

## *Metabolic Acceleration and the Evolution of Human Brain Size and Life History*

### **Contents**

Supplementary Text S1. Calculating Locomotor Costs.....	1
Supplementary Table 1. Estimated ranging costs for humans and other hominoids.....	2
Supplementary Text S2. Estimating the Costs of Reproduction for Female Hominoids.....	3
Supplementary Figure 1. Estimated reproduction energy expenditure in female hominoids.....	4
Supplementary Table 2. Comparative energy costs of reproduction and brain size.....	5
Supplementary Table 3. Multiple regression model summaries for TEE & BMR.....	6
Supplementary Figure 2. Comparison of TEE measurements across labs.....	7
Supplementary References.....	8

### **Supplementary Text S1. Calculating Locomotor Costs**

#### *Human Hunter-Gatherers & Wild Chimpanzees*

One hypothesis to explain how hominins were able to support the energy demands of larger brains and faster reproduction is via an evolutionary increase in walking economy (i.e., a decrease in the energy cost per meter traveled)<sup>1,9</sup>. Indeed, human walking is much more economical than chimpanzee walking<sup>11</sup>. This reduction in walking cost could, in principle, result in energy savings sufficient to accommodate larger brains and increased reproductive output. The daily energy costs of ranging (walking and climbing) will vary depending on season and location. However, mean daily walking and climbing distances for human foragers and for wild chimpanzees<sup>28,29</sup> are available and can be used to estimate daily ranging costs for these two groups. The metabolic costs of walking (kcal/m) is well characterized for humans<sup>30</sup> and chimpanzees<sup>11</sup>, and the energy cost of climbing (kcal/m) has been shown to be remarkably similar across primates, including humans<sup>31</sup>.

Rather than expending less energy per day on locomotion, men and women in hunter-gatherer populations have estimated daily ranging costs that are ~31% greater than those for wild chimpanzees (Supplementary Table 1). This difference is similar to the difference in body size (~35%). Human ranging costs ignore the additional cost of carrying burdens and climbing, and are therefore likely to underestimate total locomotor cost. Thus, while the energy saved through more economical walking may have played an important role in the evolution of the hominin metabolic strategy by increasing the net energy gained from foraging, improved walking economy is insufficient for providing the extra energy needed to fuel larger brains and increased reproduction. The increased daily travel distances required of hunter-gatherers would have more than outweighed the energy savings from improved walking economy (Supplementary Table 1).

#### *Cohorts in the TEE Sample*

To test whether differences in locomotor cost account for the differences in TEE among cohorts in this study, we estimated daily walking and (for apes) climbing costs for the cohorts in Table 1 (Methods). Human subjects wore accelerometers for 7 d coinciding with the TEE measurement, and their daily walking distances (m/d) were calculated from mean daytime (09:00-21:00) step-counts (females: 5832 ±3499 steps; males: 7804 ±3983 steps), assuming 2,000 steps per mile (1.6km). Daily walking (m/d) and climbing (m/d) distances for apes were calculated from 20+ hours of direct observation per animal during their TEE measurement. Walking cost (kcal/m) and climbing cost (kcal/m) was multiplied by walking and climbing distance to calculate daily locomotor costs (Table 1; Supplementary Table 1).

**Supplementary Table 1. Estimated ranging costs for humans and other hominoids.**

**a.** Human hunter-gatherers and wild chimpanzee populations. **Sources:** Mass: chimpanzees<sup>34</sup>; humans<sup>35</sup>. Daily walking distance<sup>28</sup>. Walking cost (kcal/kg/m): chimpanzees<sup>11</sup>; humans<sup>30</sup>. Climbing distance<sup>29</sup>. Climbing cost (kcal/m) estimated assuming efficiency =  $9.50\text{Mass}^{0.109}$ , following ref. 29. **b.** Cohorts in the TEE analysis (Table 1). Human walking distances estimated from accelerometer step counts; ape walking and climbing distances estimated from direct observation (Methods, Supplementary Text S1). Energy costs calculated as in **A**, using chimpanzee walking costs for all apes. \*excludes one female with exceptionally high climbing rates. See Methods and Text S1.

