PNAS | RESEARCH ARTICLE | ANTHROPOLOGY | OPEN ACCESS

Energy expenditure and obesity across the economic spectrum

Amanda McGrosky[a,b,1], Amy Luke[c,1], Leonore Arab[d], Kweku Bedu-Addo[e], Alberto G. Bonomi[f], Pascal Bovet[g], Soren Brage[h], Maciej S. Buchowski[i], Nancy Butte[j], Stefan G. Camps[k], Regina Casper[l], Daniel K. Cummings[m], Sai Krupa Das[n], Sanjoy Deb[o], Lara R. Dugas[c,p], Ulf Ekelund[q], Terrence Forrester[r], Barry W. Fudge[s], Melanie Gillingham[t], Annelies H. Goris[u], Michael Gurven[v], Catherine Hambly[w], Annemiek Joosen[x], Peter T. Katzmarzyk[y], Kitty P. Kempen[x], William E. Kraus[z], Wantanee Kriengsinyos[aa], Rebecca Kuriyan[bb], Robert F. Kushner[cc], Estelle V. Lambert[dd], Christel L. Larsson[ee], William R. Leonard[cc], Nader Lessan[ff,gg], Marie Löf[hh], Corby K. Martin[y], Anine C. Medin[ii,jj], Marian L. Neuhouser[kk], Kirsi H. Pietilainen[ll], Guy Plasqui[mm], Ross L. Prentice[kk], Susan B. Racette[nn], David A. Raichlen[oo], Eric Ravussin[y], Leanne Redman[y], Rebecca M. Reynolds[pp], Eric B. Rimm[qq], Susan Roberts[rr], Asher Y. Rosinger[ss,tt], Mary H. Samuels[uu], Srishti Sinha[bb], J. Josh Snodgrass[vv], Eric Stice[l], Ricardo Uauy[ww], Samuel S. Urlacher[xx], Jeanine A. Verbunt[x], Bruce Wolfe[yy], Brian Wood[zz,aaa], Xueying Zhang[bbb], Alexia J. Murphy-Alford[ccc], Cornelia J. Loechl[ccc], Jennifer Rood[y,1], Hiroyuki Sagayama[ddd,1], Dale A. Schoeller[eee], Klaas R. Westerterp[x,1], William W. Wong[j,1], Yosuke Yamada[fff,ggg,1], John R. Speakman[w,bbb,1], Herman Pontzer[a,hhh,1], and The IAEA DLW Database Consortium[2]

Affiliations are included on p. 7.

Edited by Daniel Nettle, PSL University, Paris, France; received October 10, 2024; accepted March 31, 2025 by Editorial Board Member James F. O'Connell

Global economic development has been associated with an increased prevalence of obesity and related health problems. Increased caloric intake and reduced energy expenditure are both cited as development-related contributors to the obesity crisis, but their relative importance remains unresolved. Here, we examine energy expenditure and two measures of obesity (body fat percentage and body mass index, BMI) for 4,213 adults from 34 populations across six continents and a wide range of lifestyles and economies, including hunter-gatherer, pastoralist, farming, and industrialized populations. Economic development was positively associated with greater body mass, BMI, and body fat, but also with greater total, basal, and activity energy expenditure. Body size–adjusted total and basal energy expenditures both decreased approximately 6 to 11% with increasing economic development, but were highly variable among populations and did not correspond closely with lifestyle. Body size–adjusted total energy expenditure was negatively, but weakly, associated with measures of obesity, accounting for roughly one-tenth of the elevated body fat percentage and BMI associated with economic development. In contrast, estimated energy intake was greater in economically developed populations, and in populations with available data (n = 25), the percentage of ultraprocessed food in the diet was associated with body fat percentage, suggesting that dietary intake plays a far greater role than reduced energy expenditure in obesity related to economic development.

energy expenditure | obesity | physical activity | doubly labeled water

Significance

Economic development is associated with increased prevalence of obesity and related health problems, but the relative importance of increased caloric intake and reduced energy expenditure remains unresolved. We show that daily energy expenditures are greater in developed populations, and activity energy expenditures are not reduced in more industrialized populations, challenging the hypothesis that decreased physical activity contributes to rises in obesity with economic development. Instead, our results suggest that dietary intake plays a far greater role than reduced expenditure in the elevated prevalence of obesity associated with economic development.

