RESEARCH ARTICLE SUMMARY

HUMAN EVOLUTION

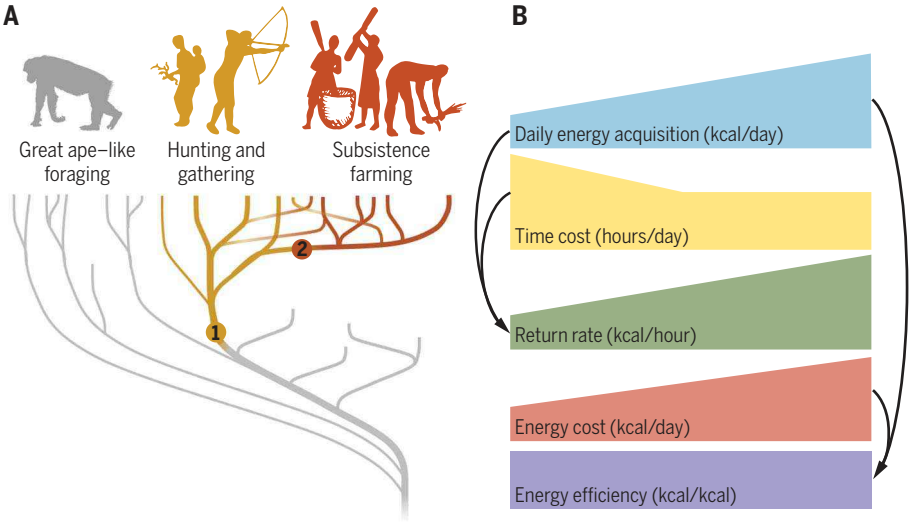
The energetics of uniquely human subsistence strategies

Thomas S. Kraft*, Vivek V. Venkataraman, Ian J. Wallace, Alyssa N. Crittenden, Nicholas B. Holowka, Jonathan Stieglitz, Jacob Harris, David A. Raichlen, Brian Wood, Michael Gurven†, Herman Pontzer*†

INTRODUCTION: Relative to other great apes, humans have large brains, long life spans, higher fertility and larger neonates, and protracted periods of childhood dependency and development. Although these traits constitute the unique human life history that underlies the ecological success of our species, they also require human adults to meet extraordinarily high energetic demands. Determining how human subsistence strategies have met such extreme energy needs, given time and energy expenditure constraints, is thus key to understanding the origins of derived human traits.

RATIONALE: Two major transitions in hominin subsistence strategies are thought to have elevated energy capture: (i) the development of hunting and gathering ~2.5 million years ago, which coincided with brain enlargement and extended postnatal growth, and (ii) the rise of agriculture ~12,000 years ago, which was accompanied by substantial increases in fertility and population densities. These transitions are associated with the exploitation of novel food sources, but it is not clear how the energy and time budgets of early human foragers and farmers shifted to accommodate expensive traits. Some evolutionary reconstructions contend that economical locomotion, cooperation, the use of sophisticated tools, and eventually agriculture increased energy efficiency (i.e., energy gained versus energy spent), beyond that of other great apes. Alternatively, unique human subsistence strategies may reduce time and improve yield, increasing return rates (i.e., energy gained versus time spent).

To test these ideas, we compared subsistence costs (energy and time) and energy acquisition among wild orangutans, gorillas, and chimpanzees with high-resolution data on total energy expenditure, food acquisition, and time allocation, collected among Tanzanian hunter-gatherers (Hadza) and Bolivian forager-horticulturalists (Tsimane). Both populations actively forage (hunt, gather), whereas the Tsimane also practice slash-and-burn horticulture, which permits exploration of further changes in the energetics of subsistence associated with farming. We also assembled a global subsistence energetics database of contemporary hunter-gatherers and horticulturalists.



Major transitions in hominoid subsistence energetics. (**A**) The shift from great ape–like foraging to hunting and gathering (1) and the adoption of subsistence farming during the Neolithic Revolution (2) involved changes in behavior and technology to allow access to novel food resources. (**B**) Through these transitions, humans paid higher energy costs in order to acquire a greater number of calories in less time; transitions from left to right are as depicted in (A). Human subsistence minimizes time costs but not energy costs, resulting in improved return rates but efficiency similar to that of other great apes.

RESULTS: Relative to other great apes, human hunter-gatherers and horticulturalists spend more energy daily on subsistence, and they achieve similar energy efficiencies despite having more economical locomotion and using sophisticated technologies. In contrast, humans attain much greater return rates, spending less time on subsistence while acquiring more energy per hour. Further, horticulture is associated with higher return rates than hunting and gathering, despite minimal differences in the amount of time devoted to subsistence. Findings from our detailed study of the Hadza and Tsimane were consistent with those from the larger cross-cultural database of subsistence-level societies. Together, these results support prior evidence that the adoption of farming could have been motivated by greater gains per time spent working, and refute the notion that farming lifestyles are necessarily associated with increased labor time.

CONCLUSION: These findings revise our understanding of human energetics and evolution, indicating that humans afford expanded energy budgets primarily by increasing rates of energy acquisition, and not through energy-saving adaptations (such as economical bipedalism or sophisticated tool use) that decrease overall costs. Relative to other great apes, human subsistence strategies are characterized by high-intensity, high-cost extractive activities and expanded day ranges that provide more calories in less time. These results suggest that energy gained from improvements in efficiency throughout human evolution were primarily channeled toward further increasing foraging intensity rather than reducing the energetic costs of subsistence. Greater energetic gains per unit time are the reward for humans' intense and behaviorally sophisticated subsistence strategies. Humans' high-cost but high-return strategy is ecologically risky, and we argue that it was only possible in the context of increased cooperation, intergenerational food sharing, and a division of labor. We contend that the time saved by human subsistence strategies provided more leisure time for social interaction and social learning in central-place locations, which is critical for cumulative cultural evolution. ■

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RESEARCH ARTICLE

HUMAN EVOLUTION

The energetics of uniquely human subsistence strategies

Thomas S. Kraft[1,2,3]*, Vivek V. Venkataraman[4,5], Ian J. Wallace[6], Alyssa N. Crittenden[7], Nicholas B. Holowka[8], Jonathan Stieglitz[4], Jacob Harris[9,10], David A. Raichlen[11], Brian Wood[2,9], Michael Gurven[1]†, Herman Pontzer[12,13]*†

The suite of derived human traits, including enlarged brains, elevated fertility rates, and long developmental periods and life spans, imposes extraordinarily high energetic costs relative to other great apes. How do human subsistence strategies accommodate our expanded energy budgets? We found that relative to other great apes, human hunter-gatherers and subsistence farmers spend more energy but less time on subsistence, acquire substantially more energy per hour, and achieve similar energy efficiencies. These findings revise our understanding of human energetic evolution by indicating that humans afford expanded energy budgets primarily by increasing rates of energy acquisition, not through energy-saving adaptations such as economical bipedalism or sophisticated tool use that decrease subsistence costs and improve the energetic efficiency of subsistence. We argue that the time saved by human subsistence strategies provides more leisure time for social interaction and social learning in central-place locations and would have been critical for cumulative cultural evolution.

In an evolutionary context, the energetic demands faced by adult humans are extraordinarily high. Relative to other hominoids, humans exhibit metabolic acceleration (i.e., elevated body size–adjusted energy expenditure) associated with the high energetic costs of maintaining large brains, a long lifespan, and high reproductive investment (both mass and number of offspring per year) (*1*). Additionally, adult humans must produce a caloric surplus to subsidize a long period of childhood dependency of their offspring (*2*). A major transition in hominin subsistence behavior was likely critical for accommodating increased energetic demands that accompanied changes in morphology, brain size, and life history ~1.5 million to 2.5 million years ago, the time period during which central-place hunting and gathering likely arose (*3*). Likewise, the rise of agriculture represents a marked shift in human subsistence that coincided with substantial increases in human reproductive rates and population densities (*4*).

Although these subsistence strategies have elevated the scale of daily human energy acquisition beyond that of other great apes (*2*), it remains poorly understood how humans manage the potentially severe energy and time costs of obtaining food through hunting and gathering or subsistence agriculture (*5*). Energy expenditure is limited by daily food intake and the amount of energy stored in the body (primarily as fat), whereas time is limited by the number of hours in a day. Both energy and time spent on subsistence activities entail opportunity costs, including energy that could otherwise be expended on bodily maintenance, reproductive investment, or provisioning kin, and time that could be invested in socialization or mating effort. Energy and time investments in subsistence therefore depend on the extent to which these currencies are limiting and the relative fitness benefits of investing those resources elsewhere (*5*–*7*).

Organisms typically pursue two alternative strategies to increase energy availability. One strategy involves increasing energy efficiency. Although efficiency has been inconsistently defined in reference to time or energy costs in the anthropological literature [(*8*), p. 185], here we follow convention from foraging ecology in referring to efficiency as the ratio of energy gained relative to energy spent on subsistence (*5*, *9*, *10*). A second strategy is to increase the net acquisition rate, the amount of energy acquired minus energy spent divided by the time spent on subsistence (*10*). Theoretical work demonstrates that the conditions under which energy efficiency or net acquisition rate are maximized depend on the interplay between the type of foraging (e.g., feeding, provisioning, storage) and ecological or physiological constraints on time and energy (*5*, *11*, *12*). Different groups of organisms maximize currencies of efficiency or rate in accordance with these principles (*11*–*15*). The legacy of metabolic acceleration in humans strongly suggests that our unique subsistence strategies are characterized by novel ways to mitigate time and energy constraints in pursuit of high-value foods that expand daily caloric acquisition beyond that of other primates.

There is substantial evidence to suggest that humans expend less energy and time on subsistence than other great apes. Humans exhibit several derived features that reduce energetic costs, including anatomical and behavioral traits that reduce the cost of walking and searching (*16*) and reductions in the size of costly digestive organs (*17*). Compared to other primates, humans also spend far less time feeding (*18*), use more sophisticated tools to acquire and process foods, and engage in cognitively complex and hypercooperative behaviors to obtain energy-dense foods that would otherwise be inaccessible (*2*). Yet it remains unknown to what extent these derived attributes actually reduce the energy and/or time costs of subsistence, thus requiring direct comparisons of the costs and benefits of food acquisition between humans and other great apes.

