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

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5

6 Bruno Simmen<sup>1</sup>, Patrick Pasquet<sup>2</sup>, Shelly Masi<sup>2</sup>, Georgius J.A. Koppert<sup>1</sup>, Jonathan C.K.

7 Wells<sup>3</sup> and Claude Marcel Hladik<sup>1</sup>

8

9 <sup>1</sup> Centre National de la Recherche Scientifique/Muséum national d'Histoire naturelle,

10 UMR 7206-Eco-anthropologie et Ethnobiologie, 1 avenue du Petit Château, 91800 Brunoy,

11 France

12 <sup>2</sup> Centre National de la Recherche Scientifique/Muséum national d'Histoire naturelle, Musée

13 de l'Homme, UMR 7206-Eco-anthropologie et Ethnologie, 17 place du Trocadéro, 75116

14 Paris, France

15 <sup>3</sup> Childhood Nutrition Research Centre, UCL Great Ormond Street Institute of Child Health,

16 30 Guilford Street, London WC1N 1EH, United Kingdom

17

18 Correspondence: Bruno Simmen, CNRS/MNHN, 1 avenue du Petit Château, 91800 Brunoy,

19 France; tel: +33 (0)1 60 47 92 33; email: [simmen@mnhn.fr](mailto:simmen@mnhn.fr)

20

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

37

38 **Key words:** allometry – food intake – energy balance – seasonal variation – hominins

39

40

41

## 42 **1. Background**

43 Humans and other large-brained hominins have been proposed to undergo an increased  
44 energy turnover during their evolutionary history and/or to evolve peculiar energy allocation  
45 trade-offs between growth, maintenance and reproduction relative to other primates (e.g. [1-  
46 3]). Comparison of basal metabolic rate between modern humans and chimpanzees, our  
47 closest living relatives, suggests that basal energy requirements increased by ~19% during  
48 hominin evolution, though the available data are very limited [1,2]. Similarly, the available  
49 data on total daily energy expenditure (TEE) in humans and apes have been interpreted as  
50 indicating greater energy turnover in humans compared to non-human primates (e.g. 27%  
51 greater than chimpanzees and bonobos, our closest relatives [2]). At some point of hominin  
52 evolution, a shift towards an energy-rich diet [1,4,5] and later towards cooked foods, with an  
53 increased energy extraction per unit mass compared with raw foods [6,7], could have  
54 sustained the increased energy demand of a larger brain (among other possible sources of  
55 energy [2]).

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

63         Clearly, additional data are needed to understand the evolution of hominin energetics  
64 and its proposed link [1-3] to the peculiar life history traits that modern humans exhibit  
65 relative to other primates. From an ecological perspective, the functioning of the brain  
66 requires continuous energy fuelling but the majority of non-human primates inhabit, and

67 evolved, in unpredictable seasonal environments that greatly challenge their energy strategy.  
68 Some authors have emphasized relationships between environmental unpredictability and the  
69 cognitive skills, brain organization and brain size [9,10], while others suggested that hominins  
70 may initially have evolved greater stability of energy metabolism, which subsequently  
71 allowed encephalization [11].

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

79

## 80 **2. Material and Methods**

### 81 (a) Non-human primate data.

82 Daily food intake data were selected from field studies undertaken since the 1970's, updated  
83 with new data (electronic supplementary material, note S1). We excluded intake data that  
84 have been pooled among adult/subadult individuals and other age classes or  
85 lactating/gestating females. We selected studies that provided an estimate of metabolizable  
86 energy intake (17 spp.; electronic supplementary material, table S1). These studies commonly  
87 assess the proportion of the different macronutrients in primate diets [12]: protein, fat,  
88 structural carbohydrates including cellulose and hemicelluloses among cell wall constituents,  
89 non-structural carbohydrates including soluble sugars and storage reserve compounds. Fibre  
90 digestibility, especially NDF (i.e. neutral detergent fibres which include cellulose,  
91 hemicelluloses and lignin) is determined in captivity for the species under investigation, or

