

Metabolic adaptation for low energy throughput in orangutans

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Energy is the fundamental currency of life—needed for growth, repair, and reproduction—but little is known about the metabolic physiology and evolved energy use strategies of the great apes, our closest evolutionary relatives. Here we report daily energy use in free-living orangutans (*Pongo* spp.) and test whether observed differences in energy expenditure among orangutans, humans, and other mammals reflect known differences in life history. Using the doubly labeled water method, we measured daily energy expenditure (kCal/d) in orangutans living in a large indoor/outdoor habitat at the Great Ape Trust. Despite activity levels similar to orangutans in the wild, Great Ape Trust orangutans used less energy, relative to body mass, than nearly any eutherian mammal ever measured, including sedentary humans. Such an extremely low rate of energy use has not been observed previously in primates, but is consistent with the slow growth and low rate of reproduction in orangutans, and may be an evolutionary response to severe food shortages in their native Southeast Asian rainforests. These results hold important implications for the management of orangutan populations in captivity and in the wild, and underscore the flexibility and interdependence of physiological, behavioral, and life history strategies in the evolution of apes and humans.

daily energy expenditure | energetics | life history | doubly labeled water

All animals require energy to grow, maintain homeostasis, and reproduce. Much of the variation in energy use among species is related to body mass; large animals generally require more energy each day than small animals (1). There are also significant differences among taxonomic groups, with birds using more energy per day than other vertebrates, eutherian mammals using more energy per day than marsupials, and reptiles using far less energy than birds or mammals (1). Still, after accounting for the effects of body mass and taxonomic class, a sixfold range of variation in daily energy expenditure, (DEE; in kCal/d) remains among vertebrate species in the wild ($N = 229$ species, ref. 1).

There is growing evidence that the variation in DEE among species reflects evolved energy-use strategies to maximize the probability of survival and reproduction in a given habitat. Both within (2) and among (3) species, increased energy throughput (i.e., calories consumed and expended per day) is associated with increased reproductive output (i.e., grams of offspring produced per year). In habitats in which food resources are abundant, organisms may benefit from adopting higher energy throughput, increasing their food requirements but providing more energy for reproduction (4–6). Conversely, if food availability is highly variable or if foraging incurs the risk of predation, it may be advantageous to decrease DEE, even at the cost of decreased reproductive rates, to avoid starvation or predation (5, 6). Indeed, several comparative studies have suggested a continuum of energy-use strategies among mammals, from high-energy throughput to low, with each species' strategy contingent upon the particular dynamics of food availability and mortality risk it faces (1, 4–6).

Great apes, including humans, display a remarkable degree of variation in growth and reproductive rates (7, 8), but it is unknown whether this variation stems from differences in energy allocation

(e.g., spending energy on repair rather than reproduction) or differences in throughput, because DEE has never been measured in nonhuman apes. Hypotheses for evolutionary divergence in growth rates, reproductive rates, or brain size in humans and other apes often invoke differences in energy allocation (9–11) based on limited evidence from studies of basal metabolic rate (BMR), which suggest that the basal energy requirements of humans and apes are similar (12, 13) and that energy throughput might be similarly constrained. Estimates of DEE have suggested differences in energy throughput among hominoids and other primates (12), but these models are based on activity budgets and cannot reliably capture the unseen metabolic demands of maintenance, growth, or reproduction (14). Instead, direct measurements of total daily energy are needed to evaluate the alternative hypothesis that observed life history differences among humans and other apes arise from evolved differences in energy throughput.

In this study, we measured daily energy use in orangutans over a 2-wk period by using the doubly labeled water (DLW) method (15) to test whether differences in life history among apes stem from differences in energy throughput or allocation. Orangutans, including species of *Pongo* on both Borneo and Sumatra, have lower reproductive rates than all other hominoids and the slowest growth rates of any primate except humans (7, 8). If these life history differences are accomplished by evolutionary decreases in energy throughput, we expect DEE in orangutans to be lower than in humans and other mammals. Such variation in DEE would indicate a substantial degree of evolutionary plasticity in metabolic physiology among humans and apes, and suggest that selection has shaped metabolic physiology as a proximate mechanism for altering hominoid life histories. If instead life history differences stem from differences in energy allocation (11), we expect similarity in DEE among humans and orangutans, as seen in comparisons of BMR among humans and other apes (13).