To clarify how unique human subsistence strategies enabled metabolic acceleration and surplus production for provisioning, we investigated whether humans achieve greater efficiency or acquisition rate relative to other great apes. We calculated subsistence costs (energy and time) and energy acquisition among wild orangutans, gorillas, and chimpanzees, and compared these measures with high-resolution data collected among Hadza hunter-gatherers in Tanzania and Tsimane forager-horticulturalists in Bolivia (Fig. 1). Both populations actively forage (hunt, gather), while the Tsimane also practice slash-and-burn horticulture, which permits exploration of further changes in the energetics of subsistence associated with farming. Whereas many studies on the ecological economics of humans are concerned primarily with the "exosomatic metabolism" that distinguishes humans from other organisms (i.e., energy flows metabolized outside of the body, e.g., from wood fuel, domestic animals, industrial processes), our focus here is on "endosomatic metabolism" (i.e., food energy used within the body) (*19*, *20*). Small-scale subsistence societies such as the Hadza and Tsimane use far more exosomatic energy than other organisms in the form of wood fuel for cooking or land management; tools for hunting, digging, food processing, or field preparation; and the occasional use of dogs for hunting (*21*–*23*). Here, however, we

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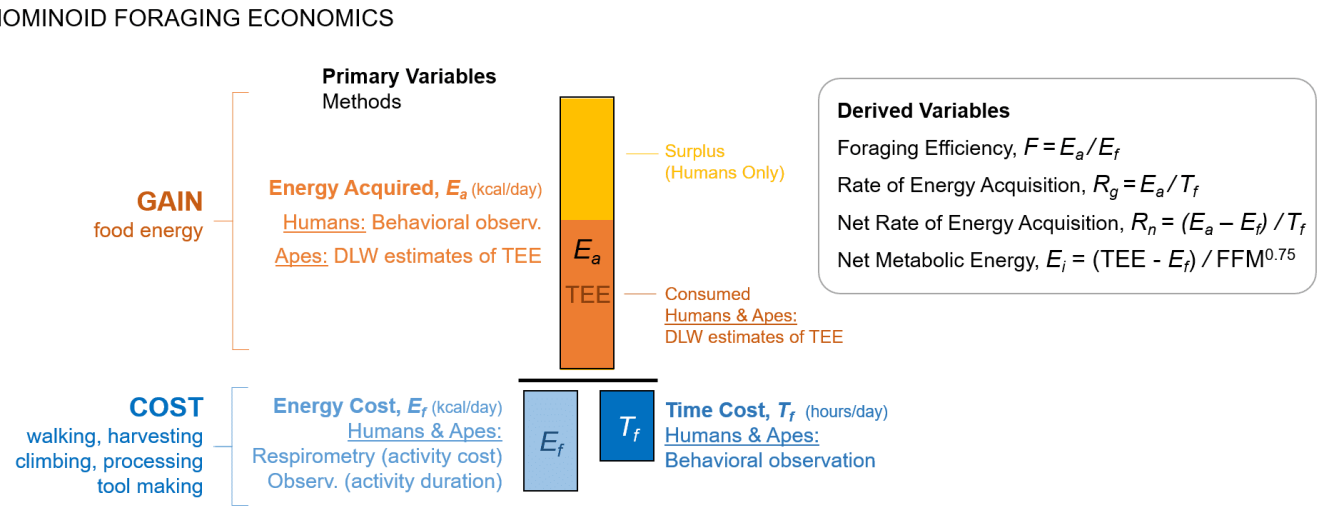

Fig. 1. Overview of methods and variables used to compare foraging economics in humans and other great apes. Energy acquired, E_a, for humans was determined through behavioral observation of food production. Humans consume some of the energy they acquire (equal to their total energy expenditure, TEE) and share or store remaining surplus. For other great apes, food sharing and provisioning are negligible (*2*, *29*–*31*), and therefore E_a = TEE. In humans and other apes, TEE was estimated from DLW measurements. The energy cost of foraging for humans and other apes, E_f, was calculated by multiplying the energy costs of foraging activities (measured using respirometry) by the time spent in each activity (determined from behavioral observation). The time cost of foraging for humans and other apes, T_f, was determined from behavioral observation. These primary variables (E_a, E_f, and T_f) were used to derive foraging efficiency (F), rate of energy acquisition (R_g), net rate of energy acquisition (R_n), and net metabolic energy (E_i). E_i is the energy consumed and available for nonforaging tasks, scaled to metabolic body size, FFM$^{0.75}$, where FFM is fat-free mass.

limit our consideration of time and energy costs to endosomatic energy flows that are critical for understanding how biological tradeoffs and constraints in energy budgets affect the ability to support expensive organs and life history traits. We therefore define system boundaries in this study to include only those behaviors that directly or indirectly contribute to tasks relating to food acquisition, processing, and consumption. We included both foraging and horticultural activities in subsistence cost estimates, as well as auxiliary behaviors such as food processing, tool manufacture, eating, and firewood/water collection. Energetic costs of subsistence tasks were calculated as net values (i.e., resting costs were subtracted) to parse out the additional costs of activities above baseline.

For the Hadza and Tsimane, we used long-term observational data on food acquisition and production to establish population-average rates of daily energy acquisition, E_a (kcal/day) for men and women, and we measured rates of energy expenditure in subsistence activities using a portable respirometry system in the field (Fig. 1). We then integrated time allocation data (scan sampling and focal follows) with respirometry-based measures of the energetic costs of subsistence tasks to estimate the following: daily energetic cost of subsistence, E_f (kcal/day); daily time spent on subsistence, T_f (hours/day); efficiency of subsistence [$F = E_a/E_f$; note that F is equivalent to the modified form of efficiency in (*12*) because foraging activities are measured net of resting costs]; and gross ($R_g = E_a/T_f$) and net [$R_n = (E_a - E_f)/T_f$] rate of energy acquisition (kcal/hour). Finally, we calculate a quantity, E_i [= (TEE – E_f)/FFM$^{0.75}$, where TEE = total daily energy expenditure in kcal/day measured using doubly labeled water (DLW), and FFM = fat-free mass], which represents the net energy available to the body for nonsubsistence purposes scaled by metabolic body mass (*24*).

We used a similar approach to calculate these variables for nonhuman great apes. Using published DLW measures of TEE for zoo-living chimpanzees, gorillas, and orangutans, we fit species-specific regressions of TEE against body mass and used them to estimate TEE for adult males and females of each species in the wild (see methods). The DLW method is considered the gold standard for measuring TEE in free-living conditions (*25*), and our DLW-based estimates of TEE for wild apes were similar to TEE estimates based on activity budget analyses in wild apes and other primates (*26*) and to DLW measurements of TEE in populations of wild primates (*27*) and other mammals (*28*) (table S1 and fig. S1). Further, the TEE–body mass relationship is similar for captive and wild primates (*27*), justifying the use of data from zoo-living animals in regressions to estimate TEE in wild apes. Nonetheless, to test the sensitivity of our results to the use of E_a estimates derived from TEE, we also used estimates of daily caloric consumption from feeding observation studies in wild apes, which are generally higher than our DLW estimates, for comparison (table S1). Results from those analyses did not substantially affect the pattern of differences between other ape species, nor between other apes and humans (see methods).

Among nonhuman great apes, average TEE = E_a because provisioning and food storage are negligible (*2*, *29*–*31*). Time spent foraging and distances traveled and climbed per day were compiled from observational studies of wild apes. These data were then used to calculate the remaining variables using locomotor costs from published respirometry studies of energy expenditure during walking in chimpanzees (*32*) and climbing in other primates (*33*) (see methods).

We tested the hypothesis that human subsistence strategies reduce both energy (E_f) and time (T_f) costs of food acquisition and increase gross energy acquisition (E_a) relative to the strategies of other great apes, thus improving the energetic efficiency of subsistence (F), gross or net energy return rates (R_g, R_n), and net energy availability (E_i). Given that agriculturalists generally have higher fertility rates than hunter-gatherers (*34*, *35*), we predicted that Tsimane horticulturalists would evince greater daily energy acquisition, efficiency, and return rates than Hadza hunter-gatherers despite potentially expending more time and energy on subsistence. Finally, to test whether the results obtained from the Hadza and Tsimane are representative of hunter-gatherers and horticulturalists more broadly, we assembled a database on efficiency, production, energy costs, and time allocation during subsistence from a global sample of contemporary hunter-gatherer (n = 14) and horticulturalist populations (n = 22) (table S2). This database allowed us to address

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debates over fundamental differences in the energetics of hunting and gathering versus farming (36, 37). All results were analyzed separately by sex to discern how the sexual division of labor characteristic of human societies affects the distribution of time and energy costs.

Subsistence energetics for humans versus other great apes

Contrary to our expectations, we found that adult human hunter-gatherers and horticulturalists exhibited higher subsistence energy costs (E_f) than other great apes (Fig. 2 and table S2). E_f for humans [mean (95% CI), men: Hadza 709 (638, 774) kcal/day; Tsimane 603 (403, 962) kcal/day; women: Hadza 474 (339, 629) kcal/day; Tsimane 253 (205, 320) kcal/day] was substantially greater than for other great apes (males: 152 to 293 kcal/day; females: 76 to 168 kcal/day). Consequently, whereas gross energy acquisition (E_a) was greater for humans, subsistence efficiency (F) was similar between humans (range: ~5 to 16) and other great apes (range: ~8 to 16) (Fig. 3). Females in all species had lower energetic costs of subsistence (E_f) than males (Fig. 2), increasing energy available for reproduction (38). The energetic efficiency of Tsimane subsistence was higher than estimates for other nonindustrial societies obtained from the literature (Fig. 3, fig. S2, and table S2) but similar to crop-specific efficiencies for tropical horticulturalists reported elsewhere [F = 10 to 20, not accounting for transport and processing costs (39)]. Notably, subsistence efficiencies for humans and other great apes are at the low end of the observed range for vertebrates, most of which exhibit F > 40 (40).