92 from primate models sharing similar fermenting digestive systems. In many cases, the  
93 calculation of readily digestible sugars or total non-structural carbohydrates (TNC) in the diet  
94 is estimated as the difference between 100% and the sum of all other nutrients (protein, fat,  
95 NDF, ash). We used results obtained with this mode of calculation as a first data set for  
96 analyzing the metabolizable energy input:body mass relationship across primates. We also  
97 used results of a second method for calculating metabolizable energy intake since TNC  
98 determined by subtraction potentially severely overestimates the true proportion of non-  
99 structural carbohydrates (electronic supplementary material, note S2). In the second method,  
100 we assessed the energy contribution of TNC to metabolizable energy intake based on a  
101 review of published data on the concentration of water soluble sugars and soluble fibres in  
102 primate foods and other tropical fruits and leaves. Results from the two ways of calculating  
103 metabolizable energy intake were referred to as the “High Energy Value of the Diet” (HEVD,  
104 involving TNC determined by subtraction in the original papers) and “Low Energy Value of  
105 the Diet” (LEVD, using a correction for TNC; electronic supplementary material, note S2 and  
106 table S1 and S3). Additional information on study sites and feeding ecology of primates  
107 tested is provided in electronic supplementary material, table S2.

108

#### 109 (b) Human data.

110 For consistency of comparisons and to reduce methodological heterogeneity in the evaluation  
111 of food intake, we focused on populations in which direct quantitative methods were applied.  
112 Strict methodological criteria were retained, including procedures in which foods or dishes  
113 consumed during a meal by adult men and women (above 20 years old) were weighed [13]  
114 (details in [14]). These criteria were met for five forest and savannah populations from  
115 tropical Africa (Yassa, Mvae, Bakola, Duupa, Koma) and three Nepalese populations from  
116 mid-altitude temperate areas (considered as a single sample in the original study). Depending

117 on the population, the diet combines farming products, natural plant resources and/or animal  
118 matter from hunting/fishing activities (electronic supplementary material, table S4). They all  
119 live at subsistence level, that is they broadly rely on self-sufficiency modes of food  
120 production/provisioning and have relatively stable energy balance in the long-term (despite  
121 seasonal variations, they do not experience substantial increase in body mass throughout most  
122 of their adult lifespan, as indicated by cross-sectional measurements across wide age ranges  
123 [15]). They do not appear nutritionally deprived according to surveys of their health status  
124 and body mass index [15-17]. We discarded populations under nutritional transition from  
125 their traditional lifestyle, rural populations practicing substantial cash agriculture, or  
126 populations showing excessive body mass index and inadequate energy balance. For  
127 consistency, we also did not retain studies that approximated individual daily food intake by  
128 weighing the mass of foodstuff brought to the village. Food measurements were made at three  
129 distinct seasons, and these data were averaged to avoid potential energy imbalance that may  
130 occur seasonally, often during the peak season of agriculture [18]. Metabolizable energy  
131 intake (electronic supplementary material, table S1) is calculated from classical nutritional  
132 composition tables for raw and cooked foods as well as from complementary analyses made  
133 for specific foods when required.

134

### 135 (c) Data analysis.

136 We tested which of the HEVD and LEVD models best reflected the actual amount of  
137 metabolizable energy available to primates and hence provided the most accurate set of data  
138 to be contrasted with human energy intake measurements. Specifically, we tested which of  
139 these models best equated total energy expenditure (TEE) measured with doubly labelled  
140 water, the gold-standard method for measuring TEE in free-ranging animals (published data  
141 for primates and analyses in electronic supplementary material, note S3 and table S5). The



142 basic assumption underlying this comparison was i) that energy fluxes should broadly equate  
143 to a balanced energy budget, and ii) that energy expenditure is maintained within a narrow  
144 physiological range, making it possible to use it as a reference value (as evidenced by a  
145 growing number of mammal studies [8,19,20]).

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

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

155

### 156 **3. Results**

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

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

164 Plotting the non-human primate LEVD energy intake data (electronic supplementary  
165 material, table S1) against species body mass yields the following phylogenetically-controlled  
166 equation:

167  $\log(\text{daily energy intake, in kJ.day}^{-1}) = 0.41 + 0.75 \log\text{BM}$  ( $N = 17$  spp), where BM is  
168 body mass. A disproportionate part (96%) of the variation of energy input was explained by  
169 body mass variation (table 1; figure 1).

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

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

187

## 188 (b) Food intake in humans versus other primates

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

191  $\log(\text{wet matter input, g.day}^{-1}) = 0.11 + 0.73 \log(\text{body mass, g}),$

192 according to phylogenetic least square regression (table 1). An allometric exponent of  $0.74 \pm$   
193  $0.16$  is found using dry matter intake (database only available for non human primates in this  
194 case; electronic supplementary material, figure S3). Each human population falls as a low  
195 outlier in the regression analysis using wet matter (with *Homo* residual  $> -3$  standard  
196 deviations). Figure 2 shows, besides the phylogenetically controlled regression for non-  
197 human primates alone, daily food intakes measured in the various human populations studied.  
198 All human groups studied consistently ingest remarkably less food than predicted from their  
199 body mass, with a conspicuously low mean value of only  $36 \pm 6\%$  (i.e. 2600 g less, on  
200 average) that expected in a non-human primate of the same body size. Only *Propithecus*  
201 *coronatus* consume very little food relative to its body mass but periods of observations were  
202 biased towards the long dry season when animals exhibited a thrifty energy strategy  
203 (reference in electronic supplementary material, table S1).