Results

Great Ape Trust orangutans used remarkably little energy compared other mammals (Table 1). Relative to body mass, mean DEE for adult orangutans ($n = 3$) was the lowest ever measured for any eutherian mammal except sloths (Fig. 1). DEE for adult orangutans was nearly three SDs (mean z -score, -2.81 ; range, -2.55 to -3.33) below the mammalian trend line, placing them in the lowest 1% of mammals; this is lower than macaques undergoing calorie restriction (z -score, -2.25) (16). Mass-adjusted DEE for Great Ape Trust orangutans was even lower than that of strepsirrhine primates using torpor to minimize energy budgets [z -scores: mouse lemurs, -0.07 (17); sportive lemurs, -0.86 (18)].

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Table 1. Orangutan DEE, body fat percentage, and RMR

Name	Sex	Age, y	Mass, kg	DEE		RMR [§] , kCal/d	Body fat, %
				kCal/d	Expected, % [‡]		
Azy*	M	30	116.6	2,052	22%	1,597	21.8%
Knobi [†]	F	27	55.0	1,628	32%	1,316	13.2%
Katy	F	19	53.2	1,570	32%	1,035	15.8%
Rocky	M	4	25.5	1,255	45%	1,031	5.5%

*August DEE, 1,965; October DEE, 2,140

[†]August DEE, 1,292; October DEE, 1,963

[‡]Percent expected calculated using the trend line for eutherian mammals; see Fig. 1.

[§]RMR measurements were taken while subjects were seated and awake, and likely overestimate true BMR by approximately 20%.

For the two adult orangutans in which DEE was measured twice (in August and October), DEE was somewhat higher in the later session (10% and 22% greater for Azy and Knobi, respectively; Table 1). This increase did not affect the overall comparison with other mammals (orangutan DEE was still remarkably low) but may reflect the cooler outdoor temperatures in October and increased caloric demands of thermoregulation. The increase in DEE during the cooler season suggests that orangutan DEE in their native tropical climates might be even lower than measured in our sample. Variation in DEE among orangutans appeared to vary with age and activity level. The young, active juvenile (Rocky) had higher mass-adjusted DEE than adults (*z*-score, -1.76), whereas the oldest, least active individual (Azy) had the lowest mass-adjusted DEE (*z*-score, -3.33 ; Table 1).

Orangutans used significantly less energy per day than humans ($P < 0.001$, Student *t* test), with body size-adjusted DEE below observed values for humans in both sedentary industrial and active subsistence/agriculture populations (Fig. 2A). This pattern holds for juveniles, which have greater size-adjusted DEE than adults as a result of the energy cost of growth (19) (Fig. 2B). The difference between human and orangutan DEE is not an artifact of small sample size: the probability of drawing orangutan DEE values from a large, low-activity level human population is less than 0.0001% (Fig. S1). Even if the lowest orangutan DEE value is excluded, the probability of drawing the other three from a human sample is only 0.002%. Nor is this difference in DEE explained by differences in lean body mass percentage. Orangutans in our sample had lean body mass percentages somewhat higher than the human mean (Table 1; see below), making the differences in DEE between these species even greater when expressed in terms of lean body mass.

The low DEE observed among Great Ape Trust orangutans is partly explained by lower resting metabolism. RMR among adult orangutans in our sample was an average of 23% lower (range, 7–35% lower) than the basal rate of metabolism predicted for their body mass, and significantly lower than BMR reported for humans (20) and chimpanzees (13) (Student *t* test, $P < 0.05$ for both comparisons; Fig. 3). This difference is likely underestimated as a result of our measurement protocol. As a matter of necessity, orangutan RMR in our sample was measured with subjects recently fed, alert, and sitting quietly. Studies of human subjects indicate that the metabolic rate in seated, alert subjects exceeds BMR by 20% or more (21). If our measurements of RMR are 20% greater than actual BMR (a conservative estimate), BMR in orangutans is approximately 36% lower than that of similarly

