PNAS RESEARCH ARTICLE | ANTHROPOLOGY

Metabolic scaling, energy allocation tradeoffs, and the evolution of humans' unique metabolism

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Edited by Christopher Kuzawa, Northwestern University, Evanston, IL; received May 16, 2024; accepted October 11, 2024

All organisms use limited energy to grow, survive, and reproduce, necessitating energy allocation tradeoffs, but there is debate over how selection impacted metabolic budgets and tradeoffs in primates, including humans. Here, we develop a method to compare metabolic rates as quotients of observed relative to expected values for mammals corrected for size, body composition, environmental temperature, and phylogenetic relatedness. Contrary to previous analyses, these quotients reveal that nonhuman primates have total metabolic rates expected for similar-sized mammals in similar environments. In addition, data from several small-scale societies show that humans evolved exceptionally high resting, activity, and total metabolic rates apparently by overcoming tradeoffs between resting and active energy expenditures that constrain other primates. Enhanced metabolic rates help humans fuel expanded brains, faster reproductive rates, extended longevity, and high percentage of body fat.

metabolism | tradeoffs | primate | human | evolution

Significance

There is debate over whether primate and human metabolic rates are lower than those of other animals and whether higher physical activity levels cause lower resting metabolic rates. Here, we describe a method for comparing metabolic rates using quotients of measured metabolic rates versus those predicted from a large sample of mammals corrected for the effects of body size and composition, environmental temperature, and evolutionary relatedness. Applying these metabolic quotients to several human populations reveal that humans evolved exceptionally high metabolic rates that, unlike other mammals including nonhuman primates, do not trade off energy allocation to maintenance versus physical activity. Humans' uniquely high metabolic rates helped fuel the evolution of our species' large brains, high reproductive rates, and extended longevity.

One longstanding problem is how humans evolved to be an energetically extravagant species that, compared to chimpanzees, our closest relatives, affords larger bodies, three to four times larger brains, 50% shorter interbirth intervals, at least three times as much body fat, longer average lifespans including several postreproductive decades, and three to five times more daily physical activity (1). Important explanations for these adaptations are that extractive foraging, hunting, cooperation, and technologies such as cooking provide humans with more overall energy (1–4). In turn, humans have uniquely high overall metabolic budgets, measured as TEE (total energy expenditure), that can potentially allow increased energy allocation to physical activity (measured as AEE, active energy expenditure) as well as to other functions collectively measured as resting energy expenditure (REE) that include growth, maintenance, fat storage, and reproduction (5). Another metabolic component is the cost of digestion, termed diet-induced thermogenesis (DIT). Thus, TEE = REE+AEE+DIT. DIT, however, is hard to measure and is almost always assumed to be 0.1 TEE. Because energy availability was limited for most humans until recently, there was likely selection during human evolution on tradeoffs among these energy allocation options to invest in our species' unique anatomical, physiological, and life history traits that ultimately maximize lifetime reproductive success (6). Those tradeoffs are therefore the subject of much research, especially the relationship between AEE and REE, which includes functions relevant to life history such as immunity and maintaining and repairing expensive tissues like the brain. In particular, all primates including humans and apes are claimed to have lower TEEs than other mammals relative to fat-free body mass (FFM) reflecting low-energy throughputs compared to other mammals (7). In addition, while many studies find or infer that REE relative to FFM is no different in nonhuman primates than other mammals (8), humans are proposed to have higher TEEs and REEs relative to FFM than other apes (5, 7). Finally, recent studies claim that constraints on TEE cause tradeoffs among humans between AEE and REE, lowering mass-specific REE in more physically active humans such as hunter-gatherers (Hadza) (9–11). This raises a question: If contemporary and presumably paleolithic hunter-gatherers have similar TEEs relative to FFM as westerners yet engage in about 10 times more physical activity and thus allocate less energy to REE, how did humans afford larger brains, shorter interbirth intervals, more body fat, greater longevity and other energetically costly dimensions of human life history?

An additional consideration is the need to reconcile constrained metabolic energy allocation (TEE = REE+AEE) with the laws of thermodynamics which dictate that the heat generated by TEE in homeotherms must be exchanged with the environment to maintain constant body temperature (12). Thus, TEE= $h \bullet A(T_a - T_b)$, where h is the heat transfer coefficient (exchange of body heat via surface area, expressed as MJ/d/m^2/°C), A is the body's effective surface area for heat exchange, and T_a and T_b are ambient and

Author contributions: A.K.Y., S.B.H., M.J.M., and D.E.L. designed research; A.K.Y., L.M.R., and D.E.L. performed research; A.K.Y., E.R.C., and D.E.L. analyzed data; S.B.H. and M.J.M. helped design study and edit the paper; E.R.C. helped edit paper; and A.K.Y. and D.E.L. wrote the paper.

The authors declare no competing interest.

This article is a PNAS Direct Submission.

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This article contains supporting information online at https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2409674121/-/DCSupplemental.

body temperatures. Note that h, A, T_a, and T_b are dynamic and affected by behaviors such as seeking shade and altering posture and levels of physical activity. As Fig. 1*A* shows, these two equations reveal that for a given TEE there must be a tradeoff between REE and AEE, whereas increasing or decreasing TEE requires changing some combination of h, A or T_b to either increase or decrease heat dissipation.

Here, we test whether metabolic rates differ among mammals, nonhuman primates including apes, and a diverse sample of human populations. We also test whether selection during primate and human evolution involved tradeoffs between AEE and REE or shifts in TEE via thermoregulation. However, testing these and other related hypotheses requires accurately comparing metabolic rates among species, populations, and individuals. The dominant factor to control is body mass, M, which explains most of the interspecific variation in a given metabolic rate, R, according to the power law $R = aM^b$, where a is a mass coefficient and b is a scaling exponent (13). Although b across vertebrates is usually close to 0.75, a and b need to be determined empirically and their values vary depending on the species or individuals used to scale R against M. It is also necessary to control for environmental temperature (T_e) when comparing animals across habitats (12). To maintain homeostasis, REE for mammals at −10 °C is approximately 40% higher than for similar-sized mammals at 25 °C (14) suggesting that primates from tropical habitats should have lower mass-specific REEs than mammals from temperate habitats. Additionally, since AEE generates heat that must be dissipated, high T_es of primates may constrain levels of AEE, but humans' unique thermoregulatory adaptations including sweating potentially mitigate this constraint. Another factor especially relevant to humans is adipose tissue, which is less metabolically active than most other tissues so that FFM correlates more closely with TEE and REE than does M (15, 16). The fat mass index (FMI, FFM/M) in nonmarine adult mammals averages 0.044 and is similar in wild primates (17–20) but adult Hadza average 0.10 to 0.25 (21), Americans with BMIs of 18 to 25 kg/m^2 have average FMIs of 0.25 to 0.38, and FMIs of individuals classified as overweight and obese exceed 0.40 (22). Finally, age, sex, resting body temperature, phylogeny, and population also influence R (23, 24).