**a. Human hunter-gatherers & wild chimpanzees**

	Sex	Mass	Daily Walking Distance (km)	Walking Cost (kcal/kg/km)	Daily Walking Cost (kcal/d)	Daily Climbing Distance (m/d)	Climbing Cost (kcal/m)	Daily Climbing Cost (kcal/d)	Daily Locomotor Cost (kcal)
Human (hunter-gatherer)	M	55.2	14.1	0.49	381	-	-	-	381
	F	47.3	9.5	0.49	220	-	-	-	220
Chimp. (wild)	M	41.7	5.0	1.06	221	104	0.68	71	292
	F	34.4	3.0	1.06	109	99	0.58	57	167

**b. TEE sample (see Table 1)**

		<i>n</i>	Mass	Daily Walking Distance (m/d)			Daily Climbing Distance (m/d)			Daily Locomotor Cost (kcal/d)
				median	mean	<i>sd</i>	median	mean	<i>sd</i>	
<i>Homo</i>	F	71	80.1		4700				183	
	M	58	73.8		6200				226	
<i>Pan</i>	F	14	46.4	914	955	380	64	73	34	102
	M	10	57.9	1070	1271	614	45	46	27	120
<i>Gorilla</i>	F	6	73.7	826	762*	224*	52	44*	43*	110
	M	4	166.4	952	995	738	15	33	45	253
<i>Pongo</i>	F	5	58.2	662	642	257	48	53	31	88
	M	6	76.7	770	808	348	93	82	39	163

## **Text S2. Estimating the Costs of Reproduction for Female Hominoids**

To place humans' increased reproductive output in the context of daily energy expenditure, we estimated the daily energy cost associated with gestation and lactation for humans, chimpanzees, gorillas, and orangutans (Supplementary Fig. 1a). We estimated the daily costs of gestation and lactation over the course of one reproductive cycle, from the start of one conception to the start of the next. Integrating this curve gives the total energy cost of one reproductive cycle (kilocalories); dividing this cost by cycle length (days) gives the average energy cost of reproduction per day for an adult female during her reproductive career.

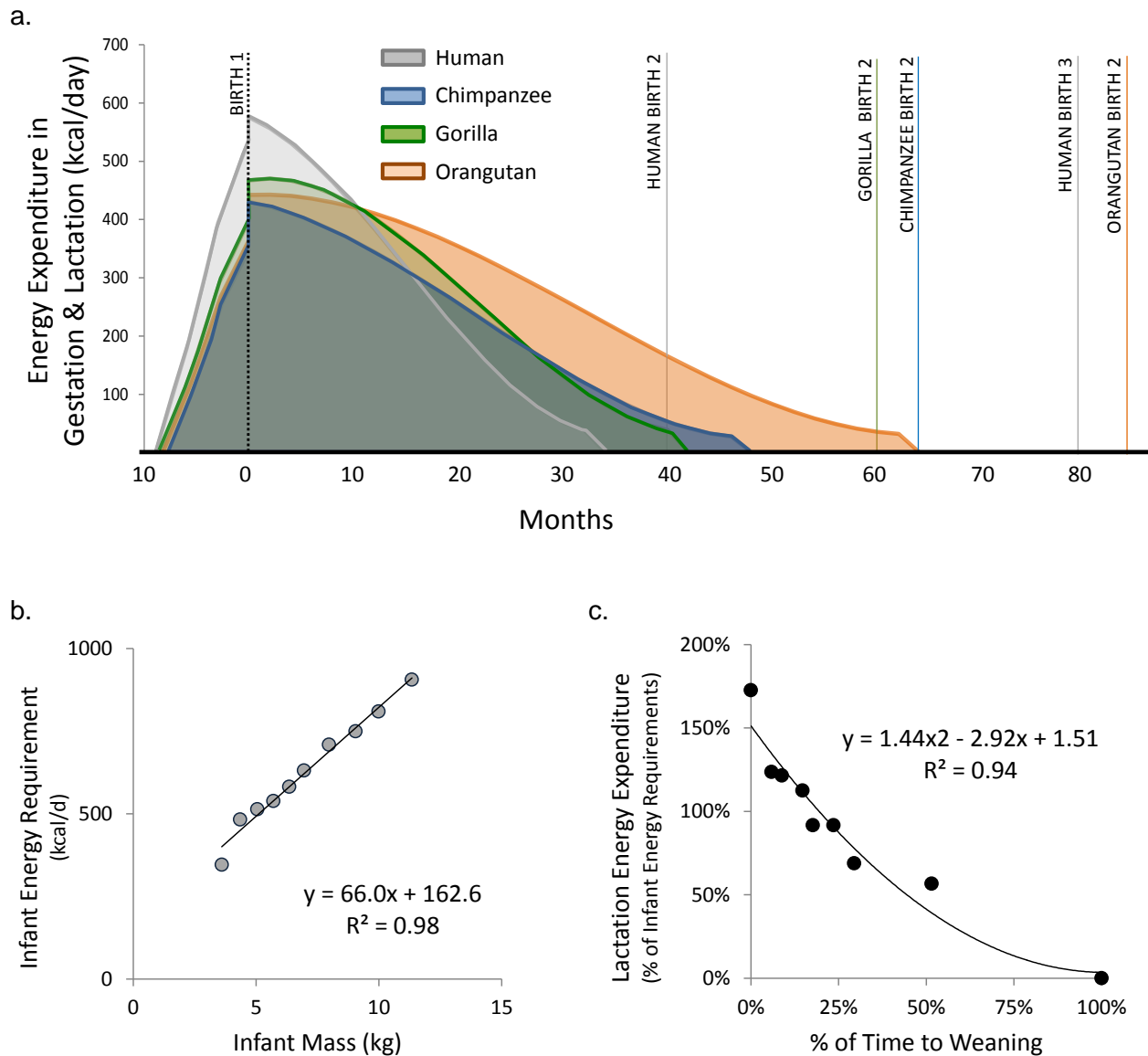
Reported inter-birth intervals for wild apes and for natural fertility human populations<sup>1</sup> were used as reproductive cycle lengths. Daily gestation costs were estimated from published mean trimester energy expenditures for humans<sup>32</sup>, assuming these mean trimester expenditures reflected the cost at the midpoint of the trimester. Ape trimester expenditures were scaled to neonatal mass<sup>1</sup>, as  $(\text{trimester expenditure}_{\text{human}} / \text{neonate mass}_{\text{human}}^{0.75}) = (\text{trimester expenditure}_{\text{ape}} / \text{neonate mass}_{\text{ape}}^{0.75})$ . Ape trimester durations were calculated as 1/3 reported gestation length<sup>1</sup>.