Humans devoted considerably less time (T_f) to subsistence than other great apes, who spend 7 to 8 hours/day on subsistence (Fig. 2). Differences in time spent on subsistence between humans and other great apes would be even greater if calculated on the basis of a more limited range of activities (e.g., excluding time spent on tool manufacture) or as a percentage of all waking hours, as humans sleep less than any other primate (41). Accordingly, both gross (R_g) and net (R_n) energy acquisition rates were substantially higher for humans than for other great apes (Fig. 3). Although energy acquisition rates for other great apes were somewhat higher when using observational data on wild food intake to estimate E_a (as opposed to DLW-based regressions for TEE), the same general pattern was observed (fig. S3). A decomposition of net energy acquisition rates reveals that these species differences were driven by reductions in both time spent on subsistence and increases in gross energy acquisition, but not reduced costs. Indeed, humans expended more energy on subsistence (E_f) than any other great apes (Fig. 2).

The fact that humans expend more energy on subsistence than other great apes, despite spending less time, indicates that humans engage in comparatively high-intensity foraging activities. Whereas other great apes expend little energy during foraging, humans engage in a diversity of specialized and energetically costly tasks with the use of tools. Hadza and Tsimane chop, dig, climb, burn, manufacture objects, and transport food, fuel, and water to central places (Fig. 4). Tsimane additionally invest in strenuous activities associated with farming, such as clearing brush, felling trees, and transporting crops. An additional database we compiled on the instantaneous energy costs (kcal/min) of common activities in nonindustrial societies reveals

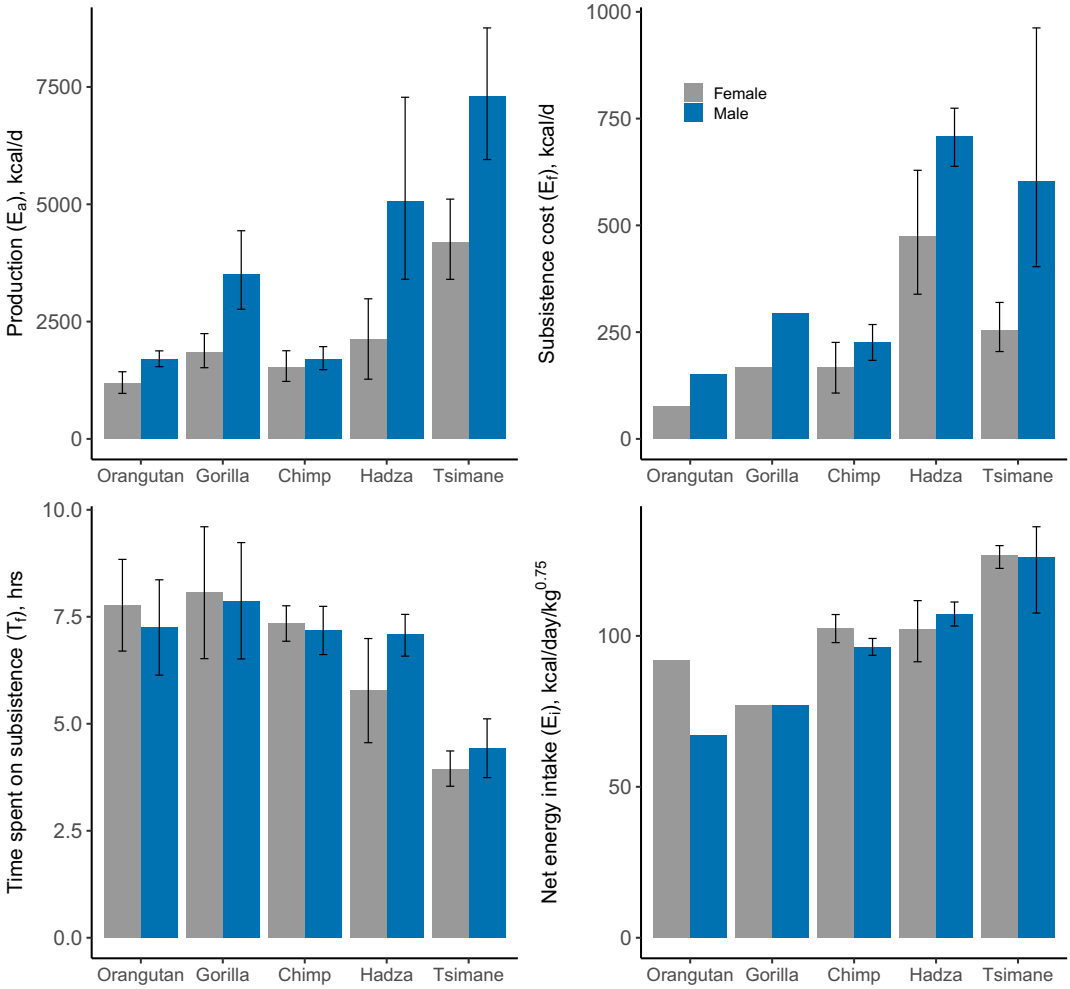

Fig. 2. Cross-species comparison of daily energy acquisition (E_a), subsistence costs (E_f), time spent on subsistence (T_f), and net energy intake (E_i). Values represent posterior medians ± 95% HDPIs (for humans) or means ± 95% CIs (for other great apes). Note that some values are missing error bars because only point metrics were available for cost calculations.

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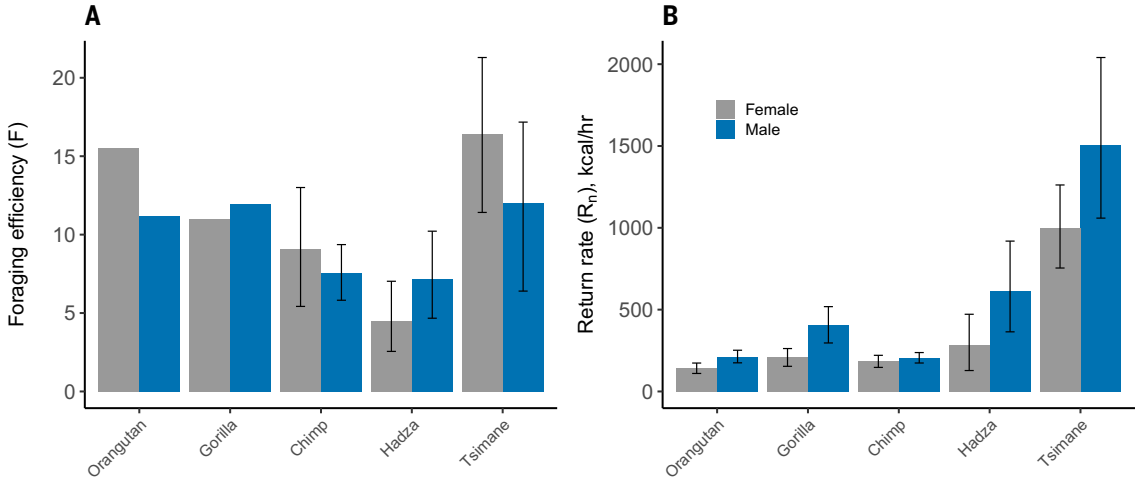

Fig. 3. Energy spent on subsistence across species/populations. (**A**) Energy acquired per unit energy; (**B**) energy acquired per unit time. Values represent posterior medians ± 95% HDPI (Tsimane/Hadza) or means ± 95% CI (all others). Tsimane and Hadza estimates represent population estimates for a 40-year-old individual.