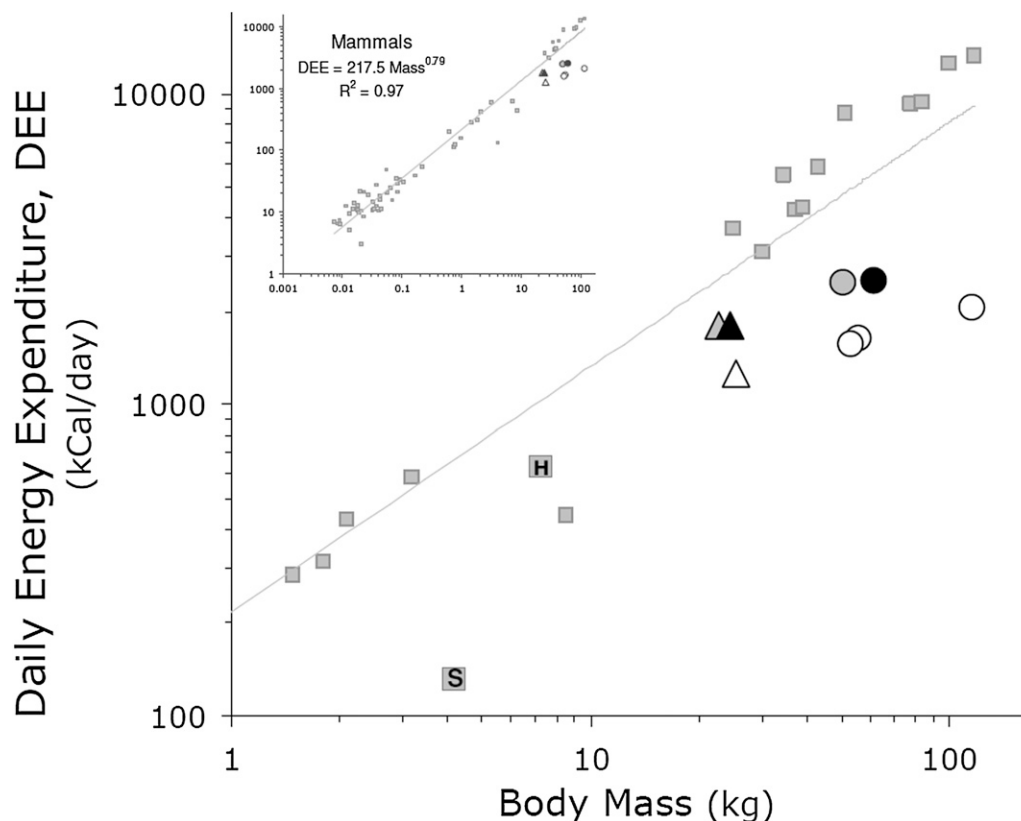


Fig. 1. DEE versus body mass for mammals. (Inset) Full comparative dataset for eutherian mammals (Table S1). Open circles and triangle represent orangutan adults and juvenile; gray circle and triangle represent human adults and juveniles in a subsistence/agricultural economy (25); black circle and triangle represent human adults and juveniles in industrial economies (33–38); gray squares represent other eutherian mammals. “S” indicates three-toed sloths (*Bradypus variegatus*); “H” indicates howler monkeys (*Alouatta palliata*).

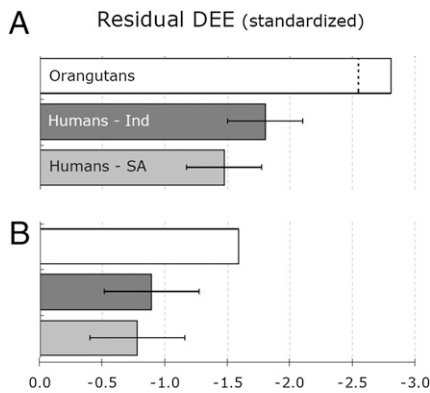


Fig. 2. Standardized residual DEE, calculated from the mammalian trend line. Orangutans (open bars); humans in industrial (Ind) economies (dark gray bars) (33–38); and humans in subsistence/agricultural (SA) economies (light gray bars) (26). (A) Adults: dashed line in the orangutan bar indicates the median of the orangutan sample ($n = 3$). Error bars indicate SD. (B) Juveniles; groups as in A.

sized mammals (Fig. 3). Decreased basal metabolism has previously been reported in other low-DEE species including sloths and aardwolves (4, 22, 23).

Low orangutan DEE does not appear to be an artifact of captivity. Great Ape Trust orangutans were very active, walking and climbing similar distances each day as their wild counterparts while maintaining similar patterns of resting, feeding, and sleeping (Fig. 4). Walking and climbing accounted for approximately 5% to 9% of DEE in adult orangutans and 13% of DEE in juvenile orangutans (*SI Methods*). By comparison, daily locomotor costs are expected to account for approximately 4% of DEE in similarly sized mammals (*SI Methods*). Although locomotor economy (i.e., meters traveled per energy consumed) in the Great Ape Trust habitat is likely greater than in the complex arboreal habitat of wild orangutans, improved locomotor economy cannot account for the exceptionally low DEE seen in Great Ape Trust orangutans. Doubling estimated locomotor costs in Great Ape Trust orangutans, equivalent to reducing locomotor economy by 50%, increases DEE by only 5% to 9% for adults and 13% for the juvenile, still significantly below the DEE of humans ($P < 0.01$) and lower than nearly all other mammals.