Methodological issues can also compromise comparisons of metabolic rates. Although many studies compare activity metabolic rates among individuals and species using the Physical Activity Level (PAL, defined as TEE/REE), quantifying AEE as a proportion of REE instead of M can introduce artifacts such as falsely finding that two individuals with the same M and AEE but different REEs differ in their level of physical activity. In addition, TEE, REE, and AEE may scale differently with M, highlighting the benefit of analyzing AEE relative to M, its primary determinant. Another concern is error from measuring or estimating the different components of metabolism (25). In particular, numerous studies analyze basal metabolic rate (BMR) instead of REE, but BMR must be measured under physiologically abnormal conditions: postabsorptive, inactive for 24 to 48 h, at the nadir of the circadian rhythm (usually upon waking), and in a thermoneutral temperature. As a result, researchers often measure REE, defined loosely as R measured under resting but not basal conditions, and assume the cost of digestion (Diet Induced Thermogenesis) is 10% of TEE, although DIT is highly variable within and between species. In addition, TEE, which is best measured using the doubly labeled water method, is subject to several sources of error including estimating rO_2 from rCO_2 as a function of an individual's respiratory quotient (RQ) (26), so a 5% error in RQ will lead to a 5% error in rCO_2, hence TEE. Most importantly, since AEE is most commonly estimated as TEE-REE, calculating metabolic compensation (tradeoffs between AEE and REE) by regressing AEE with REE causes a spurious negative correlation (regression dilution) because AEE and REE variation, including errors, are nonindependent (27).

Here, we describe a method to evaluate differences in metabolic rates among mammal species including humans, apes, and other nonhuman primates by normalizing measured metabolic measurements for a given species of population by the empirically predicted values for the average legged eutherian of the same body mass, body composition (FMI), and Te. These predicted values are calculated using standard multivariate allometric regressions using published data on TEE (n = 96) and REE (n = 476) from pooled mammal samples (20, 21) and corrected for phylogenetic autocorrelation using phylogenetic generalized least squares (PGLS; *Materials and Methods*). This method yields

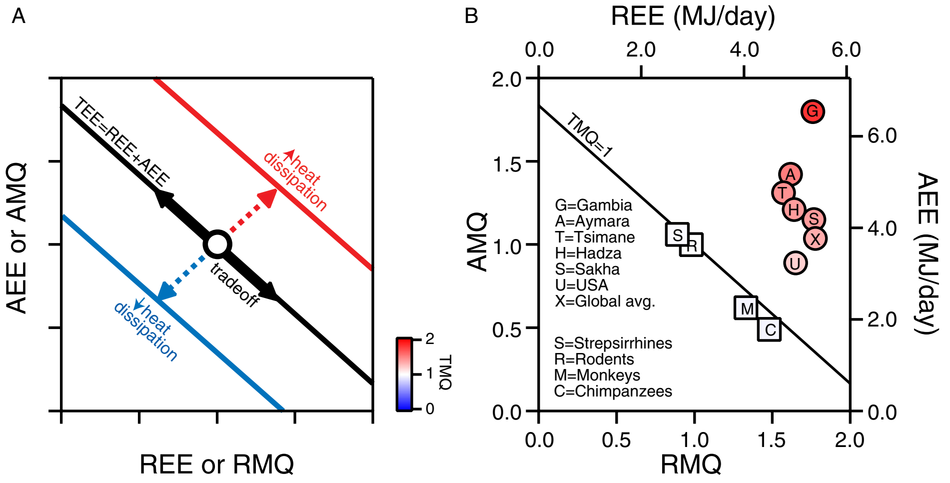

Fig. 1. Thermodynamic model of energy allocation. (*A*) Assuming that heat generated by TEE must be exchanged with the environment to maintain constant body temperature, then for a given TEE, there must be a tradeoff between AEE and REE (or their quotients AMQ and RMQ). Diverging from this gradient requires either more or less heat exchange with the environment. (*B*) Test of the model using data on nonhuman primates and mammals, all of which fall along gradient of TMQ = 1. In contrast, human populations from diverse environments and subsistence strategies all fall above the average mammalian gradient of TMQ = 1, indicating an improved ability to exchange heat thus allowing higher AEEs for a given REE. Hadza are hunter-gatherers from Tanzania, the Tsimane are forager-horticulturalists form the Amazon, the Gambia, and Aymara are subsistence farmers from tropical Africa and highland Bolivia, U represents a postindustrial American population, and X is a global average of 110 populations.

three dimensionless metabolic quotients—total metabolic quotient (TMQ), resting metabolic quotient (RMQ), and activity metabolic quotient (AMQ)—that scale to an interspecific average value of 1.0 independent of size and environmental temperature factors:

$$TMQ = \frac{TEE_{meas}}{TEE_{model}}; RMQ = \frac{REE_{meas}}{REE_{model}};$$
$$AMQ = \frac{TEE_{meas} - REE_{meas}}{TEE_{model} - REE_{model}}.$$

Note these quotients are empirical descriptions rather than mechanistic arguments, they make no assumptions about scaling, and they control for the effects of *M*, body fat, *Te*, as well as any potential phylogenetically patterned relationships. After deriving the metabolic quotients, we address three questions on the evolution of human metabolism. First, do primates have lower TMQs compared to other mammals? Second, how do RMQs, AMQs, and TMQs vary among primates including apes and humans? Third, we test the validity of using metabolic quotients derived from interspecific data for making intraspecific comparisons among humans, and then ask, are TMQs constrained to a narrow range within humans with evidence of a tradeoff between AEE and REE?

Results

Derivation of Metabolic Quotients. Fig. 2 and *SI Appendix*, Table S1 show that TEE and REE scale equivalently to $M^{0.72}$ across the reference sample of mammals (REE coefficient: 0.721 ± 0.012 SE; TEE coefficient: 0.719 ± 0.014 SE) with minimal effect from including or excluding winged and flippered species (*SI Appendix*, Table S2). Accordingly, the three metabolic quotients were calculated using the legged mammal reference sample as:

$$RMQ = \frac{REE_{meas}}{[299(1.05FFM)^{0.72} * 10^{-0.0057T_e}]},$$

$$AMQ = \frac{AEE_{meas}}{\left[1016M^{0.72} * 10^{-0.0132T_e}\right] - [299M^{0.72} * 10^{-0.0057T_e}]},$$

$$TMQ = \frac{TEE_{meas}}{[299(1.05FFM)^{0.72} * 10^{-0.0057T_e}] + \left[1016M^{0.72} * 10^{-0.0132T_e}\right] - [299M^{0.72} * 10^{-0.0057T_e}]}.$$

Note that RMQ was calculated by predicting REE using *FFM* instead of *M* because REE is primarily influenced by *FFM*; AMQ was calculated by predicting AEE using *M* because the metabolic cost of movement, hence AEE, depends mainly on inertia (i.e., *M*) (23). Since TEE is the sum of AEE and REE but AEE is dependent on *M* while REE is dependent on *FFM*, TMQ was calculated by predicting REE and AEE separately using their appropriate mass predictors (*FFM* and *M*, respectively). Although FFM is not reported for all mammals, a sensitivity analysis shows that assuming an FMI of 0.05 for a non-human mammal typically results in an error of <0.05 in RMQ (*Materials and Methods*).