204 The average energy density of the human diets (population mean  $\pm$  sd:  $6.8 \pm 1.6$  kJ.g<sup>-1</sup>  
205 <sup>1</sup> of wet diet including raw and cooked foods) was 178% greater than that of wild non-human  
206 primates (species mean  $\pm$  sd:  $2.4 \pm 0.6$  kJ.g<sup>-1</sup> of wet matter).

207

## 208 **4. Discussion**

209 Our key finding is that, with a far more rich and energy-dense diet compared to other  
210 primates, humans consume much less food to obtain the amount of calories expected relative  
211 to their mass. At first glance, these results contradict the hypothesis that the costs of brain  
212 enlargement could be compensated by extra energy input. A recent study [2] stated that  
213 humans have 27% greater total energy expenditure relative to chimpanzees and bonobos but,  
214 as shown in figure 1, the greater energy expenditure of humans relative to apes [2] emerges in  
215 part because the three ape species have similar (*Pan*) or lower TEE (*Gorilla*, *Pongo*) than  
216 predicted for their body mass. Other relatively large-brain monkeys show only moderate

217 increase of TEE relative to the expected value (e.g. *Sapajus apella*; [23]), and their TEE  
218 adjusted for body mass is much smaller than that observed in several primates with a smaller  
219 brain — e.g. some small-brain species fall above the 95% confidence limits of the slope, with  
220 a deviation of 22 to 36% above expectations (see the grey symbols and solid black line in  
221 figure 1).

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

239 In the same way, the variability around the allometric regression line drawn for  
240 energy intake does not necessarily result mainly from methodological inaccuracy but may  
241 also reflect species or population biological characteristics. We note for example the

242 important variance in the scaling of primate TEE data with body mass (see § above) despite  
243 the use of a rigorous method (doubly labelled water). Clearly, greater accuracy in future  
244 energy intake studies and standardization of these methods relative to isotopic studies should  
245 increase the robustness of comparative analyses.

246         Keeping in mind these methodological issues, our meta-analysis of primate energy  
247 intake suggests that ‘reorganization’ of the energy budget, rather than substantially increasing  
248 its total value, was probably an important step in brain evolution in the genus *Homo* [1,3].  
249 There are several different ways in which such reorganization could have been achieved.  
250 First, the classic ‘expensive tissue hypothesis’ proposed that energy was diverted to the brain  
251 through reducing size of the gut [25] but this hypothesis has not been supported across  
252 mammals in general, and across primates in particular [3,26]. However, other tissues that may  
253 have traded off against the brain include muscle or liver [1,27]. The decreased cost of  
254 digestion due to the remarkable diminution of food intake (see below) may also have  
255 contributed to the assignment of the released energy to maintaining a larger brain. Second,  
256 humans have thrifty life histories, with slow growth profiles, reducing energy demands of  
257 both juveniles and parents supporting them [28]. Third, humans may distribute energy costs  
258 socially, both overall and through cooperative breeding [29-31]. Social capital can provide  
259 ‘energy insurance’ protecting individuals from foraging failure [11]. Finally, humans may  
260 also benefit from somatic insurance, in the form of body fat stores. In contrast to social  
261 capital, body fat ring-fences energy for individual use [32]. Each of social and somatic capital  
262 can smooth over fluctuations in energy supply, reducing the need for routinely high energy  
263 intakes [33]. This generic strategy may initially have been favoured to resolve the stress of  
264 seasonality, potentially permitting the onset of encephalization in the absence of raised energy  
265 intakes [11]. Whereas subsistence human populations are able to maintain energy intake  
266 relatively stable across the year, the great seasonal variability in energy intake observed in

267 nonhuman primates — possibly implying periods of negative energy balance [34-36]  
268 (electronic supplementary material, table S1) — is a telling example of the constraints  
269 imposed by natural food resources on the expansion of energy budgets.

