet | | | | | | |
| <i>Ateles chamek</i> | SHF/ws,ds | 34* | 70 | 2945 [†] | 2456 [†] | 83 |
| C. Vegetative and/or unripe fruit diet | | | | | | |
| <i>Lemur catta</i> | GF / ds | 6.6 | 17.7 | 727 | 473 | 65 |
| " | GF / lds | 9.3 | 25.1 | 1201 | 866 | 72 |
| <i>Eulemur sp.</i> | GF / ds | 6.6 | 18.2 | 1111 | 715 | 64 |
| <i>Propithecus verreauxi</i> | GF / ds | 5.3 | 17.2 | 806 | 611 | 76 |
| " | GF / lds | 4.4 | 19.6 | 1743 | 1525 | 87 |
| " | GF / ws | 6.5 | 15.9 | 1255 | 839 | 67 |
| <i>Propithecus verreauxi</i> | DDF / ds | 4.7 | 11.5 | 740 | 492 | 66 |
| | DDF / ew | 4.8 | 15.1 | 1623 | 1365 | 84 |
| <i>Propithecus coronatus</i> | DSDF / eds | 3 | 7.4 | 905 | 557 | 62 |
| " | DSDF / ds | 4.3 | 10.6 | 982 | 614 | 63 |
| " | DSDF / ws | 3.2 | 10.3 | 1320 | 975 | 74 |
| | <i>mean:</i> | 5.3 ± 1.8 | 15.3 ± 5.1 | | | 70 ± 8 |
| overall mean: | | | | | | 74 ± 8 |

The average amount of metabolizable calories ingested daily is expressed according to two ways of estimating TNC, either by subtraction (HEVD) or taking into account the concentration of simple soluble sugars supplemented with estimates of starch and pectin concentrations (LEVD; electronic supplementary material, note S2). The comparison is made using weighted intake data and diets for which the concentration of simple soluble sugars and of total non-structural carbohydrates (by subtraction: TNC_{sub}) is available. Data are means \pm standard deviation where indicated. *: Water-soluble sugars + starch, [†]: data calculated from table II in [48].

GF: galerie forest; DSDF: dry semi-deciduous forest; SHF: semi-humid forest; DDF: dry deciduous forest. ws: wet season; ds: dry season; eds: early dry season; lds: late dry season; ew: early wet season

Table S4. Study site and food production system in human populations at subsistence level selected according to data available on food intake

| Humans | Staple food | Area | Lifestyle |
|---------------------|--|--------------------------------------|---------------------------------------|
| Yassa | cassava, fish | Southern Cameroon, coastal | fishing, farming |
| Mvae | cassava, vegetables, fruits, meat, fish | Southern Cameroon, forest | hunter-farmers |
| Bakola | cassava, meat, vegetables | Southern Cameroon, forest | hunter-gatherers, rudimentary farming |
| Duupa | cereals, legumes, vegetables, peanuts | Northern Cameroon, mountain savannah | farmers |
| Koma | cereals, tubers, vegetables | Northern Cameroon, mountain savannah | farmers |
| Tamang, Ghale, Kami | cereals, vegetables, tubers, roots, milk | Nepal, mid-altitude hills | farmers |

References: see table S1

Table S5. Daily energy intake and energy expenditure measured by doubly labeled water (dlw) or estimated by indirect calorimetry (ic).

| Non-human primates | Energy intake | | Energy expenditure | | | |
|-------------------------------|---------------------------------------|-----------------------------------|----------------------------------|--|----------------------------------|------------------|
| | (HEVD) kJ.day ⁻¹ | (LEVD) kJ.day ⁻¹ | kJ.day ⁻¹ | | | |
| <i>Lemur catta</i> | 1,201 | 866 | 626 (dlw) | | | |
| <i>Eulemur sp</i> | 908 | 611 | 610 (dlw) | | | |
| <i>Propithecus diadema</i> | 2,250 | 1,665 | 1,446 (dlw) | | | |
| <i>Alouatta palliata</i> | - | 2,292 | 2,497 (dlw) | | | |
| <i>Papio cynocephalus</i> | 3,903 | 2,888 | 3,400 (dlw) | | | |
| <i>Papio ursinus</i> * | 3,929 | 2,908 | 3,480 (dlw) | | | |
| <i>Pongo pygmaeus</i> | 10,216 | 7,559 | 6,464 (dlw) | | | |
| <i>Gorilla gorilla</i> (male) | 21,059 | 15,584 | 15,173 (dlw) | | | |
| Human populations | Energy intake kJ.day ⁻¹ | % of primate LEVD [†] | % of primate TEE [†] | Energy expenditure kJ.day ⁻¹ | % of primate TEE [†] | PAL |
| <i>Present study</i> | | | | | | |
| Yassa men | 11,416 | 116 | 125 | 11,240 (ic) | 123 | 1.67 (1.63-1.69) |
| Yassa women | 9,075 | 102 | 109 | 8,770 (ic) | 106 | 1.65 (1.63-1.68) |
| Mvae men | 10,225 | 105 | 112 | 9,500 (ic) | 104 | -(1.55) |
| Mvae women | 8,828 | 98 | 105 | 9,020 (ic) | 107 | 1.69 (1.66-1.76) |
| BaKola men | 9,827 | 116 | 124 | - | - | - |
| BaKola women | 8,803 | 115 | 123 | - | - | - |
| Duupa men | 10,648 | 121 | 130 | 11,000 (ic) | 134 | 1.77 (1.67-1.92) |
| Duupa women | 7,806 | 97 | 104 | 9,111 (ic) | 121 | 1.78 (1.64-1.90) |
| Koma men | 11,403 | 129 | 138 | 11,200 (ic) | 136 | 1.81 (1.70-2.00) |
| Koma women | 7,950 | 95 | 102 | 9,270 (ic) | 119 | 1.80 (1.71-1.94) |
| Tamang, Ghale, Kami men | 9,718 | 113 | 120 | - | - | - |
| Tamang, Ghale, Kami women | 8,774 | 115 | 122 | - | - | - |
| <i>Mean:</i> | | <i>110±11</i> | <i>118±11</i> | | <i>119±12</i> | <i>1.75±0.06</i> |