Evolution of Primate Metabolism. To test whether primates have lower TMQs compared to other mammals, we included *Te* as a covariate in our average mammal models. As previously reported, we find significant nonlinear, negative effects of *Te* on both REE and TEE (Fig. 2 and *SI Appendix*, Table S1), likely driven by heat dissipation constraints (12, 14). Although nonhuman primates live almost exclusively in warm, tropical environments, a previous mass scaling model that lacked *Te* as a covariate reported that primates have 50% lower TEEs per kg of body mass compared to other mammals (7). However, including *Te* in our model shows that mass- and temperature-adjusted TEE values among primates do not differ significantly from other legged eutherians (primates TMQ: 0.98, post hoc t test: t = −0.51, *P* = 0.61), as evident from the mass-independent partial residuals shown in Fig. 2*D*. Primate TEEs are therefore similar to those of similar-sized legged mammals from warm environments but lower than those of similar-sized species in cooler environments, following an interspecific gradient driven by heat constraints (Fig. 1*B*).

To evaluate the evolution of metabolic rates among primates including humans, Figs. 1*B* and 3 compare TMQ, RMQ, and AMQ among a rodent outgroup, strepsirrhines, monkeys, chimpanzees, and one human population (Hadza from Tanzania, see *Materials and Methods* 1.5). For all three quotients, rodents (RMQ = 0.98 ± 0.02, n = 280; TMQ = 1.00 ± 0.05, n = 44; AMQ = 1.02) and strepsirrhines (RMQ = 0.89 ± 0.08, n = 14; TMQ = 0.98 ± 0.16, n = 5; AMQ = 1.06) do not differ from the average mammal value of 1.0, corrected for *M*, *Te,* and body composition (FMI) (Figs. 1*B* and 3). Post hoc t tests confirm that RMQ and TMQ values in rodents and strepsirrhines do not differ significantly different from 1.0 (rodents: RMQ *P* = 0.157, TMQ *P* = 0.736; strepsirrhines: RMQ *P* = 0.229, TMQ p = 0.916). In monkeys, TMQ averages 0.96 ± 0.07 (n = 8), but RMQ averages 1.33 ± 0.08 (n = 11) while estimated AMQ averages 0.62 (*Materials and Methods*). This tradeoff between AEE and REE is amplified in apes: in a published sample of zoo and sanctuary chimpanzees (5) mean TMQ is 0.96 and thus typical for a mammal of its size and environmental temperature, but RMQ and AMQ are 1.48 and 0.49, respectively. These chimpanzees thus have the TEE expected for an animal of their size but apparently increase somatic investments by allocating 50% less energy to physical activity (5). Note that if wild chimpanzees were 50% more active than sanctuary chimpanzees, their AMQ would be only 0.74, still indicating a substantial tradeoff between AEE and REE. In addition, Fig. 1*B* shows that nonhuman primates trade off AMQ and RMQ (hence AEE and REE) along the same TMQ gradient. Therefore, while strepsirrhines, monkeys, and apes have different relative investments in REE and AEE, they exchange the same amount of heat corrected for *M* with their environment.

Evolution of Human Metabolism. As previously shown (5), humans are metabolically different than average mammals including primates, with higher TMQs, RMQs, and AMQs (Figs. 1*B*, 3, and 4). To explore these differences, we first compare metabolic quotients of non-human primates with published data