Physical activity levels (PAL), the ratio of DEE to BMR commonly used to gauge activity level in humans, indicate moderate levels of activity for orangutans in our study. With BMR for Great Ape Trust subjects estimated as RMR divided by 1.2 (21), mean PAL for adult orangutans was 1.7 (range, 1.6–1.8). This is com-

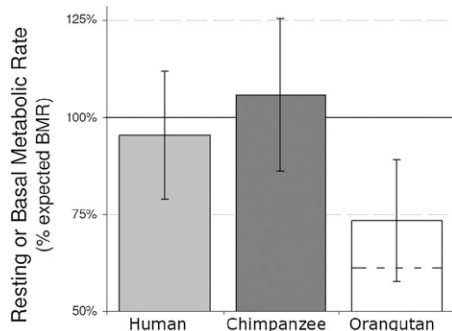


Fig. 3. Basal and resting metabolic rates in hominoids. Mean BMR for adult humans (20) and chimpanzees (13) and RMR for adult orangutans, as a percentage of the expected BMR value for mammals of similar body mass (39). Error bars indicate SD. Estimated BMR, calculated as RMR divided by 1.2 (21), is also shown for orangutans (dashed line in orangutan bar).

parable to the observed PAL of humans in physically demanding agricultural lifestyles (mean PAL, 1.9 for males; 1.7 for females) (24) and wild howler monkeys (PAL, 2.0) (25), and well above estimated PAL for wild orangutans (PAL, 1.4) (12). Body composition also suggests an active lifestyle, with mean body fat percentages in Great Ape Trust orangutans of 16.9% for adults (range, 13.2–21.8%) and 5.5% for the juvenile (Table 1). This compares favorably to mean body fat percentage in active humans engaged in subsistence/agriculture (26) (adults, 19.9%; children, 14.6%) and is considerably lower than that of less active humans (adults, 28.0%; children, 19.4%; *SI Methods*). The pattern of PAL and body composition seen in Great Ape Trust orangutans is unlike that of sedentary captive macaques involved in calorie restriction studies, including control subjects with normal diets, which have PAL of less than 1.3 and body fat percentages of 19.2% (calorie restricted) to 32.3% (normal diet) (16).

Discussion

Despite active lifestyles similar to those in the wild, orangutans in our study maintained remarkably low DEE, suggesting a physiological adaptation for minimizing energy throughput previously unknown in apes. Specifically, our results indicate that the slow life history of orangutans results from decreased energy throughput rather than changes in energy allocation. Decreased energy throughput is thought to be a risk-averse strategy for minimizing the probability of starvation in habitats where food availability is highly variable, unpredictable, and prone to long periods of shortage (4–6). The rainforests of Borneo and Sumatra, in which orangutans live, are highly stochastic environments that often experience crashes in the availability of ripe fruit, the food on which orangutans depend (27). Our study suggests that orangutans have adapted by becoming consummate low-energy specialists, decreasing their daily energy needs to avoid starvation in food-poor times. Observations in the wild support the hypothesis that ecological food constraints have had widespread repercussions on the physiology, behavior, and life history of orangutans. In addition to their low rates of growth and reproduction (8), orangutans live solitary lifestyles, avoiding the increased foraging costs incurred in large groups (8, 28), and use locomotor strategies that minimize the cost of travel through the canopy (29).

The link between DEE and life history in orangutans may also shed light on the evolved energy use strategies of other primates. Primates generally have low rates of growth and reproduction relative to other mammals (9). Although this slow primate life history strategy is commonly thought to reflect an energy allocation strategy of increased somatic investment and decreased mortality (9), our results suggest that low growth and reproduction rates may also stem at least in part from decreased energy throughput. Indeed, the limited DEE data for primates indicates many species, including mouse lemurs, sportive lemurs, howler monkeys, humans, and orangutans, have lower DEE than expected for their body mass (as discussed earlier; Fig. 1). More measurements of primate DEE are needed to test this hypothesis thoroughly.