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

281         We calculate that the increased energy costs of harvesting/processing foods (300-700  
282  $\text{kJ}\cdot\text{d}^{-1}$  according to the hunter-gatherer societies considered; electronic supplementary  
283 material, Note S5) could easily be offset by lower costs of digesting smaller food volumes. In  
284 humans, digestion costs represent  $\sim 10\%$  of TEE (e.g. [41,42]) and increase basal energy  
285 expenditure by  $\sim 25\%$  [43]. Based on predictive equations incorporating meal size and body  
286 mass, a human consuming the reduced amount of food we report here, relative to the primate-  
287 predicted amount ( $-64\%$ ), would experience  $\sim 600 \text{kJ}\cdot\text{d}^{-1}$  lower costs of digestion (electronic  
288 supplementary material, Note S5). Experimental studies on animal models with a digestive  
289 physiology similar to humans, such as pigs, indicate that further meal reductions can reduce  
290 digestion costs much more ( $\sim 1600 \text{kJ}\cdot\text{d}^{-1}$ ; [44]). We note that this energy saving could  
291 compensate for both the higher cost of foraging for energy-dense foods, and for maintaining a

292 large brain (the increased energy cost of the human brain compared to a chimpanzee is  
293 estimated at  $\sim 800 \text{ kJ d}^{-1}$  [2]; electronic supplementary material, Note S5) among other  
294 metabolically costly organs. Moreover, on an evolutionary scale, the transition from a  
295 relatively fibrous diet toward softer edible foods in the genus *Homo* [4] likely led to an  
296 additional decrease in the energy cost of digestion [45].

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

305

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

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

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318

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437 **Table legends**

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

441

## 442 **Figure legends**

443 Figure 1. Scaling of daily energy intake and total daily energy expenditure (TEE) with species  
444 body weight in non-human primates and subsistence-level humans. Main figure: the solid  
445 orange regression line,  $y = 0.75(\pm 0.04)x + 0.42(\pm 0.15)$ , refers to the “Low Energy Value of  
446 the Diet” (LEVD: filled circles) database for non-human primates (averaged for each species  
447 where seasonal data or different population data are available; electronic supplementary  
448 material, table S1). The solid black line shows the scaling of TEE (measured using doubly  
449 labelled water; diamonds) with body mass in primates,  $y = 0.73(\pm 0.03)x + 0.45(\pm 0.12)$  (after  
450 [8]). Recent additional TEE results for apes [2] include data combined for chimpanzees and  
451 bonobos (*Pan*\*). The average energy intake of human populations tested in this study (blue  
452 circle;  $N = 6$ ) is shown. Regressions using best-fit models are derived from phylogenetically  
453 controlled analysis (table 1). The dotted lines show the 95% confidence interval for each of  
454 the two regression lines. Box: details of human deviation from the TEE:body mass  
455 relationship (populations averaged for men and women; Y: Yassa, M: Mvae, D: Duupa, T:  
456 Nepalese, B: Bakola, K: Koma).

457

458 Figure 2. Relationship between daily food intake and body weight of primates. The regression  
459 line is calculated for free-ranging non-human primate species using the best-fit model derived  
460 from the phylogenetically controlled analysis (table 1). Human populations are figured  
461 separately. The dotted lines show the 95% confidence interval for the regression line.