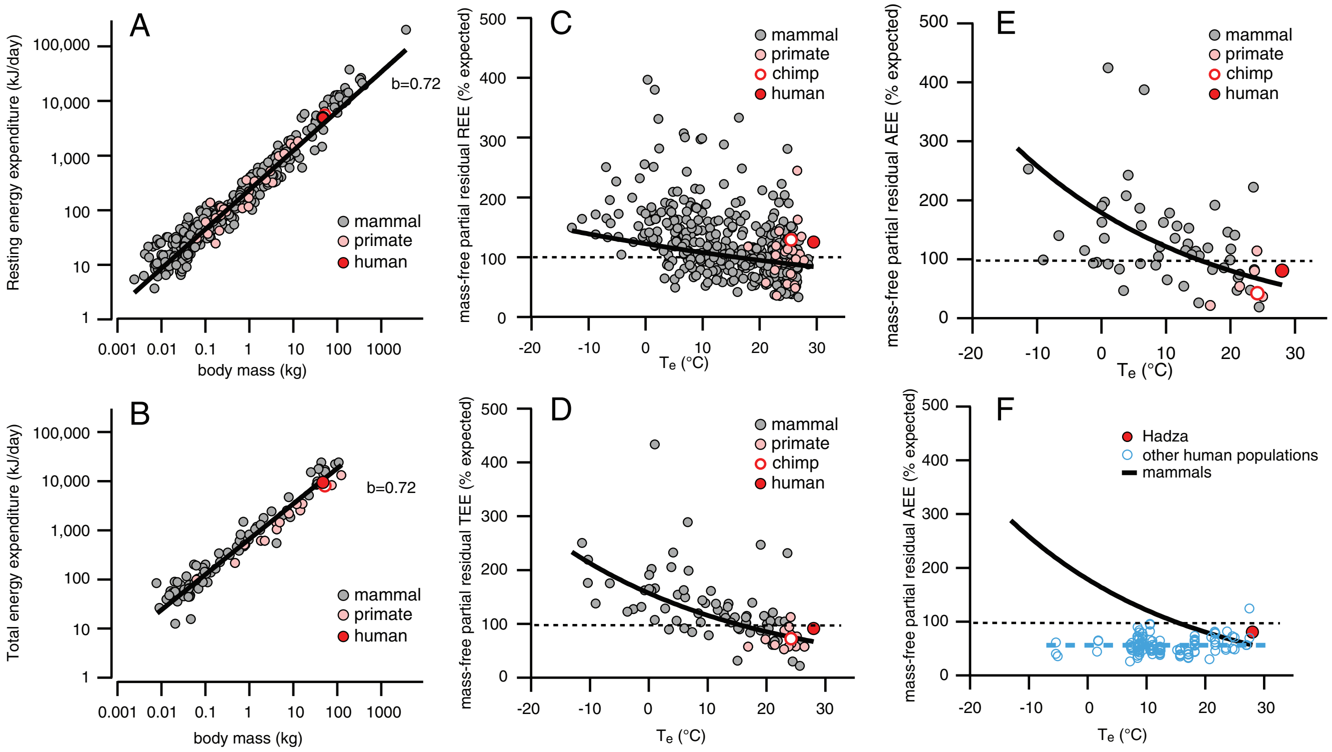

Fig. 2. Allometric regression models. Total, resting, and active energy expenditure relative to body size and environmental temperature. (*A* and *B*) Logarithmic plots of total (*A*) and resting (*B*) energy expenditure versus body mass. Hadza are indicated by the dark red closed circle, chimpanzees by the dark red open circle, other primates by light red, and nonprimate legged eutherian mammals by gray. Both resting and TEE scale to body mass with an exponent of 0.72. (*C*–*E*) Resting total and active energy expenditure as a function of environmental temperature (*Te*). All expenditures are partial residuals that correct for body mass using the relationships shown in *A* and *B* and are reported as the percentage expected based on mass alone. Note that AEE declines with *Te* in mammals (*D*) but is independent of *Te* in humans (*F*), with Hadza indicated by the dark red closed circle and 116 other human sample means plotted in blue.

on Hadza hunter-gatherers (n = 30, 17F, and 13 M; ref. 9) whose activity levels, energy expenditures, and *Te* are hypothesized to be representative for humans over the past several My (9, 29). We then compare metabolic rates and tradeoffs among diverse human populations.

Figs. 3 and 4 show that the average Hadza AMQ of 1.24 is more than twice as high as the AMQ of chimpanzees (0.49) and monkeys (0.62). But instead of being constrained by a tradeoff between AMQ and RMQ, RMQ is 11% higher in Hadza hunter-gatherers (1.64, estimated using a mass-based regression equation) than in chimpanzees (1.48). The combined increases in Hadza RMQ and AMQ also result in high mean TMQs (1.42), with Hadza in the 88th percentile of the legged mammal TMQ sample (Fig. 4*A*). To illustrate these differences in terms of energy, Fig. 3*B* compares these AEEs and REEs as MJ/d standardized to the same *M*, *FMI*, and *Te*. While the hypothetical chimpanzee spends ~2.1 MJ/d on AEE, the average Hadza of the same size and FMI in the same *Te* spends ~4.5 MJ/d on AEE—2.1 times greater than the average chimpanzee, 1.6 times higher than the average monkey, and 1.2 times higher than the average legged eutherian.

Before comparing metabolic rates among humans, we use two methods to test whether metabolic quotients derived from an interspecific sample of mammals accurately correct for size intraspecifically among humans. First, we calculated R^2 of the regression between size-corrected quotients against *M* or *FFM* (*SI Appendix*, Fig. S3 and Table S3). For all three quotients, R^2 was less than 0.014. Next, we compared our quotients to size-corrected values of AEE, REE, and TEE derived using intraspecific variation from a sample of postindustrial Americans (n = 274, 136F, and 138 M; *Materials and Methods*). We used multivariate regression with *M*, *FFM*, age, and sex as predictors to calculate size-independent residuals and then tested these residuals' correlation with the appropriate quotients. In all cases, r was greater than 0.91 and R^2 was greater than 0.83 indicating that the interspecific-derived quotient method is valid for intraspecific size correction in humans.

To explore variation in metabolic rates among human populations, we first compare TMQ, AMQ, and RMQ between the Hadza hunter-gatherer and postindustrial American samples using nonparametric Mann–Whitney tests with the null hypothesis of values sampled from a common distribution. As Figs. 3*C* and 4 show, TMQ in Americans is 14% lower than that in the Hadza (1.20 versus 1.42, Mann–Whitney U = 2297, $P < 0.0001$), while AMQ is 30% lower in Americans compared to the Hadza (0.87 versus 1.24, U = 2486, $P = 0.0002$) with no difference in estimated RMQ. When standardized by *M*, *FFM*, and *Te*, as shown in Fig. 3*D*, an average postindustrial American spends approximately 1 MJ/d (240 kcal/d) less on physical activity than an average Hadza, with no difference in REE. Note, however, that variation in both TMQ and AMQ is large within the Hadza and American samples, spanning almost the entire interspecific legged mammal ranges for these quotients (Fig. 4).

In order to evaluate Hadza metabolic rates in the broader context of other small-scale, nonindustrial populations, we used published data on four additional populations from diverse environmental contexts: Tsimane forager-horticulturalists from the Amazon, subsistence farmers from the high-altitude Andes (Aymara) and the Gambia, and Sakha (Yakut) pastoralists from Siberia (*Materials and Methods* 1.5). We also include a global average from 110 industrial populations that vary in income level (28). To facilitate comparisons, Fig. 3*D* and *SI Appendix*, Table S4 also report estimated energy expenditures in MJ/d