In captive settings, the low energy needs of orangutans likely make them prone to overfeeding and obesity, even where sufficient enrichment is available to ensure an active lifestyle. Caretakers should reference our data in planning orangutan nutritional schedules, and consider direct measures of energy use in managing the well being of other ape species. In the wild, the low energy requirements of orangutans should allow them to survive well in low-productivity habitats. Data from the wild support this hypothesis for Bornean orangutans, which appear to withstand selective logging reasonably well, but data on Sumatran orangutans are less clear (30). More research on the energy requirements of each species is needed to understand potential differences in their susceptibility to habitat disturbance.

Finally, our results open a line of inquiry in the study of human and ape evolution. Modeling studies based on activity budgets

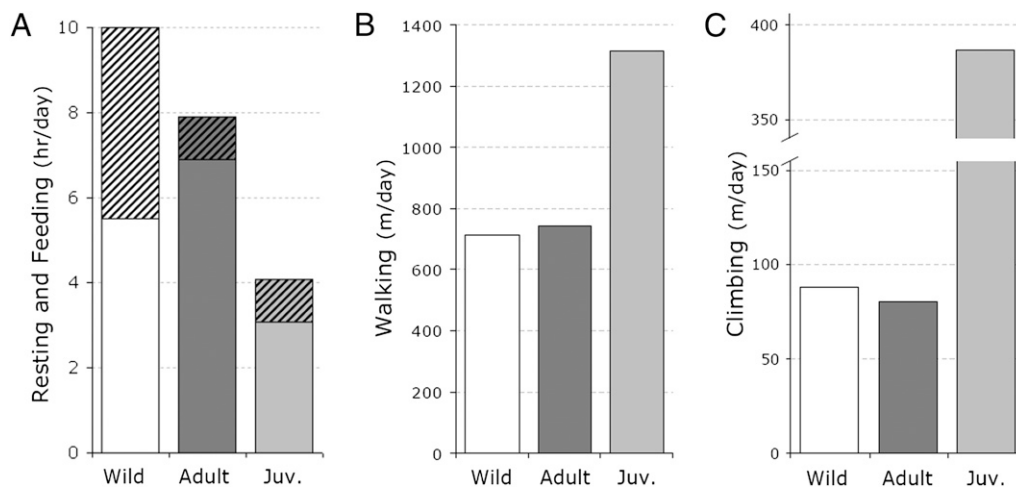


Fig. 4. Activity profiles for orangutans in the wild and at the Great Ape Trust (adults, $n = 3$; juvenile, $n = 1$). (A) Feeding and resting. Hashed area indicates time spent feeding. Wild and Great Ape Trust orangutans also sleep approximately 12 h each night. Wild data are from populations in masting forests (i.e., forests that experience periodic crashes in food availability) (40). (B) Walking, which includes the horizontal distance traveled in the canopy and, for Great Ape Trust subjects, the distance traversed along enclosure walls. Wild data are from both Borneo and Sumatra [$n = 8$ sites; mean, 712 m/d; range, 162–1,077 m/d (41)]. (C) Climbing, which includes all vertical travel (ascent only). Wild data (mean, 88.3 m/d; range, 55.7–121.4 m/d) from full day follows of eight adults (*SI Methods*). Great Ape Trust data shown in [Table S3](#).

and life history schedules have long suggested that critical changes in hominin evolution arose from changing patterns of energy use (7, 9, 12). Measurements of energy throughput in living hominoids will help expand and inform these evolutionary reconstructions. For example, whereas orangutans appear to be energy minimizers, the comparatively high DEE of humans may suggest our species is adapted to relatively high energy throughput. An accelerated metabolic rate in the hominin lineage would be consistent with humans' high rate of reproduction (7) and large brains (9, 11) relative to other apes. If increased throughput is linked to decreased variance in food availability as proposed previously (4, 6), the adoption of provisioning behaviors may ultimately explain why human reproductive rates diverged from those of other hominoids. Direct measures of daily energy use in other apes, as well as human foragers, are needed to test these evolutionary hypotheses.