The physical activity level (PAL), ie the ratio of daily energy expenditure to basal metabolic rate, is given as mean and range across 3 seasons excepted for Mvae men where only dry season data are available. Other species or population data presented as means. *Non-human primates*. Paired-comparison between daily energy intake (using HEVD and LEVD modes of calculation; see Main text and Note S2) and total energy expenditure (TEE) across species. Subjects have approximately similar body size, except in *Papio cynocephalus* where the energy intake of adult males was rescaled according to body mass^{0.75} for comparison with female TEE in this dimorphic species; *: TEE data for *Papio anubis* (omnivorous diet and body mass similar to *P. ursinus*); †: percent of expected values is calculated from the Energy intake(LEVD):body mass regression (this study, table 1) or from the TEE:body mass regression in [65] ($\log(\text{TEE, in kCal.day}^{-1}) = 2.032 + 0.734 \log(\text{body mass, in g})$), with TEE converted in kJ.day⁻¹ using a 4.18 multiplication factor).

Same references as in table S1, except for primate TEE [65].

Supplementary figures

Figure S1. Phylogenetic tree built for phylogenetic least square regression analyses.

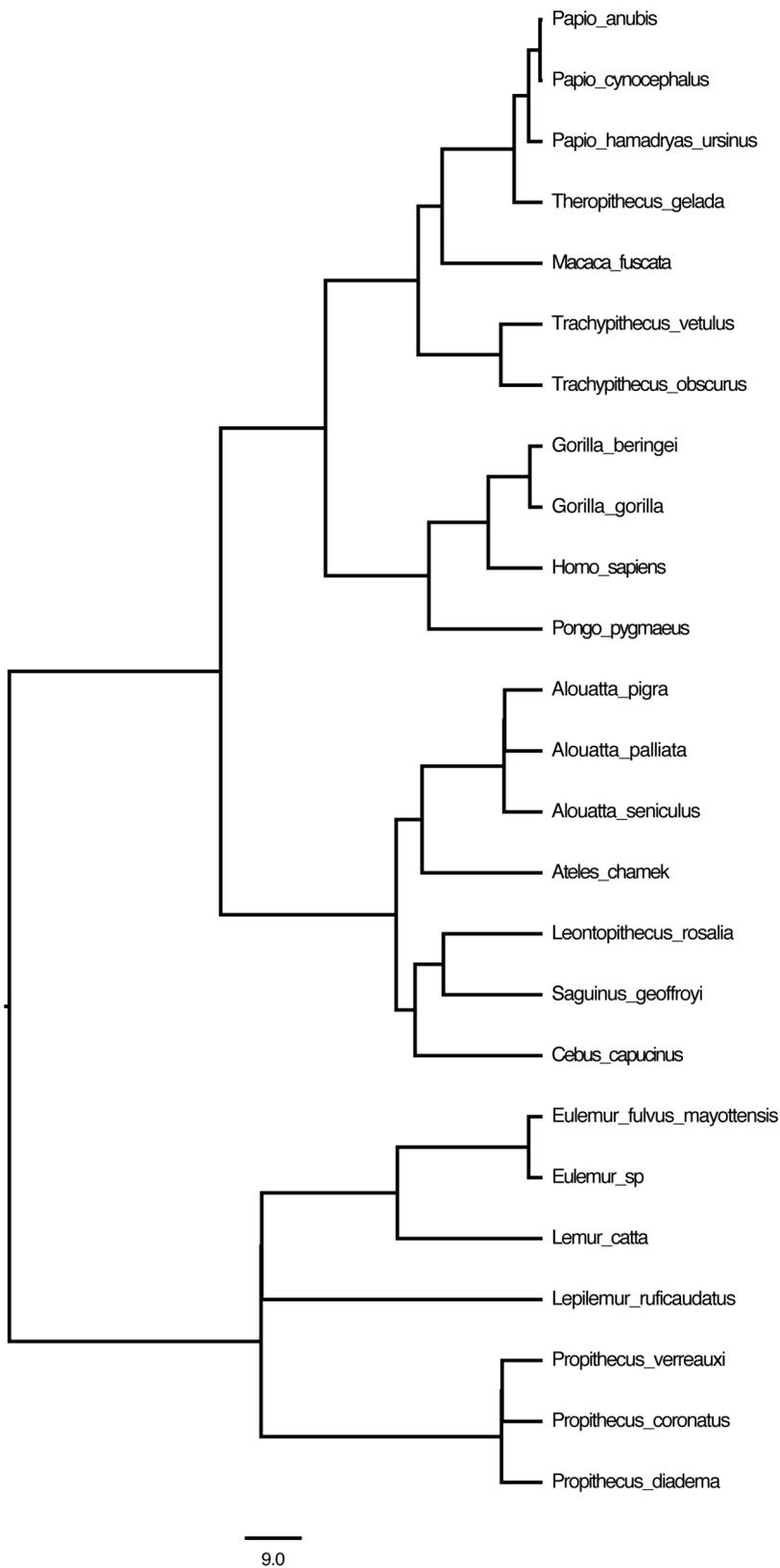


Figure S2. Relationship between daily energy intake, total energy expenditure (TEE) and species body weight in primates. The solid yellow and orange regression lines refer respectively to the “High Energy Value of the Diet” (HEVD: squares) and “Low Energy Value of the Diet” (LEVD: circles) databases for non-human primates (Material and Methods). The solid black line shows the scaling of TEE (measured with doubly labelled water) with body mass in captive and wild primates (diamonds), after [65]. Regressions using best-fit models are derived from phylogenetically controlled analysis.