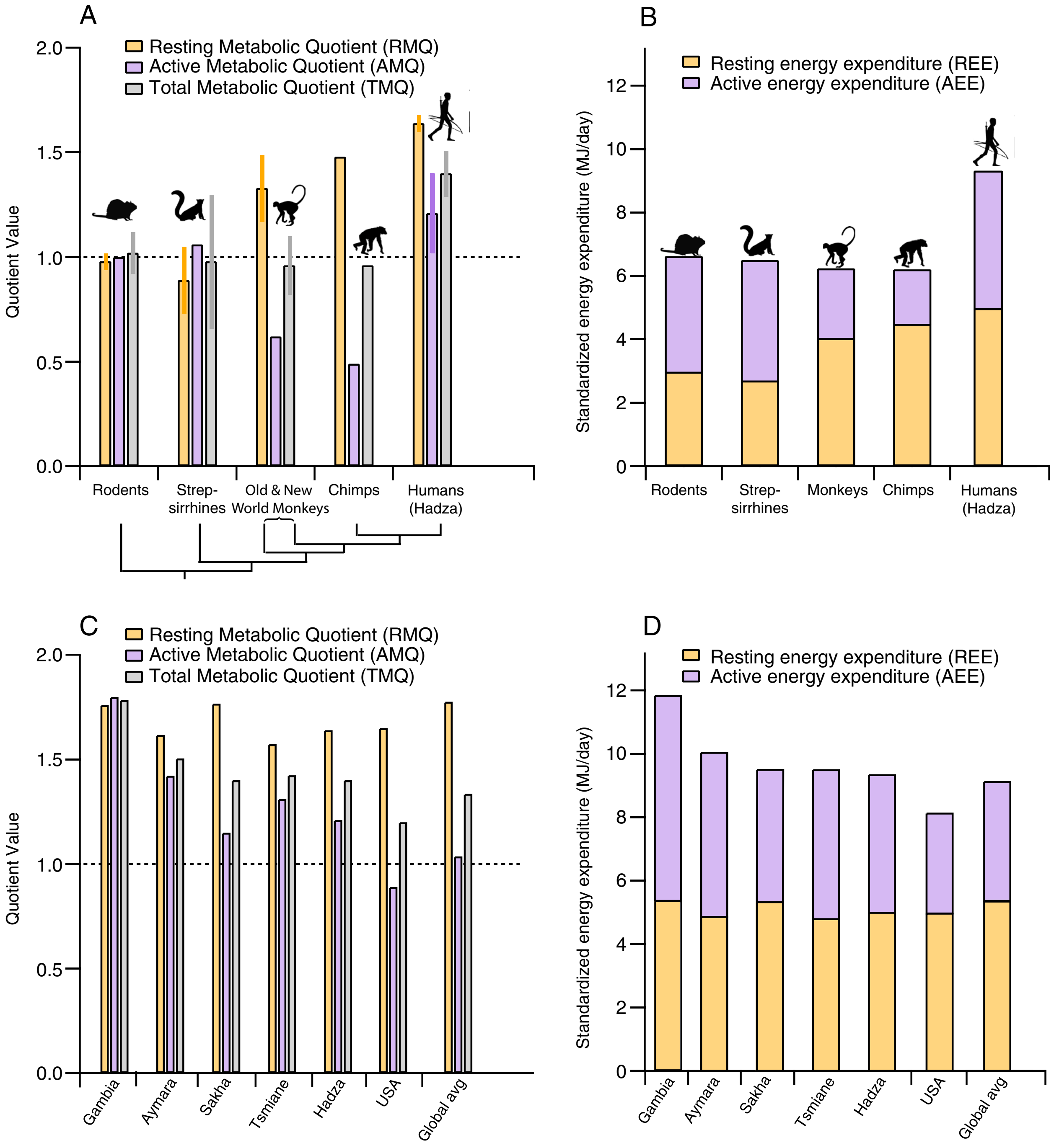

Fig. 3. Interspecific and intraspecific variation in resting, active, and TEEs. (*A*) Evolution of resting, active, and TMQs (RMQ, AMQ, and TMQ) for select primate clades including a human hunter-gatherer population represented by the Hadza (from ref. 9) and with rodents as an outgroup (see *Materials and Methods* for data sources). All data are averages of males and females with 95% CI shown when available. In monkeys and chimpanzees, TMQ values are not significantly different from the average mammal value of 1.0, but RMQs are higher and AMQs are lower; in contrast, RMQ, AMQ, and TMQ in the hunter-gatherer population are significantly above 1.0. (*B*) Estimated resting and active energy expenditures in MJ/d of the same taxa standardized to a 47.2 kg body mass, 39.7 kg fat-free mass, and 28 °C. (*C* and *D*) Metabolic quotients (*C*) and standardized resting and active energy expenditures in MJ/d (*D*) for five nonindustrial populations including the Hadza, a sample of Americans, and a global sample of 110 populations (from ref. 28). Although AMQ varies widely among human populations with only Americans being less active that similar-sized mammals, TMQ and RMQ are substantially above expected values for similar-sized mammals, and there is minimal variation in daily REE after standardizing for size, body composition, and environmental temperature. See *Materials and Methods* for details on how values were derived for each clade.

standardized to the same *M*, *FMI*, and *Te*. Of the nonindustrial populations, the Hadza, Aymara, Sakha, and Tsimane all have similarly high TMQs (1.40 to 1.50) and AMQs (1.15 to 1.42), and the Gambian farmers have an extraordinarily high AMQ of 1.80, causing an equivalently higher TMQ of 1.78. In contrast, the TMQ and AMQ for the global sample were 1.34 and 1.04, respectively, and the US sample was even lower with a TMQ and AMQ of 1.20 and 0.87, respectively. Note also the similarity among estimated RMQ (1.57 to 1.78) and size-corrected REE values (4.78 to 5.39 MJ/d) for these populations despite differences in body size, FMI, measured activity levels, and subsistence.