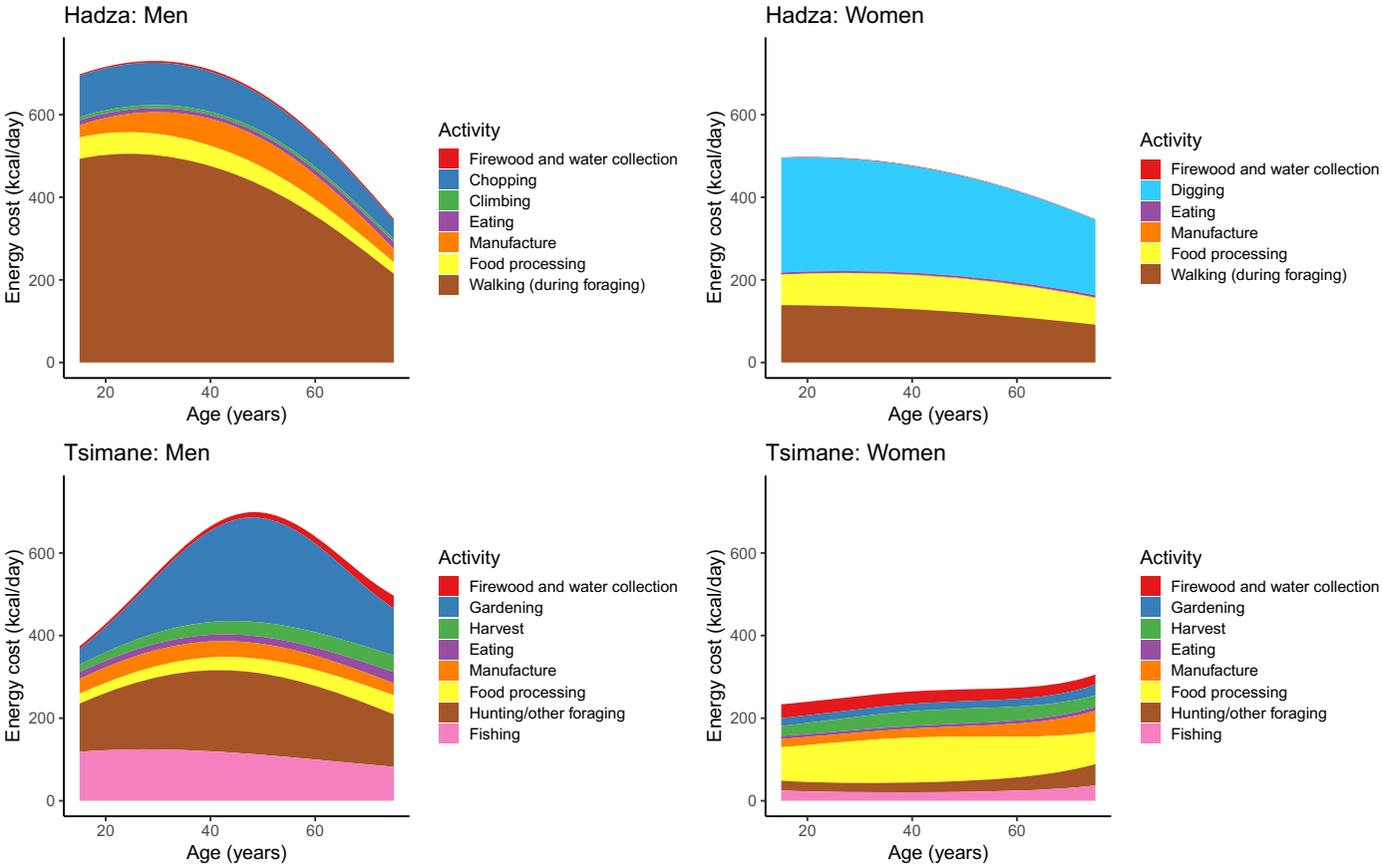

Fig. 4. Subsistence costs for Hadza and Tsimane over the life course. Costs (kcal/day) reflect the time that individuals of different ages spend on activities as well as the relative energetic costs of engaging in those activities.

that many human subsistence activities are energetically costly, and that tasks associated with farm work bear marginally higher costs than those associated with foraging (including walking) (Fig. 5).

Net energy availability (E_i) scaled by fat-free body mass (*1*, *24*) was generally greater among humans than other great apes, especially for Tsimane (Fig. 2). Human subsistence, and particularly strategies including farming, thus yields more energy that can be used by the body for diverse purposes other than subsistence, even though humans spend a greater absolute proportion of their TEE on subsistence (Fig. 6). This greater net energy availability likely enables

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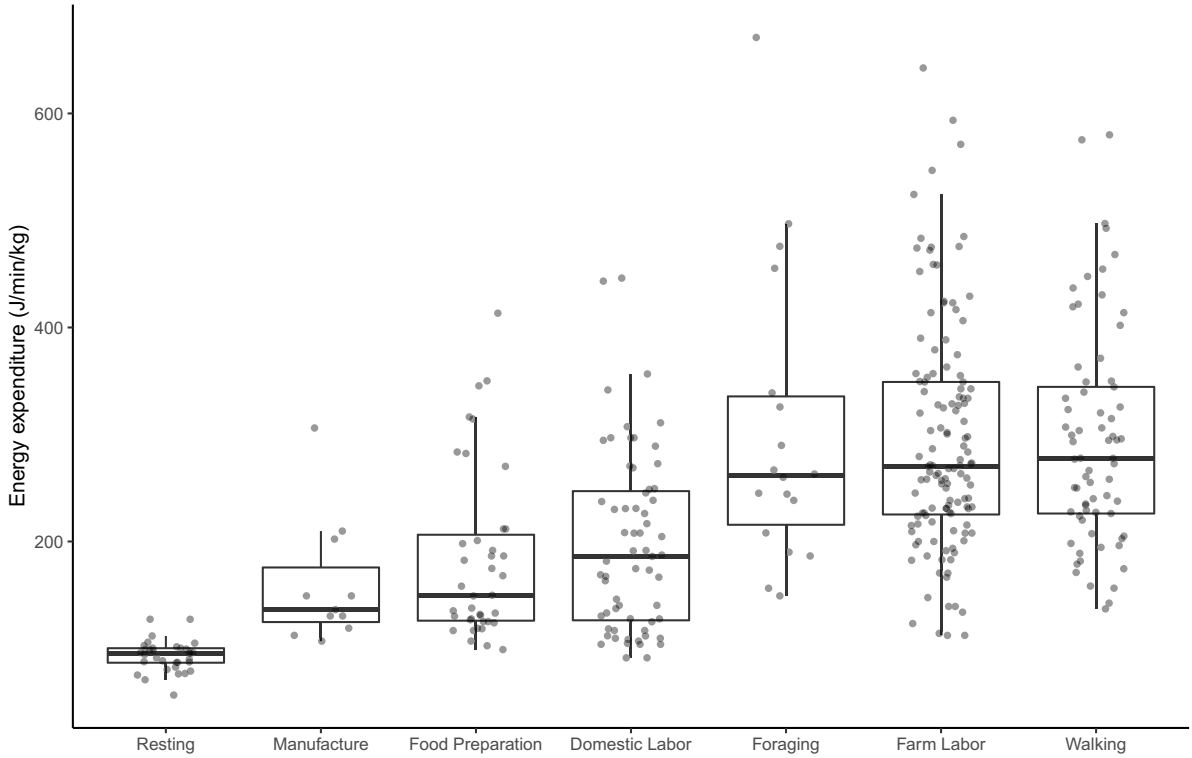

Fig. 5. The instantaneous metabolic cost of activities undertaken in traditional subsistence societies. Values were either measured empirically for this study or derived from the literature (table S5). Data from field activities are measured using respirometry. Many foraging activities involve walking but were categorized under foraging according to their original designations in the literature. Costs are presented for both men's and women's activities and are standardized per kilogram of body mass.

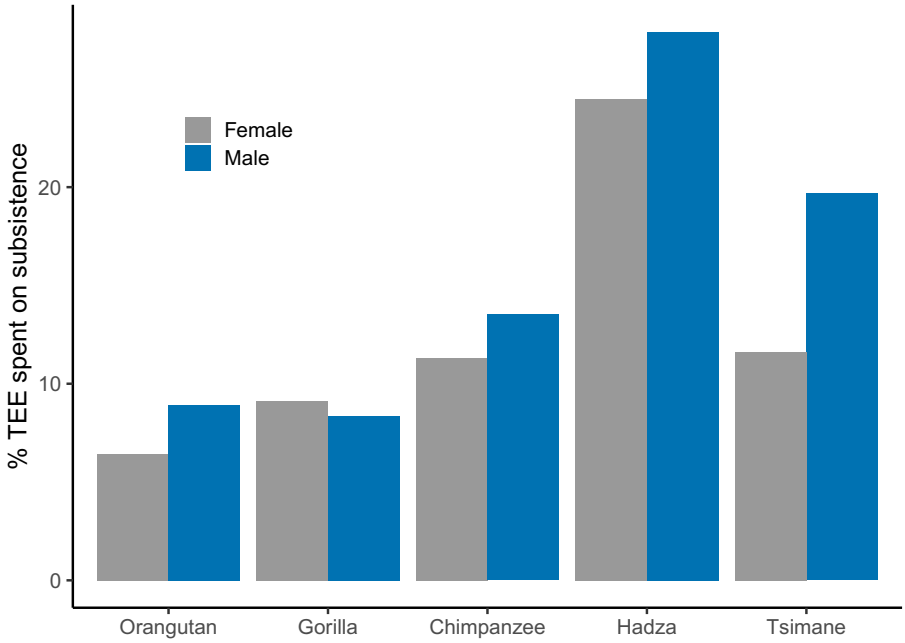

Fig. 6. The percentage of total energy expenditure (TEE, kcal/day) spent on subsistence costs across species/populations.

humans to afford the high maintenance costs of large brains and elevated reproductive investment (*1*), although the substantial energy costs of human subsistence limit interspecific differences in E_i and suggest that the primary energetic benefit of human subsistence strategies is obtaining surplus energy for provisioning children, reproductive females, and other group members. Unlike other great apes, humans exhibit extensive surplus production by adults (E_a > TEE), which is critical for provisioning females bearing the energetic costs of reproduction (*42*, *43*) and young offspring that are net consumers (*2*), thus enabling elevated fertility despite compound offspring dependency (*44*, *45*). Provisioned children and reproductive-aged women also have lower subsistence costs (*46*) and thus have more energy available during critical periods of brain growth and development (*47*) and gestation and lactation, respectively.

Our results indicate that horticulture may improve efficiency (*F*) relative to hunting and gathering, especially for females (Fig. 3). Horticulture also reduces time costs and increases daily gross energy acquisition, leading to substantially higher daily and hourly return rates (by a factor of ~1.5 to 2; Figs. 2 and 3). These differences persist across ontogenetic development (Fig. 7). Within-population comparisons further demonstrate that activity-specific energetic return rates from horticulture exceed those of hunting and gathering in mixed economies (table S3). These results are consistent with previous comparisons between Amazonian horticulturalists and hunter-gatherers (*48*–*52*). The potential for elevated energetic return rates could therefore have favored the adoption of incipient agriculture, particularly in environments suffering from depletion of profitable wild food resources (*37*).