Lactation expenditure was also based on human costs. Measurements of human infant TEE and growth<sup>33</sup> indicate a strong relationship between infants' body mass and daily energy requirements (Supplementary Fig. 1b). This regression equation (Supplementary Fig. 1b) was used to estimate daily energy requirements for human and ape infants from birth until weaning, assuming linear growth from birth (mass=neonatal mass) to weaning (mass=weaning mass), and using published values for neonate mass, weaning mass, and weaning age<sup>1</sup>. Measurements of human mothers' expenditure on lactation<sup>32</sup> show a decrease in cost, measured as % infant energy requirements, from birth (mothers' cost  $\approx$  173% infant energy requirement) to weaning (mothers' cost  $\approx$  0). This relationship (Supplementary Fig. 1c) was used to determine ape mothers' daily lactation costs from birth to weaning of their neonates.

The resulting estimates of gestation and lactation costs for human and ape mothers (Table S2) are first approximations. Nonetheless, it appears that human costs peak higher (Supplementary Fig. 1a) and average roughly 50% more per day than those of the apes (Table S2). The energy savings associated with the earlier age at weaning in humans is offset by humans' shorter inter-birth intervals. Direct measures of energy expenditure during gestation and lactation in apes are needed to test the accuracy of these estimates.

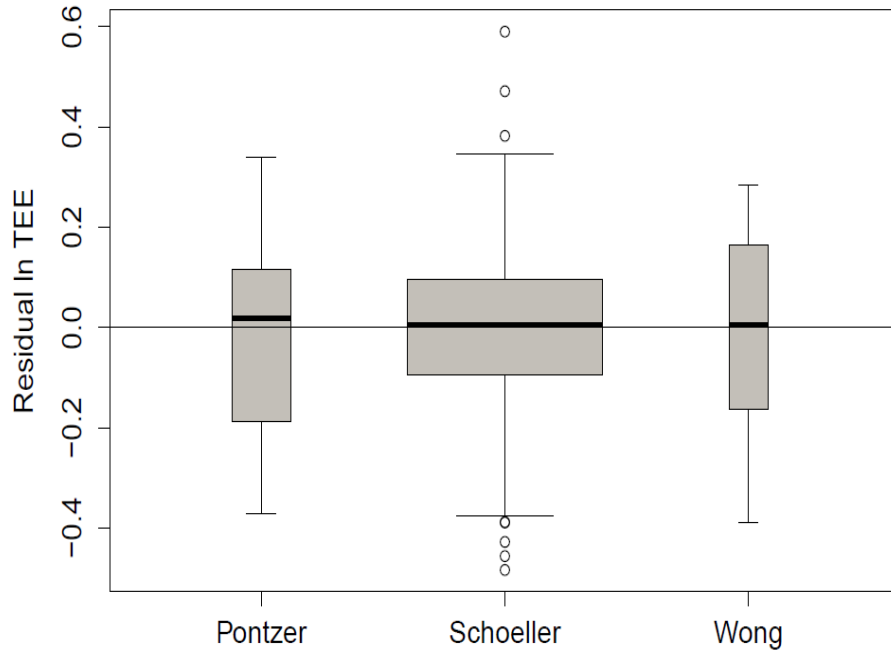
**Supplementary Table 2. Comparative energy costs of reproduction and brain size.** Brain size and interbirth interval from ref. 1. Pregnancy and nursing costs from Supplementary Figure 1. Brain costs are a first approximation assuming similar mass-specific organ costs ( $\text{kcal g}^{-1} \text{s}^{-1}$ ), following ref. 8. Comparisons of TEE and BMR suggest these mass-specific costs likely differ among genera; see main text.