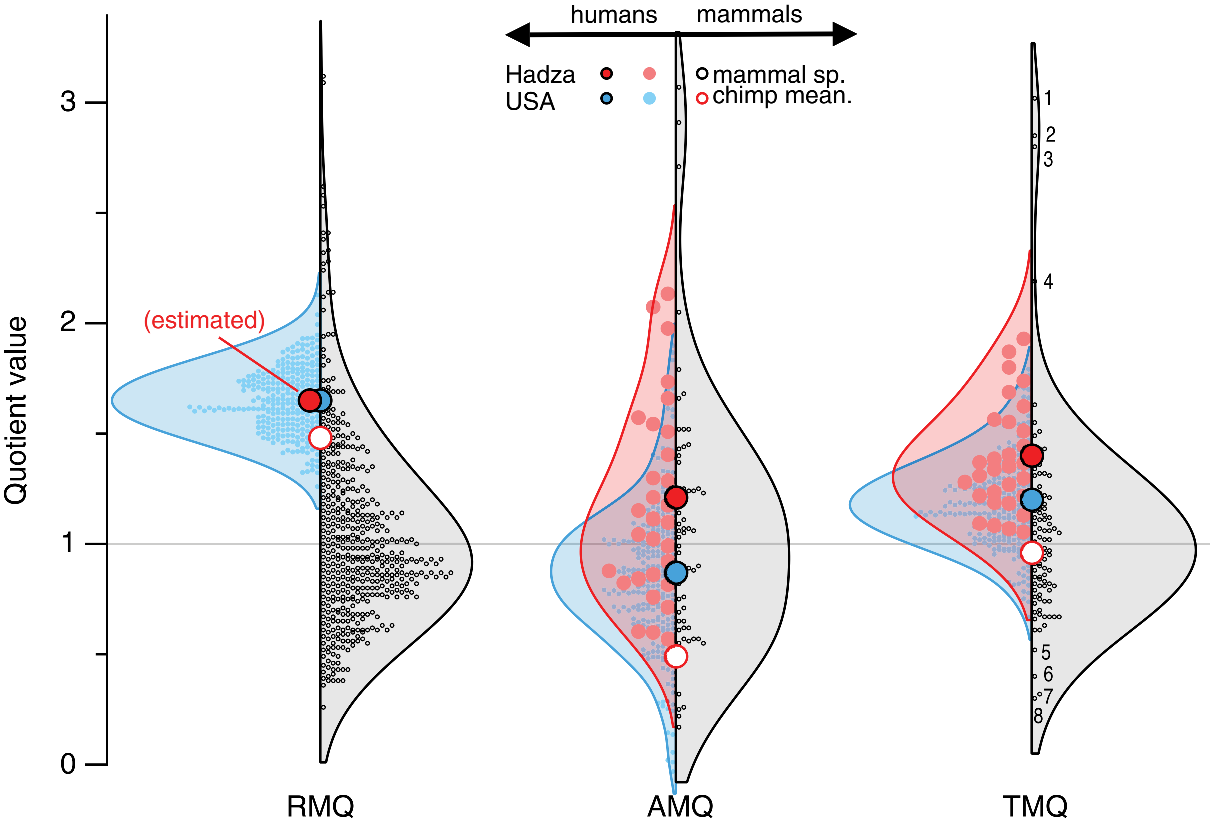

Fig. 4. Human metabolic quotients are high for mammals and vary widely within populations. Resting, active, and TMQs (RMQ, AMQ, and TMQ) are shown as dimensionless vertical scales. Mean quotient values for the Hadza (red), USA (blue), and chimpanzees (white) are plotted on the scales along with the expected value of 1.0 based on the average mammal. Violin plots show the distributions of quotient values along the scales: Gray distributions to the right represent interspecific variation within the legged mammal dataset, while red (Hadza) and blue (USA) distributions to the *Left* represent intraspecific variation within the two human populations. Mammal species means are also indicated by black open circles to the right of the scales, while human individuals are indicated by opaque red and blue closed circles to the left of the scales. Note that the Hadza RMQ value comes from REE data estimated by anthropometric equations rather than measured by indirect calorimetry as in the USA sample. Eight species with TMQ values at the extremes of the interspecific distribution are indicated by numbers: 1) African wild dog (*Lycaon pictus*), 2) Springbok (*Antidorcas marsupialis*), 3) Common shrew (*Sorex araneus*), 4) Mountain beaver (*Aplodontia rufa*), 5) Cairo spiny mouse (*Acomys cahirinus*), 6) Brown-throated sloth (*Bradypus variegatus*), 7) Grant's golden mole (*Eremitalpa granti*), and 8) Common rock rat (*Zyzomys argurus*).

Discussion

Metabolic quotients provide novel insights into the evolution of nonhuman primate and human metabolism by correcting for mass, body composition (FMI), environmental temperature (*Te*), and potential effects of phylogenetic relatedness without making assumptions about scaling. They also correct appropriately for body size for both inter- and intraspecific comparisons, avoid errors from comparing PALs or from regression dilution caused by regressing REE, AEE, and TEE against each other or against measures of body mass within the same sample (27).

Metabolic quotients suggest that the first stage in the evolution of humans' unique metabolism was likely increased REEs within non-human primates that helped make possible selection for increased investment in longer lifespans, slower ontogenies, and larger brains. While strepsirrhines have total, resting, and active metabolic rates typical of other mammals for their size and environment (TMQ, RMQ, and AMQ ≈ 1), monkeys and apes evolved RMQs that are 33% and 48% higher, respectively, than expected. Contrary to claims that primates have lower TEEs than other mammals of the same size (7), correcting for the effects of *Te* shows that their overall total metabolic rates are typical of similar-sized mammals in warm environments. Instead, increased investment in higher primate REEs appears to have been made possible by tradeoffs with physical activity. Old and New World monkeys have 38% lower AMQs than expected and this tradeoff is exaggerated in chimpanzees whose AMQs are 51% lower than expected.

Metabolic quotients add to previous evidence that innovations in food procurement, food processing, and cooperative behaviors increase energy availability, thus permitting mass-specific energy expenditure in humans to be higher relative to our closest ape relatives (5). Most importantly, humans were apparently selected to increase RMQ by a further 11% over chimpanzees while simultaneously increasing rather than decreasing AMQ, altogether leading to 45 to 85% higher TMQs among a diverse sample of nonindustrial human populations. These data accord with previously published comparisons of physical activity. While wild chimpanzees walk on average 3 to 4 km/d, climb 100 m/d, and rarely sprint for only short distances, average hunter-gatherer females and males walk 9 and 15 km/d, respectively, often carrying heavy burdens, engage in other physical activities such as digging, and sometimes long-distance running (4, 29, 30). Similarly, high levels of physical activity are also documented among humans in other small-scale societies from a variety of environmental contexts (4). A global sample of humans and relatively sedentary Americans have 2.1× and 1.81× higher AMQs, respectively, than sanctuary and zoo chimpanzees. Estimated locomotion costs in wild and captive chimps suggest that wild individuals expend ~500 kJ/d more than captive populations (5), yielding an estimated AMQ of 0.58, similar to monkeys (0.62). Even if wild chimpanzees were 50% more active than sanctuary and zoo chimpanzees, their estimated AMQ would be 0.74, in the 34th percentile of the mammal sample.

Although metabolic quotients cannot directly test how selection enabled humans to overcome the tradeoff between REE and AEE that constrains TEE in monkeys and apes, one likely factor is thermoregulation. As Fig. 2*E* shows, mammals in warmer environments have lower AEEs presumably because physical activity generates heat that is hard to dissipate (note that AMQ corrects for this temperature trend; Fig. 2 *E* and *F* show AEE versus *Te* corrected for only *M*). Compared to other primates including chimpanzees, humans evolved a unique, unparalleled ability to dump heat during physical activities in warm environments thanks to loss of fur combined with a 10-fold increase in eccrine gland number (31, 32). As a result, nonindustrial human populations including subsistence farmers and hunter-gatherers can average AMQs that are 2.3 to 3.7× higher than a chimpanzee of their size, despite living in habitats with *Te*s as high as 28 °C. Another contributing factor is locomotor efficiency: During walking, humans spend 50% fewer calories and thus generate less heat per unit distance and mass than chimpanzees (33). These adaptations were likely present by 2 Mya in the genus *Homo* (34), or possibly earlier (31). Since then, humans have spread across the globe, but as Figs. 1*B* and 2*F* show, mass-corrected AEEs from diverse human populations in a wide range of environments diverge from the TMQ gradient between AMQ and RMQ, and 116 human sample means of mass-corrected AEEs (from ref. 34), see *Materials and Methods*) are independent of *Te* unlike the observed negative trend with *Te* across mammals. While most mammals are less active in the higher T_e (12), humans have adaptations to overcome this constraint; similarly, while most animals are more active in lower T_e, humans do not need to elevate their metabolisms as much in colder environments because of technologies such as clothing and fire (35).