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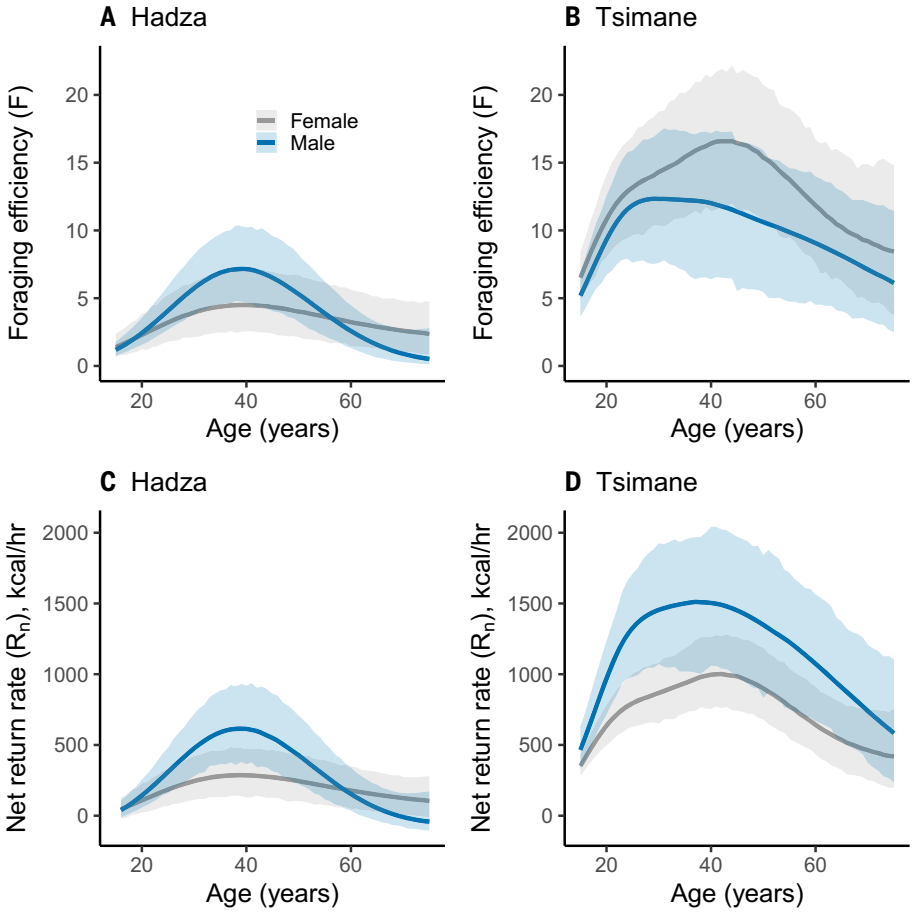

Fig. 7. Efficiency (*F*) and net return rates (R_n) across the life course in Hadza and Tsimane. (**A** and **C**) Hadza *F* and R_n; (**B** and **D**) Tsimane *F* and R_n. Data are separated by sex (blue = male, gray = female). Lines and shaded regions represent predicted mean values and 95% CIs based on composite calculations. Tsimane exhibit greater net return rates than Hadza across all ages (in years).

Cross-cultural energetics of human hunter-gatherers and horticulturalists

Our cross-cultural database of traditional hunter-gatherers and horticulturalists ($n_{\text{hunter-gatherer}}$ = 14, $n_{\text{horticulturalist}}$ = 22) confirms our findings from detailed study of the Hadza and Tsimane (table S2). Specifically, we found further evidence that humans of both subsistence modes produce more calories per day, spend less time on subsistence, and have higher return rates than other great apes (Fig. 8; see fig. S4 for results using observational acquisition data for nonhuman great apes). The few available published estimates of efficiency in subsistence horticulturalists also support the observation that human efficiencies are not elevated above those of other great apes (fig. S2). Among humans, cross-cultural analyses also show that horticulturalists produce more daily calories [combined sexes for all societies; mean (kcal/day) = 7520 versus 3061, $t(10.3) = 2.4$, $P = 0.048$], spend similar amounts of time on subsistence [mean (hours/day) = 4.1 versus 4.5, $t(21.4) = -0.7$, $P = 0.48$], and have higher return rates [mean (kcal/hour) = 2162 versus 729, $t(9.2) = 2.2$, $P = 0.052$] than hunter-gatherers, in general agreement with results for the Hadza and Tsimane. Sex differences in the cross-cultural sample were minimal for the amount of time spent on subsistence and return rates (all $P > 0.2$), but among hunter-gatherers, daily production was higher in men than in women [mean (kcal/day) = 3879 versus 2243, $t(17.9) = 3.3$, $P = 0.004$].

Despite fairly large average differences between hunter-gatherers and horticulturalists, cross-cultural estimates indicate a great deal of variability within subsistence mode for all variables assessed (Fig. 8). For example, the amount of time spent on subsistence ranges from 2.6 to 7.0 hours/day for hunter-gatherers and from 1.8 to 8.5 hours/day for horticulturalists (pooled sexes). Likewise, although return rates are generally higher for horticulturalists than hunter-gatherers, the distributions of outcomes overlap between subsistence modes. This suggests that hunting and gathering can be equally or even more profitable than farming, depending on the local environment, and may help to explain overlap in total fertility across subsistence modes (*35*) as well as flexibility and reversions in subsistence patterns (*37*).

Energetics and the origins of hunting and gathering

Overall, our results point to a revised understanding of the evolution of hunting and gathering. Whereas complex technology and behavioral innovations undoubtedly reduce the energy costs of particular subsistence tasks (*53–59*), they are used in pursuit of resources that are energetically costly to acquire (e.g., meat, tubers, baobab) and necessitate greater day ranges than those of other primates (Fig. 4) (*26*, *60*). Humans therefore accommodate the energetic demands of metabolic acceleration and surplus energy acquisition for provisioning not by decreasing subsistence costs and increasing energetic efficiency, but instead by expending larger amounts of energy to rapidly attain larger amounts of energy from the environment (Figs. 2 and 3). The emergence of hunting and gathering could have been favored despite increased energy costs, as long as they increased net acquisition rates and total energy gained (*9–11*, *61*). Thus, hunting and gathering likely evolved with a focus on high-quality dietary resources made available by extractive foraging and complex processing (*2*) in combination with behaviors and technologies leading to the minimization of time spent foraging (T_f) at the expense of increased energy (E_f) costs.

The finding that humans are not particularly efficient foragers runs counter to a prevailing assumption in the anthropological literature, which presumes that the suite of human adaptations (e.g., complex tool use, bipedalism) and our unique ability to harness exosomatic energy have served to reduce endosomatic expenditure (*62*, *63*). However, the results of this study are consistent with the predictions of optimal foraging theory. Human subsistence is best contextualized using foraging models of provisioning, in which an organism seeks to maximize total daily energy delivery subject to meeting its own energetic requirements (*11*). In the absence of constraints, an optimal forager maximizes the net rate of energy gain (R_n). Under energetic or time constraints, however, a forager may do better to maximize efficiency, particularly when limited by the amount of energy the forager can assimilate/expend or a low self-feeding rate (rate at which food is acquired to self-provision) (*5*, *11*, *64*).

Human foraging exhibits characteristics that promote optimal rate-maximizing behavior under either energy or time constraints. Metabolic acceleration (including increased TEE), coupled with economical bipedal locomotion, large fat stores, and enhanced heat dissipation capacity, increases the ceiling on the maximum daily energy expenditure of a forager while simultaneously decreasing the rate at which that

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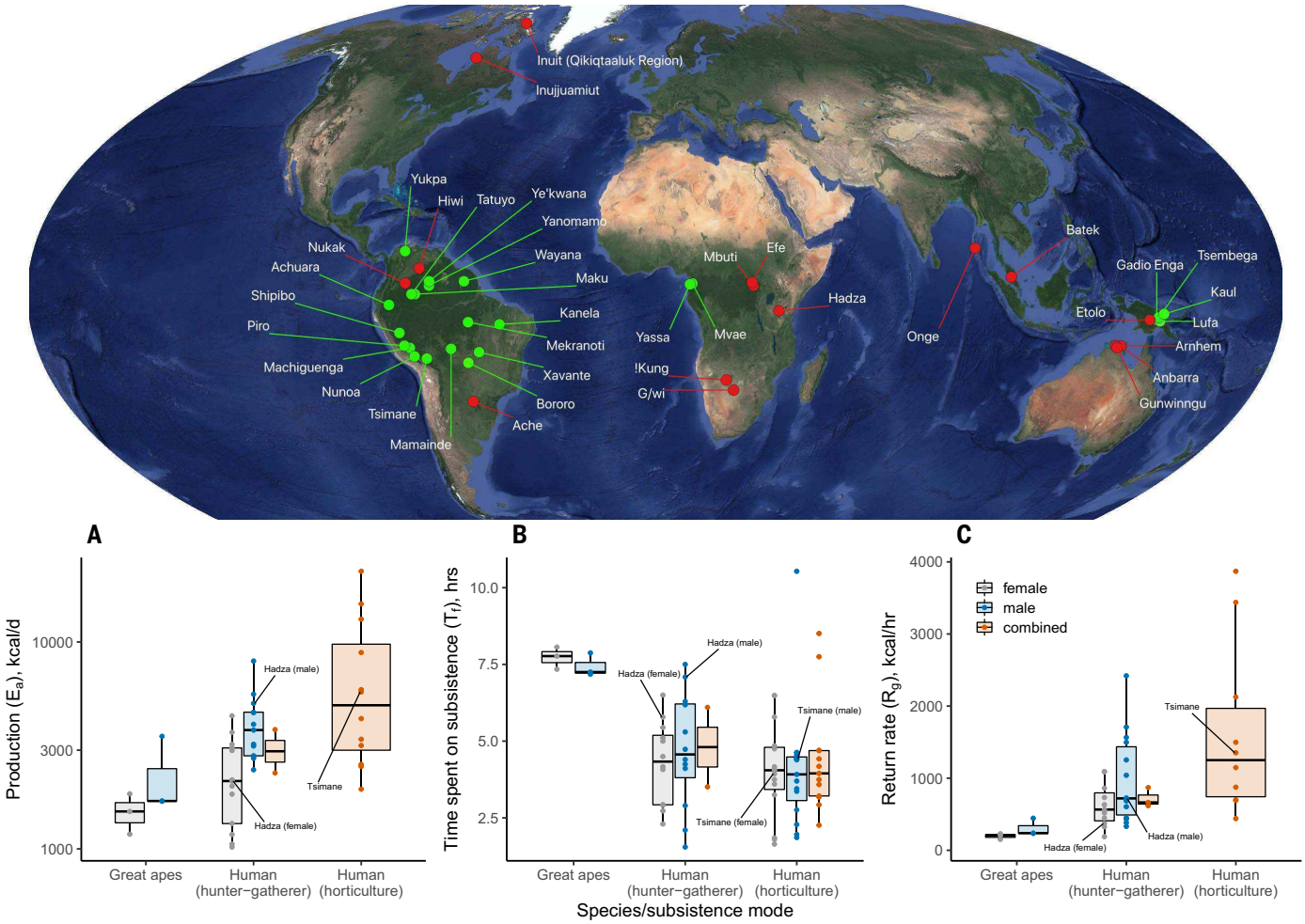