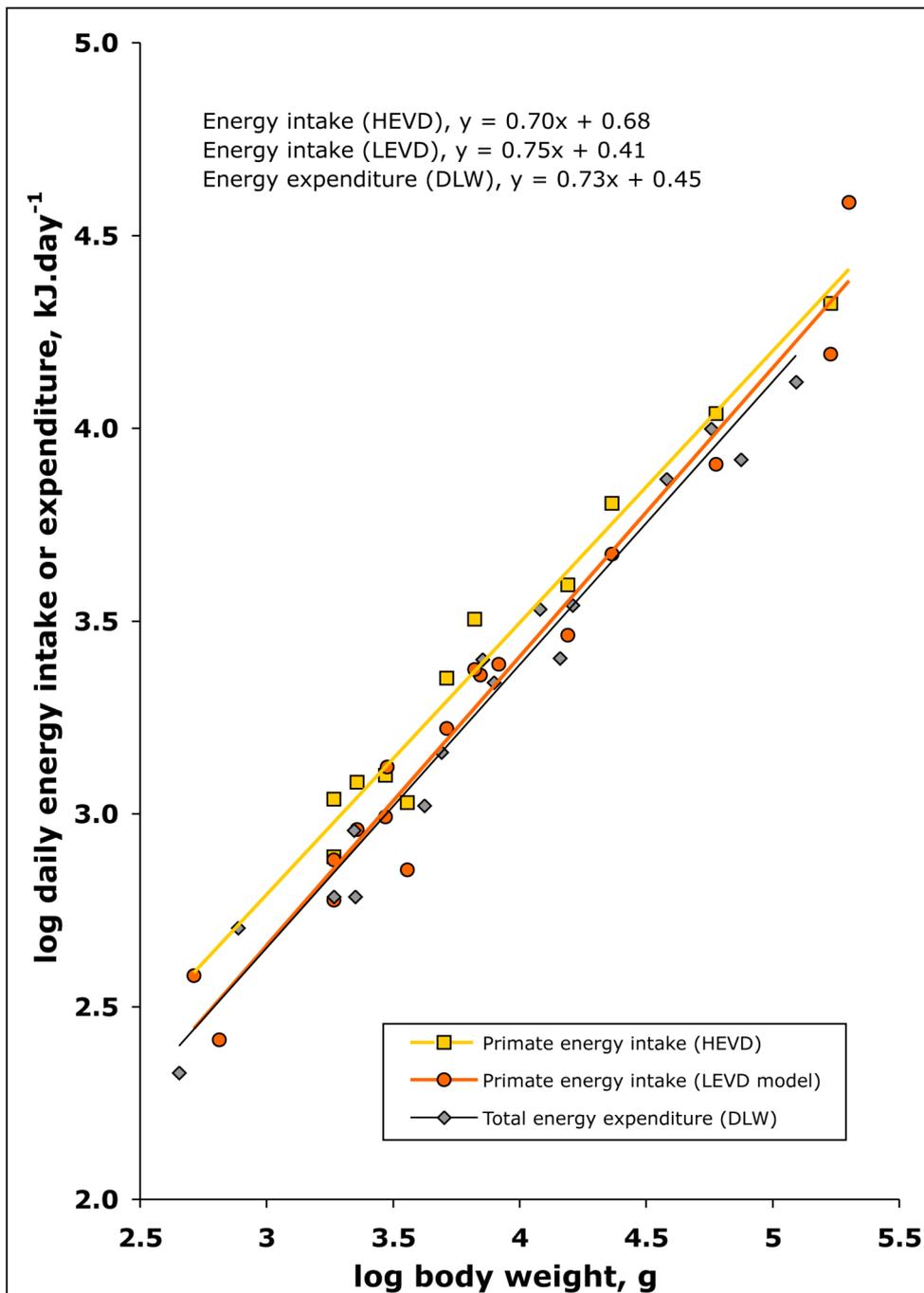
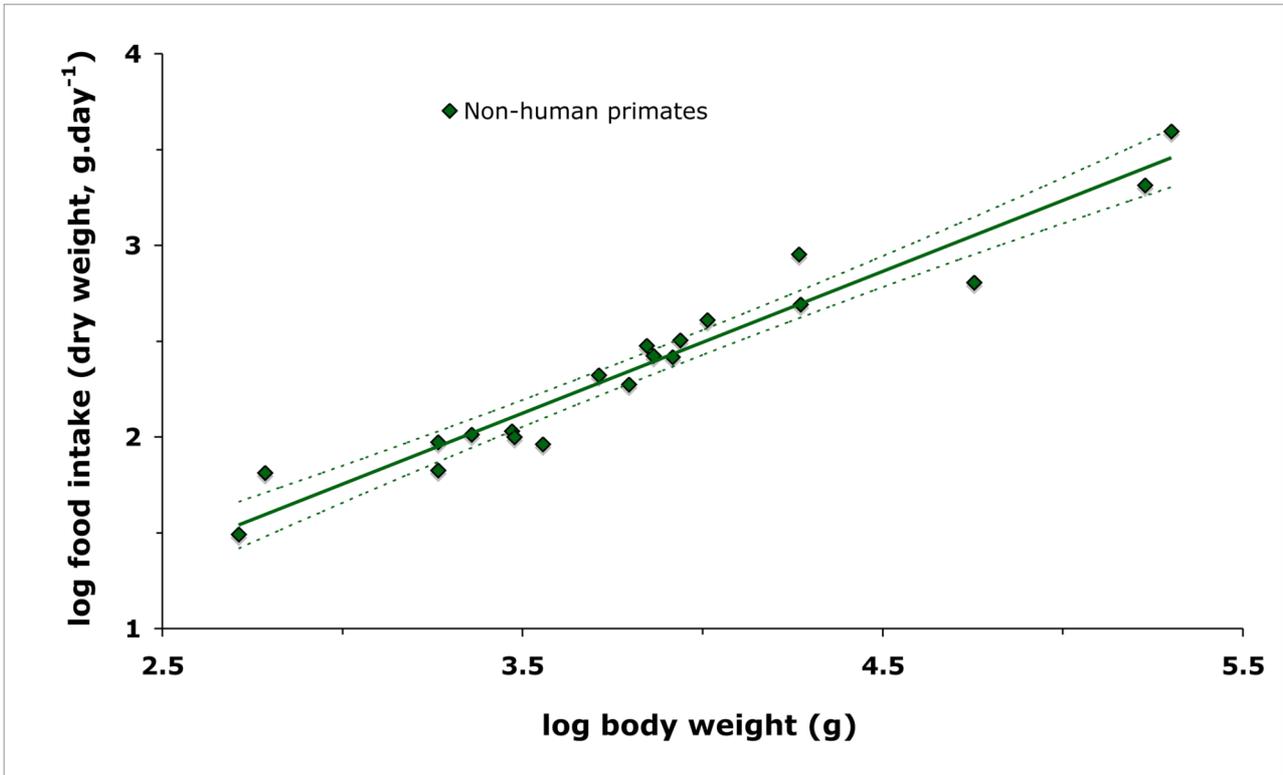


Figure S3. Daily food intake (as dry matter ingested) in wild non-human primates. Regression using the best-fit model derived from phylogenetically controlled analysis (table 1). The dotted lines show the 95% confidence interval for the regression line.



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