Humans' unique ability to overcome tradeoffs between REE and AEE that constrain other primates has profound implications. High human AMQs reinforce multiple lines of evidence that hominins were selected to travel long distances to forage and hunt daily for high-quality foods, helping hunter-gatherers such as the Hadza to achieve a stunning 65% higher RMQ and a 40% higher TMQ than expected for an average, same-sized mammal. Subsistence farmers from diverse environments have even higher energetic budgets. In turn, elevated energy budgets combined with high-quality diets, cooking, and other cooperative behaviors such as food-sharing that increase energy availability apparently released constraints on energy allocation tradeoffs. Altogether, high AMQs and RMQs (hence TMQs) reflect selection to invest more energy in critical human traits that increase reproductive success such as shortened inter-birth intervals, large brains, and increased investment in somatic maintenance and repair that extend postreproductive lifespans by several decades compared to chimpanzees (1). Of these investments, the three to four-times larger human brain is particularly notable, increasing REE by approximately 200 to 300 Kcal/d (36). Although not captured by metabolic quotients, human foragers (aided in part by increased brain size) can acquire so much energy that they also share surpluses with children and grandchildren, increasing their reproductive success (1, 2). Finally, by having more than twice as much body fat as chimpanzees, humans, especially females, can engage in comparatively high levels of sustained physical activity (as measured by AMQ) during extended periods of negative energy balance without compromising costly, critical investments in large brains or reproductive functions such as lactation (as measured by RMQ), helping explain selection for human females to store about 10% more fat than males.

In short, metabolic quotients add to previous evidence that humans are metabolically special (5). Compared to other mammals including apes, humans uniquely evolved to burn lots of energy while being physically active in hot environments, and thus have higher active, resting, and total metabolic expenditures per unit body mass. Metabolic quotients also resolve the apparent conundrum raised by comparisons of PALs and regression analyses of TEE against body mass that find no systematic differences in TEE relative to body mass across human populations including between hunter-gatherers and market societies despite obvious and marked differences in PA levels (9). When observed metabolic rates are compared to those expected for legged mammals corrected for body mass, FMI, and *Te*, substantial and significant differences are evident between postindustrial populations such as the USA and a diverse sample of nonindustrial populations in terms of active (AMQ) and total metabolic expenditures (TMQ) but not estimated resting metabolic expenditure (RMQ). Although this study does not test for tradeoffs between REE and AEE within the human populations analyzed, these metabolic differences accord with evidence that postindustrial societies are characterized by declining levels of physical activity combined with increased food energy availability and adiposity and more time in thermoneutral environments from air-conditioning and heating. Persistent sedentariness is thus an evolutionary mismatch. By spending less energy on physical activity which allocates energy toward repair and maintenance mechanisms, sedentary individuals funnel more energy toward excess fat storage and higher levels of reproductive hormones (37). Consequently, moderate levels of physical activity independent of diet effectively help prevent weight gain (38) as well as decrease the risk of many noncommunicable diseases such as atherosclerosis, hypertension, type 2 diabetes, and some cancers (39).

Materials and Methods

Allometric Regression Models. Interspecific scaling models were constructed from a mammalian dataset of REE, TEE, and T_e along with associated M for the two metabolic measurements (Dataset S1). REE and M_{REE} were downloaded from AnAge and Pantheria public databases for all available eutherian species, while most TEE and M_{TEE} values were compiled from three recent scaling studies that utilized the same data to a large extent (7, 13, 39–42). The Hadza community in Tanzania (9) were chosen as the representative population for humans, while TEE and REE data for hominids were taken from ref. 5. T_e was assigned to each species from Pantheria when available, defined as the mean annual temperature in the center of the species' geographic range, and for humans, the mean temperature of the Hadza's home territory of 28 °C was used (29). The dataset was then split into functional categories based on limb design. Winged mammals (Dataset S1) were defined as order Chiroptera, while flippered mammals (Dataset S1) were defined as pinnipeds (within order Carnivora) and order Sirenia (no cetacean data were included). The remaining species were categorized as legged mammals and compose the primary comparative dataset and analyses.

The compiled legged mammal dataset included 513 species, with 476 REE values and 96 TEE values. Fifty-nine species had values for both EE variables, although due to the separate provenance of the REE and TEE data some species had measurements obtained from separate populations with different masses. Eighty-four winged mammal species (80 REE values, 16 TEE values) and 15 flippered mammal species (nine REE, eight TEE) were also available in the larger dataset. Following (13), we modeled EE using an allometric function with M and T_e as the predictors:

$$EE = aM^b * 10^{cT_e}. \qquad [1]$$

Taking the log of the allometric function in Eq. **1** allowed for linear regression to determine the mass-scaling terms a and b and the temperature factor c:

$$\log(EE) = \log(a) + b * log(M) + c * T_e. \qquad [2]$$

We ran separate regressions on REE and TEE for the legged mammals (*SI Appendix*, Table S1), as well as regressions including all mammals in the dataset (*SI Appendix*, Table S2). Including winged and flippered mammals in the models had minimal effect on the regression coefficients, so we only used the legged mammal model to construct the metabolic quotients. Because phylogenetic autocorrelation can influence the regression parameters, we used PGLS models to construct the prediction equations. PGLS models were conducted using the "caper" package (43) in R Studio, and parameters were estimated via maximum likelihood. The mammalian supertree of Bininda-Emonds et al. (44) supplied the phylogenetic structure for comparative analyses of species in this dataset. Several species from the full dataset were not included in the molecular tree, so for PGLS regression, there were n = 409 legged REE and n = 78 legged TEE samples and n = 481 mammal REE and n = 98 mammal TEE.

Quotient Derivations. The results of the legged mammal regressions (*SI Appendix*, Table S1) yielded the prediction equations for REE, TEE, and AEE (units of kJ/d):

$$REE_{pred} = 299M^{0.72} * 10^{-0.0057T_e},$$

$$TEE_{pred} = 1016M^{0.72} * 10^{-0.0132T_e},$$

$$AEE_{pred} = (1016M^{0.72} * 10^{-0.0132T_e}) - (299M^{0.72} * 10^{-0.0057T_e}).$$

These prediction equations then formed the basis for RMQ, TMQ, and AMQ, which were calculated for each species that had the available data. Because REE and TEE data came from different sources and potentially different populations of different M, to calculate AMQ, we first estimated REE at M_{TEE} (REE*):

$$REE^{*} = RMQ * 299M_{TEE}^{0.72} * 10^{-0.0057T_e}.$$

Then using REE* and TEE, we calculated AEE at M_{TEE} followed by AMQ.

We note there is debate whether the relationship between mass and metabolism deviates from the standard power-law form and whether the scaling relationship is fixed between species or varies with phylogeny (13). We tested for these effects in our dataset and found no evidence of nonlinearity in the dataset and small variation in scaling exponents across orders or superorders with the exception of Eulipotyphla (hedgehogs, shews, and moles) (*SI Appendix*).