Fig. 8. Comparison of nonhuman great apes, hunter-gatherers, and horticulturalists using the cross-cultural sample. World map shows the location of societies (red = hunter-gatherer, green = forager-horticulturalist) included in the cross-cultural sample. In (**A**) to (**C**), novel values for Tsimane and Hadza from the current study are included and labeled for reference. Male and female values for Tsimane were averaged for measures of production (E_a) and gross return rate (R_g) because no separate values were available from the literature by sex. Note that the *y* axis is on a $\log_{10}$ scale in (A). In (C), one high outlier is omitted for "Human (horticulture)" for visualization purposes.

ceiling is approached (*1*). Humans also have a number of traits that increase the self-feeding rate, which is critical for supporting high-intensity foraging (*11*). Whereas other primates eat raw foods that require long digestion times, humans target energy-dense foods (*65*) that become highly digestible with processing (*66*, *67*) and produce large surpluses that can be pooled, stored, and distributed. A human forager may effectively experience less self-provisioning risk because of the expectation that other family or camp members will bring surplus resources back to a central place for later consumption, thereby enabling rate-maximizing foraging strategies that would otherwise be too risky (i.e., high potential gain, but also high potential for failure) (*11*). In addition, hunter-gatherers are known to consume easily digestible, high-energy foods out of camp while foraging, which can rapidly provide energy to sustain further food acquisition; our data indicate that Hadza men and women consume approximately 80% and 20% of daily TEE while out of camp, respectively (*68*).

High-intensity foraging strategies are not unique to humans and have arisen numerous times throughout the tree of life. The best examples come from social insects. For instance, ants exhibit great variation in the "tempo" of foraging, in which high foraging intensity correlates with increased resource abundance, colony size, and caste polymorphism (*69*), or the availability of excess carbohydrate resources from the exudates of aphids that may enable high-energy activities without compromising colony growth (*70*). Intriguingly, farming (of fungal cultivars) has emerged in hundreds of ant species (*71*), and it would be interesting to determine whether the energetic advantages obtained mirror the apparent impact of the domestication of plants and animals by humans (e.g., increased population growth rates). Asian honey bee species also show marked differences in mass-specific metabolic rates and the rate of performance of colony tasks, a pattern that appears to be linked with the demands of provisioning and defense of open versus cavity nests (*72*). More generally, parental care may have driven the remarkable convergent evolution of endothermy and the associated ability to sustain vigorous exercise among birds and mammals (*73*).

High-intensity foraging and cooperative energetics

A high-throughput foraging strategy in humans coevolved with cooperative provisioning and alloparental care to produce our characteristic life history strategy. In the human case, this shift occurred within the context of an existing scaffolding of cognitive abilities, incipient tool use, advanced food processing, and extractive foraging (*2*, *74*). The resulting energy system was in a sense risky and was made possible only by lifting the foraging time constraints that characterize other great apes while simultaneously increasing tolerance for high

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daily energetic costs. Our findings thus help to unify and shed light on two dominant theories in human evolutionary studies: (i) the embodied capital model, which attributes large brain growth and a long developmental period in humans to the need to learn and develop difficult skills associated with extractive food acquisition (2), and (ii) the cooperative breeding hypothesis or pooled energy budget model, which posits that many derived features of human behavior, intelligence, and cognition are linked to a cooperative provisioning system that arose after the evolutionary split with the *Pan* lineage (38, 75, 76). Our findings suggest that increased daily production associated with extractive foraging in humans (2) was enabled by increased foraging intensity that reduced the time cost, but not the energy cost, of food acquisition. Such a strategy is unlikely to be tenable in the absence of a cooperative production and provisioning system with widespread sharing, divisions of labor, alloparental care, and prosociality. As we have shown, human subsistence strategies demand a large proportion of TEE (Fig. 6) and (at least in hunter-gatherers) the proportion of days in which individuals fail to produce food can be high (fig. S5). Humans are thus more prone to fatigue and starvation than other great apes when expected returns fail to materialize, especially given that humans often pursue high-risk/high-reward foods, such as large game (77). Some high-intensity activities (e.g., climbing or running) may also put foragers at an elevated risk of injury. Age-related increases are evident in the energetic efficiency of subsistence and in rates of energy acquisition among humans (Fig. 7), with intergenerational transfers of surplus calories by individuals at ages of peak productivity buffering risks of energetic shortfalls. These transfers, along with divisions of labor, the capacity for storage, and pooled energy budgets (38), allow for wide distribution of surplus resources to buffer adults as well as offspring. The pooled energy budgets and food storage capabilities of humans thus render it profitable to pay high energy costs and pursue high-risk and/or slow-to-master foraging behaviors in order to capitalize on lucrative return rates.

We argue that the extraordinary energy surpluses produced by adult humans, and our expensive encephalized brains, are unattainable for an organism with a foraging strategy and locomotor economy like those of other great apes. In order to achieve the same proportional surplus of a 40-year-old Hadza male (99% increase above TEE), for example, an adult male chimpanzee would need to forage ~14.3 hours/day; an adult female chimpanzee would have to forage ~14.0 hours/day to achieve the same surplus (91% increase above TEE) of a 40-year-old Tsimane woman. Human day ranges would also introduce prohibitive locomotor costs if terrestrial locomotion were as uneconomical as that of a chimpanzee: For a 50-kg human moving the same daily distance traveled by male Hadza [~14 km (78)] with the locomotor economy of a bipedal chimpanzee (1.06 kcal kg^{-1} km^{-1}), daily travel costs alone would be ~750 kcal/day, which would be ~30% of TEE, and nearly 3 times the cost of traveling that distance with a standard human locomotor economy (~270 kcal/day; 0.39 kcal kg^{-1} km^{-1}).

Superficially, these calculations seem to support the argument that the evolution of greater walking economy helped to facilitate encephalization in human evolution by reducing travel costs and thereby making more energy available for an increasingly expensive brain (62, 63, 79). In this scenario, the reduced cost of bipedal walking in early members of the genus *Homo* would have enhanced foraging efficiency, helping to pay for a larger brain. However, enhanced walking economy would not by itself save much energy without a change in subsistence strategy. For example, imagining a 50-kg male hominin with fully human-like walking economy but retaining chimpanzee-like foraging and daily travel distances [~2.5 km/day (80)], we estimate that this individual would have saved only ~80 kcal/day compared to the costs for a chimpanzee traveling the same distance. This saving, while not trivial, likely could not have improved foraging efficiency enough to fuel the increased encephalization that occurred with the appearance and evolution of *Homo*. However, lower walking costs in bipedal hominins could have rendered the longer travel distances required in hunting and gathering to be more energetically feasible, ultimately allowing early members of the genus *Homo* to adopt a subsistence strategy dependent on long day ranges. High-intensity foraging activities, in addition to greater day ranges, would have favored the evolution of a high-endurance phenotype in humans relative to other apes (81–83). In this scenario, the great energy gains needed to fuel increasing hominin brain sizes would have been achieved not through greater foraging efficiency (F), which remained low and similar to other great apes, but instead through the ability to engage in hunting and gathering strategies that required high daily travel costs but yielded very high energy rewards at a fast rate.

Thermal (exosomatic input from fire) and nonthermal (e.g., pounding, winnowing, fermenting) food processing would likewise have helped to enable high-intensity foraging strategies. Processing, the intentional external modification of a food resource to alter its physical and/or chemical attributes in preparation for consumption (22), can improve energy capture in several important ways. Even minimal food processing can effectively increase digestibility and bioaccessibility, reduce pathogens, and denature toxins (67, 84, 85). Thermal processing, particularly cooking, not only alters the nutritional quality of foods, but also begins the externalized phase of digestion (84, 86). Cooking can substantially reduce the costs of meat digestion, absorption, and assimilation (87) and reduces the physical structure of plants (starch, inulin, cellulose), increasing digestibility of their basic nutritional elements. Nonthermal processing is also likely a key component of high-intensity foraging and works in many of the same ways, with the addition of particle size reduction prior to ingestion (22). Our findings suggest that although some food processing activities can be energetically intensive (Fig. 5), overall amounts of time and endosomatic energy devoted to processing remain relatively low (Fig. 4). Given the ability to increase edibility and digestibility of foods, processing should thus yield a high efficiency or return on investment. Although our analyses do make use of caloric estimates of food items after undergoing thermal and nonthermal processing, a limitation of the current study is that our measures of subsistence costs do not include the energetic cost of digestion and thus any potential cost savings that humans experience digesting processed foods.

A central finding here is that humans devote less time to subsistence activities than other great apes (Figs. 2 and 8). Humans are also the only primate species that can afford to take rest days (days in which individuals voluntarily choose not to forage) on account of our reliance on cooperation, sharing, and pooled energy budgets. With less time spent foraging, ancestral hominins would have experienced greater opportunities for alternative activities (10, 88, 89), including cultural production and exchange, by loosening constraints on the demanding foraging time costs observed in other great apes. Through improvements to technology and social exchange of information, such investments would have enabled further increases in energy acquisition rates, in turn freeing more time to invest in nonsubsistence pursuits. These include quintessential human behaviors that occur in the context of central-place foraging—social learning, object manufacture, and symbolic/ritual activities—which, combined with social tolerance and bilateral networks, could collectively favor ongoing processes of cumulative cultural evolution (90, 91).

Energetics and the origins of farming

Energetic and time considerations lie at the heart of theories to explain the origin and spread of agriculture. In particular, it has been hypothesized that the adoption of farming could have been a response to a higher marginal return on labor (36, 37). Using high-resolution measurements of subsistence energetics from the Hadza and Tsimane in combination with a cross-cultural sample, our results indicate that horticulture is generally associated with higher

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return rates compared to hunting and gathering, despite there being little difference in the amount of time devoted to subsistence (Fig. 8). As such, higher return rates arise primarily from greater caloric production within the same amount of time. These results support prior evidence that the adoption of farming could have been motivated by economic factors, primarily greater gains per amount of work (time) spent on labor (*37*). Technological improvements such as the shift from stone or wooden tools to metal tools may decrease the time required for agricultural work and improve return rates (*55*, *59*). Estimated return rates and efficiencies for contemporary subsistence populations may therefore be higher than they would have been for early humans lacking modern technology (e.g., machetes), although some modern environments may also be more depleted (*92*).