Obesity is a leading cause of global mortality and morbidity, accounting for more than 4 million deaths and 140 million disability-adjusted life years worldwide each year (1). The causes of the modern obesity crisis remain a focus of debate in public health research but appear to be related to economic development. Obesity was rare in the 1800s in the United States (2), for example, and remains so in traditional farming and foraging communities today, but has become common over the past century among most industrialized populations (3–5).

Fundamentally, weight gain results from consuming and absorbing more calories than are expended. Public health organizations typically attribute this imbalance to both reduced physical activity energy expenditure (AEE) and dietary changes promoting overconsumption, but assessing the relative contributions of expenditure and intake has proven challenging. Industrialized populations are much less physically active than traditional farming and foraging communities (4), and daily physical activity has declined within industrialized populations over the past few decades as economic development increased (6, 7). However, comparisons between populations and over time indicate that activity decline does not necessarily lead to corresponding reductions in total energy expenditure (TEE) (i.e., the total energy expended per 24 h) (8–11). Similarly, while industrialization and economic development have irrevocably changed our environments and the foods we eat, the salient obesogenic aspects of modern lifestyles and diets and the importance of increased intake relative to declining expenditure are unclear (12). Clarifying the relative importance of reduced energy expenditure and increased energy consumption and absorption in unhealthy

The authors declare no competing interest.

This article is a PNAS Direct Submission. D.N. is a guest editor invited by the Editorial Board.

[1]To whom correspondence may be addressed. Email: amcgrosky@elon.edu, aluke@luc.edu, jennifer.rood@pbrc.edu, sagayama.hiroyuki.ka@u.tsukuba.ac.jp, k.westerterp@maastrichtuniversity.nl, wwong@bcm.edu, yosuke.yamada.c1@tohoku.ac.jp, j.speakman@abdn.ac.uk, or herman.pontzer@duke.edu.

[2]A complete list of the IAEA DLW Database Consortium can be found in the *SI Appendix*.

This article contains supporting information online at https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2420902122/-/DCSupplemental.

Published July 14, 2025.

weight gain with economic development would help inform public health efforts to prevent obesity.

A major challenge in resolving the contribution of intake and expenditure is the lack of empirically measured expenditure, intake, and body composition across diverse populations. Most broad population comparisons of obesity prevalence lack empirical measures of energy expenditure (5). Conversely, most studies of total daily energy expenditure (MJ/d) have examined individual nonindustrial populations (8, 9, 13) or have lacked measures of adiposity (i.e., body fat percentage) (14). Diet assessments across populations have relied largely on surveys or country-level consumption (15, 16), which are insufficient for establishing accurate measures of energy intake (17).

In this study, we investigated the relative contribution of expenditure and intake to obesity across a global, economically diverse sample of 34 populations, using empirical measures of TEE (MJ/d) and body composition for 4,213 adult individuals between the ages of 18 and 60 y (*SI Appendix*). These populations represent a wide spectrum of economic development, including hunter-gatherers, pastoralists, farmers, and people in industrialized countries. We used the United Nations Human Development Index (HDI) (18), which integrates measures of wealth, longevity, and education, to further categorize the industrialized populations into Low-, Mid-, and High-HDI economies (*SI Appendix*, Table S8). Following previous work with the International Atomic Energy Agency Doubly Labelled Water Database (19), TEE was determined using the doubly labeled water method. Basal energy expenditure (BEE) was measured using indirect calorimetry or, when no measures were available, estimated from body size (*SI Appendix*). Following previous work (19), AEE was estimated as [0.9(TEE) – BEE], which assumes 10% of daily calories are expended on digesting and metabolizing food; see *Materials and Methods* for additional detail. Body composition was assessed as body fat percentage, which was measured by isotope dilution, and we also examined body mass index (BMI; mass/height^2), a common clinical metric for assessing obesity status.