The scaling models use total body mass (M) as the size predictor, but in some cases, size may be more appropriately controlled for using fat-free mass (FFM), especially for REE. We therefore used the scaling models found in Antol and Kosolowski (17) to modify the mass predictor variable and allow for quotients standardizing for *FFM* instead of *M*. Using a sample of 100 mammal species (including four marsupials and two bats), Antol and Kosolowski report isometric scaling between adipose tissue mass and FFM, resulting in a constant average ratio across all body sizes. From their regression coefficients, the average ratio of adipose/FFM in mammals is 0.05. The relationship between FFM and M in the average mammal is thus: M = 1.05*FFM. If FFM is known for the measured individual, the term (1.05*FFM) can therefore be used instead of M in the quotient equations to standardize the energy measurements to an average mammal of the equivalent FFM instead of M. For most species, the error using total mass and the FFM correction is less than 0.05 RMQ (*SI Appendix*).

Primate Comparisons. We used post hoc *t* tests to compare model residuals of primates and nonprimate legged mammals after correcting for *M* and *Te*. Residuals were analyzed in the form of log (TEE) to maintain normality in the distribution. The mean residual for primates was −0.03, while the mean residual for nonprimates was −0.008. We tested the null hypothesis that primate residuals come from the larger-legged mammal distribution using a two-tailed t test. ANOVA failed to reject the null hypothesis (t = 0.73, *P* = 0.47), and we found no support for systematic differences in primate TEE compared to nonprimate mammals.

We used metabolic quotients in the comparative dataset to broadly compare ecological energetics in primates, with rodents as an outgroup. First, we extracted quotient data into three interspecific, paraphyletic clades: rodents, strepsirrhines, and monkeys (catarrhines and platyrrhines). Note that for several of the primate species including chimpanzees, the data come from sanctuary or zoo populations (5), although the values are likely broadly representative of wild populations (5). For each clade, we calculated mean TMQ and RMQ from the available species data. There were few specific AMQ values within each clade, and the available species cannot be assumed to be representative, so we modeled the mean clade AMQ as a point estimate using mean TMQ and RMQ. An arbitrary mass and temperature (1 kg and 15 °C) were used to convert TMQ and RMQ to energetic units, allowing for the calculation of AEE and AMQ.

We also included two individual species in the comparison: chimpanzees and humans. Using published mean values from 27 chimpanzees (*Pan* sp.) from sanctuaries and zoos that included TEE, REE, M, and FFM (5), we calculated mean RMQ, TMQ, and AMQ. The values for males and females were calculated separately and averaged for an equal sex balance. Because individual data were not available, we only report mean estimates without confidence measures for the chimpanzees. Humans were represented by published data from individual Hadza hunter-gatherers (9), where TEE, estimated REE, M, and FFM were all available allowing for individual RMQ, TMQ, and AMQ values to be calculated and the sample variation described. Thirty Hadza were included in our analysis from published data (9). The sample was imbalanced by sex: 17 females and 13 males. There were also notable differences in mean AMQ (F: 0.99, M: 1.48) and TMQ (F: 1.27, M: 1.56) between sexes, so reported mean values for the Hadza quotients are sex-weighted averages. In contrast, the statistical tests and computed distributions shown in Fig. 3 are based on the unweighted samples and are therefore more conservative than expected for an equally weighted sample. Note that the unweighted averages were only slightly less than weighted values (AMQ: 1.19 v. 1.24, TMQ: 1.40 v. 1.42). [In contrast, the US sample (see more details in the following section) was balanced by sex so reported values are simple averages across the entire sample.]

Quotients were also converted to energetic units of MJ using the mean Hadza as a standard: 47.2 kg M, 39.7 kg FFM, 28 °C to facilitate a more direct comparison.

Human Comparisons. Metabolic quotients from the Hadza sample described above were compared to a postindustrial sample from the United States. Deidentified human data were abstracted from the Pennington Center Longitudinal Study, which includes research participants that enrolled in nutrition, weight loss, and other physiologic interventional or observational clinical trials conducted at Pennington Biomedical Research Center since 1992. Only data that pertained to a baseline testing period (i.e., prior to an intervention) or a cross-sectional study is included in the database. The current cohort was derived from a data query that specified adults (>18y), 14-d doubly labeled water data, body composition (FMI from DXA, various instruments), and resting metabolic rate (Deltatrac II, ventilated hood metabolic cart) if it occurred within 30 d of the doubly labeled water measurement. Demographic information including age, height, and sex were also included. Pennington Center Longitudinal Study procedures and the data abstraction for this study were reviewed by the Pennington Biomedical Research Center Institutional Review Board (PBRC311EX). The initial query yielded individuals ranging from ages 18 to 74, followed by a large age gap and 67 additional samples between the ages of 89 and 101. The older subsample was dropped from the dataset to avoid confounding issues with advanced aging. In total, 274 individuals were included in the sample population for this study. The average age was 38 ± 16 y (SD), average M was 82.6 ± 19.2 kg, average FFM was 57.2 ± 12.9 kg, average FM was 25.3 ± 12.5 kg, and average F% was 30.0 ± 10.4%. rCO_2 values were converted to TEE in energetic units using an assumed average RQ value of 0.86 for all individuals (*SI Appendix*).

Hadza and USA quotients were compared using individual data and nonparametric Mann–Whitney tests to account for log-normal quotient distributions. We also compared the mean quotient values to the mean values from four small-scale, subsistence populations with the necessary data found in the literature: Tsimane (Bolivia), Aymara (Bolivia), Sakha (Russia), and Gambian farmers. Mean data for the Tsimane came from Gurven et al. (45) while data for the latter three populations were obtained from the meta-analysis of Dugas et al. (28). Because Dugas et al. split samples from the same studies by sex, all groups were analyzed separately by sex and averaged (*SI Appendix*, Table S5). We similarly calculated quotients for 110 industrial populations from Dugas et al. and used the means as the "global averages". Note that because data were reported by sex, the 110 "populations" came from a smaller number of studies. In addition, values from both the small-scale and industrial populations were paired with *Te* estimates at the study site (World bank data for countries, NOAA data for USA states) and were used to plot Fig. 2*F*.

Mean age, height, body mass, BMI, and TEE were extracted for each population analyzed. FFM was reported for the Tsimane; for all other groups, we used a BMI regression equation (46) to estimate body fat percentage and thus FFM. Because respirometry-based estimates of REE are highly dependent on study design and conditions, we used the Mifflin-St. Jeor Equation (47) to estimate REE followed by AEE using subtraction. TEE, REE, and AEE values were then converted to quotients using a common human *Te* of 28 °C matching the Hadza. We also translated the quotients into energetic units for direct comparison using the mean Hadza as a standard in the same manner as the primate comparison.

Data, Materials, and Software Availability. All study data are included in the article and/or supporting information.

ACKNOWLEDGMENTS. We thank Alex Harris, Nicholas Holowka, Tim Kistner, Herman Pontzer, Joel Ramirez, Ben Sibson, Ali Yawar, Ian Wallace, and the editor and reviewers for their insightful comments on the project and manuscript.

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