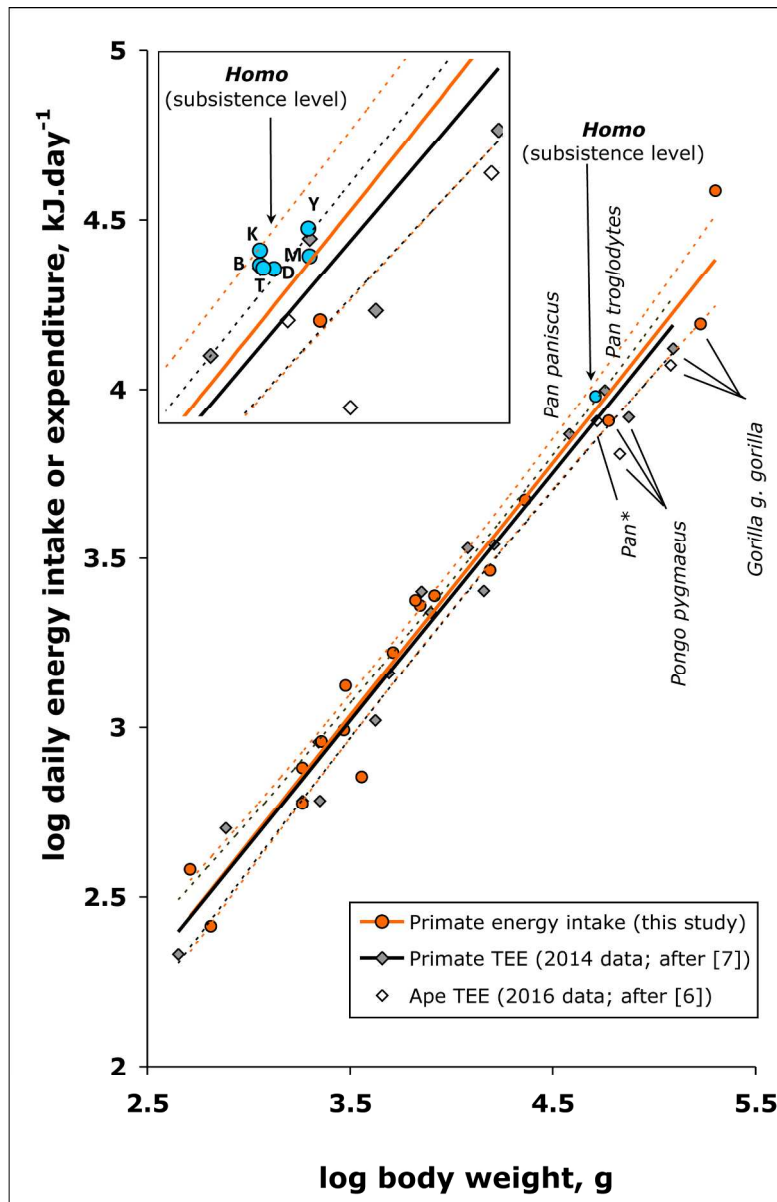


Figure 1. Scaling of daily energy intake and total daily energy expenditure (TEE) with species body weight in non-human primates and subsistence-level humans. Main figure: the solid orange regression line,  $y = 0.75(\pm 0.04)x + 0.42(\pm 0.15)$ , refers to the “Low Energy Value of the Diet” (LEVD: filled 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,  $y = 0.73(\pm 0.03)x + 0.45(\pm 0.12)$  (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).

156x240mm (300 x 300 DPI)



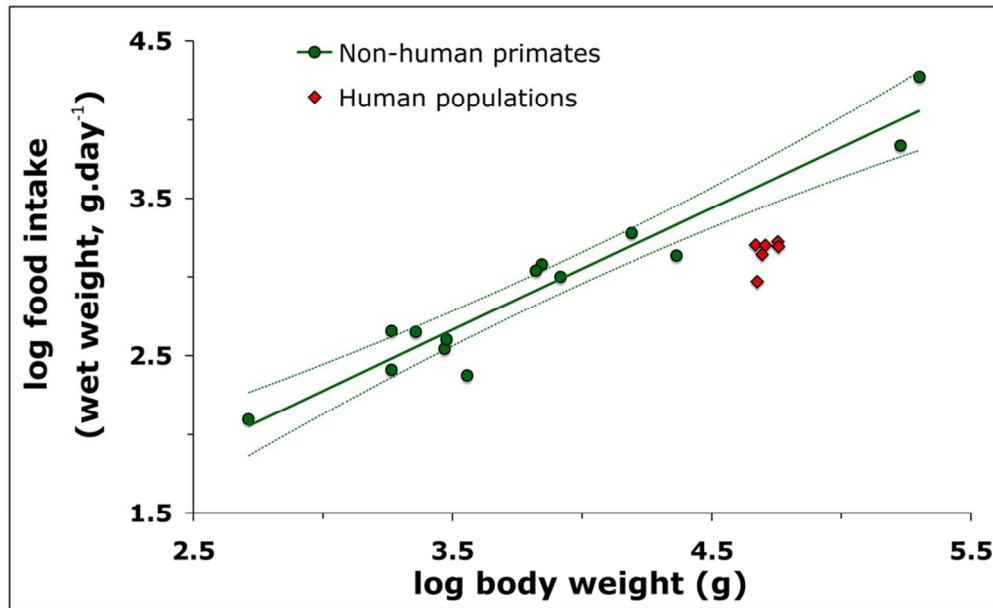


Figure 2. Relationship between daily food intake and body weight of primates. The regression line is calculated for free-ranging non-human primate species using the best-fit model derived from the phylogenetically controlled analysis (table 1). Human populations are figured separately. The dotted lines show the 95% confidence interval for the regression line.

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