Our results further contradict any notion of the "original affluent society," according to which hunter-gatherers work ~15 hours/week (*93*, *94*): Hadza men and women work ~50 and 40 hours/week and other hunter-gatherer men and women work ~33 and 28 hours/week on average, respectively, based on our cross-cultural sample (table S2). Agriculture compared to hunting and gathering is also not necessarily accompanied by increased working time, as has been hotly debated (*95*). Although some farming groups do work more hours, on average there is no difference in total work time between modes of subsistence (Fig. 8). The wide range of times devoted to subsistence among both hunter-gatherers and horticulturalists suggests that local ecological and social factors, rather than subsistence mode, dictate available leisure time.

Our results also provide a proximate mechanism to explain the elevated reproductive rates often associated with the shift to agriculture (*4*, *96*), which has been linked to increased available energy for women to invest in reproduction. Tsimane women expend 47% less energy on subsistence than Hadza women (Fig. 2), devote less than half the amount of TEE to subsistence (Fig. 6), and have more energy available for reproduction scaled to body mass (E_i; 18% greater). Reductions in energy expenditure may result from Tsimane women engaging primarily in tasks that require little energy, such as food processing and domestic labor (Fig. 5), in contrast to Hadza women, who spend nearly 40% of time out of camp engaged in intensive digging for underground plant foods (table S4). The relative subsistence costs for Hadza and Tsimane women correspond to observed differences in total fertility rates [TFR_{Hadza} = 6.2 (*21*), $TFR_{Tsimane}$ = 9.1 (*97*)].

Recent changes in human energetics

We have shown that human subsistence has evolved to capture ever-greater amounts of surplus energy quickly, but at the expense of high energy costs. Such high costs persist even though humans have economical locomotion (the primary energetic cost of foraging for most animals) and use tools that reduce the costs of particular foraging activities relative to the cost of the same activity performed without tools. This suggests that energy gained from improvements to efficiency in human evolution were primarily channeled toward further ramping up foraging intensity rather than reducing the energetic costs of subsistence. This unintuitive view of energy use in relation to efficiency finds a parallel in the Jevons Paradox, a macroeconomic principle by which the introduction of more efficient technologies leads to increased consumption rather than savings in human systems (*98*).

Our results also provide deeper evolutionary context for understanding modern trends in human time and energy budgets. Exosomatic energy accounts for a relatively minor portion of the "social metabolism" of small-scale societies (*20*). For example, hunter-gatherers and horticulturalists rely directly or indirectly on biomass generated by solar energy and, with the notable exception of occasional landscape burning practiced in some cultures (*99*), do not participate in systematic large-scale management of ecosystems (*100*). The intensification of agriculture introduced greater exosomatic inputs, primarily in the form of domesticated animals for draft power. Since the Industrial Revolution, fossil fuels and mechanization have increasingly externalized energy production (*101*). Paralleling these changes, the ratio of exosomatic to endosomatic energy flows has risen from less than 5 in hunter-gatherer societies to more than 90 in highly developed industrialized societies (*102*). This has allowed for an unprecedented increase in the energy return on investment of labor (ratio of food energy produced to endosomatic energy invested in labor) for modern agriculture since the 1950s (*103*–*106*). With the subsequent decoupling of industrial production from human and animal labor, industrialized populations have continued to experience reductions in the time costs of "subsistence." For example, the proportion of income spent on food for Americans decreased from ~25% to 12% between 1928 and 1998 (~1.4 and 0.7 hours/day, respectively, assuming a 40-hour work week), mainly due to lowered monetary costs of food (*107*). With large increases in food production alongside increasingly sedentary lifestyles, humans have experienced a fundamental shift in our relationship with energy, setting up one of the major health challenges of our time: the rise of chronic noncommunicable "diseases of civilization" such as obesity, metabolic syndrome, and cardiovascular disease. Unburdened by the high physiological costs of food production, a human body that evolved to expend large quantities of energy to acquire food has now found itself in a potentially deadly mismatch.

Materials and methods

Foraging energetics of nonhuman great apes

To calculate energy budgets of nonhuman great apes, total daily energy expenditure (TEE) was used as a proxy for daily energy acquired from food (kcal/day) under the realistic assumption that energy input and output are approximately equal among nonprovisioned animals in energy balance (*2*, *27*). Food sharing and provisioning are very rare among nonhuman apes in the wild, even between mothers and offspring (*2*, *29*–*31*), and therefore each individual's average daily food energy acquisition must match their average TEE. A lack of surplus production in other great apes is underscored by the fact that humans exhibit elevated fat deposition compared to chimpanzees and gorillas, and that the fat reserves of orangutans fluctuate in accordance with boom and bust seasonal cycles and supra-annual mast fruiting events (*1*, *108*, *109*). TEE was determined for each great ape species by fitting regressions to empirically measured TEE and body mass data for healthy adults (10+ years old) from DLW studies in zoo and sanctuary ape populations (*1*, *110*). We note that TEE for captive primate populations does not differ from that of wild populations in analyses accounting for body size (*27*, *111*). Natural logarithm–transformed values were used for mass and TEE because previous work has demonstrated that, as in other species, TEE increases in a power-law manner with body size in apes (*1*). Regressions were as follows (data presented in fig. S6):

Chimpanzees: ln(TEE) = 0.602 ± 0.196 ln(mass) + 5.197 ± 0.792 (model: adj. r^2 = 0.23, p = 0.005, SE = 0.195, df = 28)

Gorillas: ln(TEE) = 0.726 ± 0.160 ln(mass) + 4.432 ± 0.741 (model: adj. r^2 = 0.66, p = 0.001, SE = 0.212, df = 9)

Orangutans: ln(TEE) = 0.467 ± 0.128 ln(mass) + 5.402 ± 0.544 (model: adj. r^2 = 0.34, p = 0.001, SE = 0.223, df = 23)

We used these regressions to calculate mean (95% CI) TEE for wild males and females of each species using adult body masses reported for wild populations [chimpanzees: males 40.4, females 32.8 (*112*); gorillas (Western lowland): males 170.4, females 70.5 (*113*); orangutans (Borneo): males 78.5, females 35.8 (*113*)]. These estimates for TEE were, in turn, used as estimates of daily energy acquisition, assuming that food provisioning and storage among adult nonhuman great apes is negligible.

To calculate energy expenditure associated with foraging in each species, measurements of average daily distances of terrestrial travel and arboreal climbing were compiled from prior studies (*80*, *114*–*117*) and distances were converted to energy costs (kcal/day) using

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established cost of transport values (kcal kg^{-1} m^{-1}) from respirometry studies of chimpanzee quadrupedal walking and nonhuman primate climbing (*16*, *33*). The kinematics and locomotor anatomy of nonhuman great apes are broadly similar across species (*118*), and thus walking costs (kcal kg^{-1} m^{-1}) determined from respirometry studies of chimpanzees also provide a reasonable estimate for those of gorillas and orangutans. Further, the cost of transport (kcal kg^{-1} m^{-1}) for climbing is similar across primates, and indeed across mammals (*33*), and thus the cost of transport for climbing derived from respirometry studies in nonhuman primates provides a reliable estimate of climbing costs in great apes. The time cost of foraging was defined as the daily time spent feeding and moving to acquire food and was calculated by sex for each species by averaging data from prior studies (table S5). Estimates of TEE and behavioral data on foraging in nonhuman great apes were derived from different samples.

To check our regression-based approach for estimating TEE, we compared our estimates to those from (i) activity budget analyses for wild great apes and other primates (*26*), (ii) DLW measurements of wild primates (*27*), (iii) DLW measurements of wild nonprimate mammals (*28*), and (iv) estimated daily energy acquisition values from studies observing feeding behavior in wild great apes (table S1) (*119*–*128*). To facilitate comparisons across the wide range of body sizes in these analyses, we examined the ratio of TEE to basal metabolic rate (BMR; kcal/day), which provides both a body size–adjusted measure for comparison of TEE and a rough measure of daily physical activity (the TEE/BMR ratio is sometimes termed "physical activity level") (*28*, *129*). BMRs were estimated from body mass using published regression equations for nonhuman great apes and other primates (*1*, *26*) (table S1). Our regression-based TEE estimates yielded TEE/BMR values for wild great apes that were similar to activity budget–based estimates, DLW measurements in wild primates, and DLW measurements in wild nonprimate mammals (table S1 and fig. S1). The agreement between our approach and other measures and estimates of daily expenditure supports our use of DLW-based regression estimates of TEE here. However, estimates of food acquisition from behavioral observations of wild great apes (*119*, *124*, *126*, *127*), in at least some studies, yield higher estimates of TEE and TEE/BMR (table S1 and fig. S1). We note that estimates of energy acquisition from feeding observations require estimates of intake rate for each food, average nutritional content of each food, digestibility of each food, and average daily feeding time across partial-day follows, and that analytical error in each of these estimates can lead to compounded errors in estimated TEE; we therefore favor the DLW regression-based approach used in this study. Nonetheless, as a sensitivity analysis, we reran analyses using energy acquisition estimates from wild nonhuman great ape feeding studies. Even if energy returns were somewhat greater than our estimates, as suggested by estimated return rates from feeding observations in wild nonhuman great apes, the pattern of results is unchanged: human foraging efficiencies (F) would compare even more unfavorably to those of other great apes, while hourly return rates remain higher for humans (figs. S3 and S4).