Methods

We measured DEE (in kCal/d) over a 2-wk period in four orangutans: one adult male (Azy, age 30 y, mass 116 kg), two adult females (Knobi, age 27 y, mass 56 kg; and Katy, age 19 y, mass 53 kg), and one juvenile male (Rocky, age 4 y, mass 25 kg). All subjects were hybrids of Bornean and Sumatran *Pongo* species. DEE was measured twice in Azy and Knobi, once during a 2-wk period in August, and once during a 2-wk period in October 2008; the mean of the measurements from these two periods was used for subsequent analyses. DEE was measured during the October session for Katy and Rocky. Institutional Animal Care and Use Committee permission was obtained from the Great Ape Trust and Washington University before conducting the study, and institutional guidelines were followed throughout. Subjects were weighed daily throughout the course of the study with a digital weighing platform. All subjects were weight-stable (i.e., <2 kg fluctuation) over the course of the study, and had been weight-stable during the preceding 6 mo.

The Great Ape Trust houses orangutans in a large indoor/outdoor habitat ([Fig. S1](#)). Indoor enclosures are maintained at 25 °C and consist of 900 m² of living space divided into four main areas. The building is 15 m tall, and enclosure walls are made of heavy-gauge metal fencing that permits climbing. Outdoor areas consist of an enclosure (15 m × 15 m × 15 m) with climbable walls and fire hoses to encourage climbing, and a three-acre forested area. Orangutans sleep indoors, but spend a large portion of daytime hours outside.

DLW doses were administered orally. Adult females and the juvenile were each given 17.7-g doses of deuterium oxide-¹⁸O (D, 49.8atom%; ¹⁸O, 54.3 atom%; Isotec); the adult male was given a 35.4-g dose. Doses were mixed into a small portion of sugar-free iced tea, which the subjects then drank; the same investigator (R.W.S.) administered the dose to each animal to ensure all of it was consumed ([Fig. S2A](#)). The drinking cup was refilled with iced tea only

and drunk two additional times to ensure that the entire DLW dose was consumed. To track DLW enrichment, urine samples for each subject were collected (i) before dosing, (ii) 4 h after dose administration, and (iii) each morning for the subsequent 15 d. Urine was collected by asking each subject to urinate into a clean, dry paper cup ([Fig. S2B](#)); all subjects were trained for this before the study. Care was taken to avoid contamination. Samples were immediately transferred to 2-mL cryovials (Sarstedt) and frozen at –10 °C. Samples remained frozen until analysis using gas-isotope MS (William Wong, Houston, TX). An aliquot of the DLW batch used for the doses was used for calibration. A ²H dilution technique was used to calculate lean body mass (15). The rates of ²H and ¹⁸O depletion ([Fig. S2C](#)) were used to calculate the rate of CO₂ production and hence DEE (15).

CO₂ production was converted to metabolic energy expenditure using a food quotient (FQ) of 0.95, which was calculated from Great Ape Trust orangutans' weekly diets ([Table S2](#)). FQ must equal respiratory quotient (RQ) over long periods (i.e., several days) in weight- and nutrient-stable subjects (31), and are therefore preferable to RQ measurements from relatively short (approximately 20 min) RMR trials. This value is higher than the RQ of 0.85 generally used in studies of humans and other mammals (14). We note, however, that even substantial variation in the assumed RQ does not significantly affect comparisons with humans and other mammals: if an RQ of 0.85 is assumed, orangutan DEE in our sample was still significantly lower than that in humans ($P < 0.001$) and lower than all other eutherian mammals except sloths.

RMR was measured by using open-flow methods described previously (32). Subjects sat quietly with their face resting on or near the open-mesh wall of their enclosure. A vacuum hose was then held with its aperture within 10 cm of the subject's face ([Fig. S3](#)). Air was drawn at a high rate (500 L/min) through the vacuum to collect all expired air. The stream of collected air was sampled continuously and analyzed for oxygen and CO₂ content (Sable Systems). Trials were accepted for analysis if the rate of oxygen consumption and CO₂ production remained stable for at least 8 min. A minimum of three trials, collected on separate days, were analyzed for each subject; results are shown in [Table S4](#). The rate of oxygen consumption was converted to kCal/d assuming 1 L of oxygen was equivalent to 20.1 kCal. Subjects were not sleeping or necessarily prone for these trials.

Orangutan DEE and RMR were compared with published values for humans and other mammals (*SI Methods*). Activity data, including time spent resting and feeding as well as walking and climbing distances were recorded for each subject for a subset of days during the 2-wk DEE measurement period. Hourly rates of resting and feeding (minutes/hour) and climbing and walking (m/h) were converted to daily rates for further analysis and comparison with activity data for wild orangutans. Daily locomotor costs for Great Ape Trust orangutans were calculated by applying walking and climbing costs published for other primates to distances walked and climbed each day (*SI Methods*).

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