	brain (g)	brain cost (kcal/d)	brain cost (%TEE)	pregnancy cost (kcal)	nursing cost (kcal)	reproduction cost (kcal)	interbirth interval (days)	reproduction cost/day (kcal)	reproduction cost (%TEE)
Human	1213	276	12.6%	74980	305508	380488	1215	313	14.3%
Chimpanzee	357	81	4.7%	42124	321815	363939	1982	184	10.7%
Gorilla	434	99	4.9%	52773	344831	397604	1825	218	10.7%
Orangutan	337	77	5.2%	46996	474237	521233	2683	194	13.2%



**Figure S1 | Estimated reproduction energy expenditure in female hominoids. a.** Comparison of estimated energy costs of reproduction for humans, chimpanzees, gorillas, and orangutans. Humans reproductive cycles are shorter but more frequent, with a higher peak energy requirement, resulting in greater daily energy costs for reproduction compared to apes, averaged over a female's reproductive career. Ape costs were estimated from human measurements<sup>32,33</sup> assuming that gestation and lactation costs are proportional to neonate mass, and that the curves are bounded temporally between conception and weaning. Data on neonatal mass, weaning mass, gestation length, and weaning age from ref. 7. See Text S2 and Table S2. **b.** Human infant daily energy requirements (which include growth costs) as a function of infant mass, reported for girls in table 1 of ref. 33. **c.** Lactation energy expenditures, calculated as a percentage of the infant's daily energy requirements as (milk production cost / infant energy requirement), for human mothers. Milk production cost was taken from table 14 in ref. 32 for mothers in developing countries (exclusive breastfeeding 0-8 months, partial 9 – 23 months). Infant energy requirements at each age (as a % of weaning age) were taken from table 1 in ref. 33.





**Figure S2 | Comparison of TEE measurements across labs.** Residual ln TEE was calculated from a general linear model with ln FFM, ln fat mass and genus (Table S3, model C). Results obtained using Cavity Ring Down Spectrometry in the Pontzer Lab (Hunter College) were similar to those from Isotope Ratio Mass Spectrometry (Schoeller Lab, Univ. of Wisconsin, and Wong Lab, Baylor School of Medicine). Box width is proportional to sample size.

## Supplementary References

28. Marlowe, F.W. Hunter-gatherers and human evolution. *Evol Anth.* **14**, 54–67 (2005)
29. Pontzer, H., Wrangham, R.W. Climbing and the daily energy cost of locomotion in wild chimpanzees: Implications for hominoid locomotor evolution. *J Hum Evol.* **46**, 315 – 333 (2004)
30. Rubenson, J. *et al.* Reappraisal of the comparative cost of human locomotion using gait specific allometric analyses. *J Exp Biol.* **210**, 3513-3524 (2007)
31. Hanna, J.B., Schmitt, D., Griffin, T.M. The energetic cost of climbing in primates. *Science.* **320**, 898 (2008)
32. Butte, N.F., King, J.C. Energy requirements during pregnancy and lactation. *Public Health Nutrition.* **8**, 1010-1027 (2005).
33. Butte, N.F. Fat intake of children in relation to energy requirements. *Am J Clin Nutr.* **72**, 1246S–52S (2000)
34. Carter, M.L., Pontzer, H., Wrangham, R.W., Peterhans, J.K. Skeletal pathology in *Pan troglodytes schweinfurthii* in Kibale National Park, Uganda. *Am J Phys Anthropol.* **135**, 389-403 (2008)
35. Walker, R.S. *et al.* Growth rates and life histories in twenty-two small-scale societies. *Am J Hum Biol.* **18**, 295-311 (2006)