Measurements of subsistence energetics among Hadza hunter-gatherers

To calculate energy expenditure during subsistence-related activities among the Hadza, a portable respirometry system (Cosmed, K4b2) was used to measure breath-by-breath oxygen consumption and carbon dioxide production. Hadza participants (total: $n_{male} = 9$, $n_{female} = 5$) performed various subsistence tasks for 5 to 10 min while wearing the respirometer, and average rates of energy expenditure for each task were calculated once steady-state energy expenditure had been reached. Mass-specific energy expenditure (J kg^{-1} m^{-1}) was converted to net energy cost (kcal/min) by multiplying by the caloric coefficient (20.1) and body mass (kg), and then subtracting the participant-specific resting metabolic rate (i.e., the energy cost of rest in a sitting position). Resting energy expenditure was measured for 5 to 8 min immediately prior to the work task measurement with the subject either standing (for climbing, chopping, pounding, and walking) or kneeling (for digging). For activities lacking respirometry measurements (e.g., tool manufacture, eating) we used values from the literature for similar tasks (table S6).

To assess time spent on subsistence-related activities, scan samples of Hadza adults [n_{male} = 135 (26,498 observations), n_{female} = 179 (37,433 observations)] were collected in 16 camps between 1995–1996 and 2003–2005. Scan-sampling data were collected across all seasons between 7 a.m. and 7 p.m. To generate estimates of time spent in different subsistence activities, we used Bayesian multilevel, multinomial logistic regression models on time allocation data (*130*). In short, this technique models the probability of an individual engaging in a specific behavior (the multinomial response outcome) as a function of independent variables while accounting for repeated observations of individuals and correlated random effects that characterize individual-level trade-offs in the probability of engaging in different behaviors. In our analysis, outcome behaviors were divided into categories representing the major subsistence activities (with different per–unit time costs), and we included age, age^2, time of day, and time of day^2 as fixed effects, as well as random intercepts and their correlations for individual, community, and month. Men and women were analyzed separately. Models were fit using Hamiltonian Monte Carlo algorithms in the *RStan* package in R 3.5.0. To improve mixing of the Hamiltonian Monte Carlo chains, fixed effects were centered and scaled prior to analysis, and weakly informative priors for the fixed effects parameters were used.

After ensuring proper mixing and convergence of the models, model estimates were converted to sex- and age-specific probabilities of engaging in an activity using a custom link script and the softmax function (which normalizes the K predicted probabilities to sum to 1), with random effects set to 0. Given that sampling took place between 7 a.m. and 7 p.m. (when the vast majority of subsistence activity occurs), probability functions for each activity were integrated across time of day to calculate the number of minutes spent on a given activity per day by age and sex.

Because scan sampling occurred within camps, a large proportion of observations fell into a generic activity category for work outside of camp. To categorize out-of-camp activities, we used a database of focal follows in which observers followed individuals on out-of-camp trips and continuously recorded behavior (figs. S7 and S8). Men's time allocation out of camp was based on 46 focal follows collected between 2006 and 2014 among 27 different men (mean age = 33, SD = 11) in eight residential camps. On average, individual focal follows for men lasted 5.3 hours (SD = 2.8). The out-of-camp follow data were categorized into times spent walking, running, chopping, digging, resting, and in other activities (fig. S7 and table S7). "Other activities" include generally low- to moderate-level physical activities, including lying in wait while hunting, scanning the landscape for animals, inspecting trees for bee nests, processing foods, and eating. The energetic cost of "other activities" was ascribed an average value for non-baobab food processing [1.9 kcal/min, for average category of "food preparation" in (*131*)]. We also used observations from these follows to estimate the mean height climbed per day to extract honey (10 m/day).

Hadza women's out-of-camp time allocation while foraging was recorded during 27 focal follows of 14 women (mean age = 45, SD = 14) collected between 2011 and 2014 in three residential camps. Follows of women foraging lasted on average 3.7 hours out of camp (SD = 2). Time allocation during these follows has been categorized into times spent walking, running, chopping, digging, resting, and in other activities (fig. S8 and table S4). "Other activities" are generally low- to moderate-level physical activities and were also ascribed the energetic cost of non-baobab food processing (as above).

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During focal follows of both men and women, we recorded every time the observed Hadza subject consumed food, noting the species of food, its directly weighed or visually estimated amount (e.g., volume of honey, numbers of berries, mass of meat), and the source of the food. Analyzing these data, we find that men and women consumed, on average, an additional 306 kcal/hour (SD = 479) and 70 kcal/hour (SD = 60), respectively, while out of camp.

To estimate task-specific daily energy expenditure, respirometry measurements for specific activities were combined with daily time allocation data from scan sampling and focal follows. Total time spent foraging was then calculated by summing time spent on subsistence behaviors both in and out of camp.

Food acquisition in human populations cannot be adequately assessed using TEE from DLW measurements because frequent provisioning and sharing occur within the context of surplus production by some individuals. Food acquisition for the Hadza was estimated using data on foraging in which daily activities were recorded and all food brought to camp was either directly weighed or visually estimated. Data were collected between 2005 and 2009 on a total of 100 women and 79 men from seven camps, and were integrated with caloric density values for each food to calculate the total daily caloric value of food acquisition. Caloric density values of Hadza foods were estimated based on published nutritional values for honey, berries, tubers, baobab, and marula nuts (*68*, *132*, *133*). For Hadza foods where no published values were available, we used USDA values for closely related foods (*134*). These included quail eggs as a proxy for crested francolin eggs and beet greens as a proxy for leafy greens. To estimate the caloric value of animal carcasses, we used an intermediate value of 1.7 kcal/g for all species.

To generate production curves for the Hadza, foraging returns (kcal/day) were modeled as a function of age (third-order polynomial), sex, and age × sex interaction, with random intercepts for individual, camp, and month. Given the large number of zeros and highly skewed distribution of foraging returns, we used a Bayesian lognormal hurdle model (a commonly used alternative, the gamma hurdle model, produced similar results) (fig. S5) (*135*). Estimation was performed using the *brms* package in R using weakly informative priors (run with four chains with 3000 iterations, 1500 of which were devoted to warmup). Finally, total daily acquisition was obtained by summing in-camp returns with out-of-camp consumption (by multiplying the number of hours spent out of camp and the average per-hour consumption estimates above, scaled to the productivity age profile).

TEE among the Hadza was measured in a sample of 27 adult men and 24 adult women using the doubly labeled water method (*136*). Fat-free mass was measured by multiplying average body mass by 1 − (% body fat), with percent body fat measured using bioimpedance.

Measurements of subsistence energetics among Tsimane horticulturalists

Energy expenditure during subsistence-related activities among the Tsimane was measured using the same respirometry procedures used among the Hadza but applied to Tsimane subsistence tasks (Tsimane participants: $n_{\text{male}} = 7$, $n_{\text{female}} = 5$). Resting energy expenditures for Tsimane were similarly measured in standing or sitting position prior to performing subsistence activities.

To estimate time spent in subsistence activities, we analyzed adult time allocation data (n = 35,500 observations) collected from 2002 to 2007 as part of a longitudinal study of the Tsimane (*137*). Time allocation data represent instantaneous scan samples collected at 30-min intervals. Villages were partitioned into household clusters that were monitored for 2- or 3-hour time blocks between 7 a.m. and 7 p.m. If a residing individual was not present at the time of sampling, interviews with other residents were used to assess out-of-camp activities (follow-up direct observation indicated that reported behaviors were highly accurate). Data were collected across all seasons in nine villages. Analyses were restricted to adults between the ages of 15 and 75 ($n_{\text{male}} = 282$, $n_{\text{female}} = 243$), and the same analysis and post-processing procedures reported for Hadza above were employed using multilevel, multinomial logistic regression models to calculate time spent in different activities. Finally, time spent in each subsistence activity was multiplied by net energy costs from respirometry to estimate the daily cost (kcal) of subsistence (E_f).

For some subsistence tasks (e.g., rice processing by men), there were not enough observations to accurately estimate separate parameters in the models. In such cases, outcomes were combined into the most closely related category and energetic costs of those activities were recalculated as a weighted mean based on the raw proportion of each observed activity (e.g., if rice processing has a net cost of 300 kcal/hour, general processing costs 100 kcal/hour, and rice processing accounts for one-fourth of observations in either category, then the combined cost assigned would be 150 kcal/hour).

Estimates of Tsimane gross energy production (E_a, kcal/day) from foraging and horticulture, separated by sex and age, come from reanalysis of data from previous studies (*138*). TEE among the Tsimane was measured in a sample of 18 adult men and 22 adult women using the doubly labeled water method (*97*). Fat-free mass was measured in the same manner as described for the Hadza.

Global data on human subsistence energetics

To generalize beyond the Hadza and Tsimane and to facilitate cross-cultural comparisons, a literature search was conducted for published estimates of food/energy acquisition from subsistence activities, the energetic costs of subsistence activities, time devoted to subsistence, foraging efficiency, and return rates in hunter-gatherer and horticulturalist societies around the world (table S2). Values were disaggregated by sex whenever possible, but in many instances were available only in combination (e.g., many horticulturalist production systems, where it is difficult to disentangle production within a household unit). In order to be included in our analysis, a study needed to present at least one of the quantities of interest (E_a, E_f, T_f, F, $R_{g/n}$) in a form that was commensurate to those estimated for our study populations. Return rates were calculated to include processing whenever possible. Time allocation estimates for other auxiliary subsistence activities, however, including tool manufacturing, eating, and water and firewood collection, were unavailable for most societies besides the Hadza and Tsimane and thus were not included in the cross-cultural analyses. A detailed description of how all values in the cross-cultural sample were derived is provided in the additional methods.

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SUPPLEMENTARY MATERIALS

science.org/doi/10.1126/science.abf0130
Materials and Methods
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Figs. S1 to S8
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Details of the cross-cultural sample

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Science

The energetics of uniquely human subsistence strategies

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Efficiency leads to leisure

Humans are animals—merely another lineage of great apes. However, we have diverged in significant ways from our ape cousins and we are perennially interested in how this happened. Kraft *et al*. looked at energy intake and expenditure in modern hunter-gatherer societies and great apes. They found that we do not spend less energy while foraging or farming, but we do acquire more energy and at a faster rate than our ape cousins. This difference may have allowed our ancestors to spend more time in contexts that facilitated social learning and cultural development. —SNV

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