Body composition reflects long-term energy balance, and previous work has shown that total daily energy expenditure is highly repeatable and stable within individual adults, even when activity levels fluctuate (10, 20). Therefore, if reduced physical activity leads to lower TEE and greater adiposity with economic development, measures of TEE should vary across populations accordingly and variation in expenditure should explain variation in body composition in multivariate regression models. Variation in body composition with economic development that is not explained by differences in energy expenditure may be provisionally attributed to variation in energy intake (i.e., calories consumed and absorbed).

Results

Economy and Body Size. As expected, absolute body mass, body fat percentage, and BMI were greater in more economically developed populations (Kruskal–Wallis $P < 0.05$; Fig. 1 and *SI Appendix*, Tables S1 and S2). Obesity, when identified by a BMI ≥ 30 kg/m^2, was also more common in Mid-HDI and High-HDI populations, particularly among female cohorts (*SI Appendix*, Table S1). Adiposity and BMI increased with age (*SI Appendix*, Fig. S2), and fat percentage was greater in women (Fig. 1), but the associations of both body fat percentage and BMI with economic development remained after accounting for age and sex effects ($P < 0.01$; *SI Appendix*, Table S2). Notably, the increase in BMI with economic development was largely driven by greater fat-free mass (FFM) in more-developed populations. Economy, age, and sex explained only 7% of the variance in BMI, but adding FFM to the model increased the explained variance to 51% (*SI Appendix*, Table S2). In comparison, 35 to 36% of the variance in body fat percentage was explained by economy, age, and sex, and adding FFM to the model only increased the explained variance by 2 to 3% (*SI Appendix*, Table S2). Further, in multivariate analyses with sex, age, and FFM, the High-HDI category consistently had higher body fat percentage than hunter-gatherer, agropastoralist, horticulturalist, and low HDI populations, but did not always have the highest BMI (*SI Appendix*, Table S2). The increase in obesity with economic development is more reliably captured by measures of body fat percentage than BMI.

Economy and Energy Expenditure. Like body size, TEE was greater in more economically developed populations ($P < 0.001$, Fig. 2 and *SI Appendix*, Tables S1 and S3). BEE and AEE also increased with economic development in analyses using HDI rank, as did the physical activity level (PAL) ratio of TEE/BEE (*SI Appendix*, Table S3). The development-related increase in expenditure was a function of larger body size in more developed populations, as all measures of expenditure increased with FFM (*SI Appendix*, Fig. S3 and Table S3).

In multiple regression including FFM, fat mass (FM), sex, and age, TEE was lower in more developed economies ($P < 0.001$, *SI Appendix*, Table S3), but the effect was small and largely attributable to differences in BEE. When economic development is treated as a rank-order variable (*SI Appendix*, Table S3*B*), linear models with FFM, FM, age, and sex predict a 6% decrease in TEE from the lowest to highest ranked populations in our dataset. Similar analyses predict an 11% decrease in BEE, but no significant change ($P > 0.05$) in AEE or PAL (*SI Appendix*, Table S3). When economies were grouped into categories for analyses, the SD for body size–adjusted TEE for all economic groups except horticulturalists overlapped with the High HDI group (*SI Appendix*, Table S1). Body size–adjusted BEE for horticulturalists was similarly elevated (*SI Appendix*, Table S1).

At the population level, variation in lifestyle did not correspond closely with body size–adjusted TEE. Hadza hunter-gatherers and Daasanach agropastoralists in equatorial Africa had size-adjusted TEEs equivalent to the US and Norwegian cohorts (Fig. 2). Tuvan agropastoralists in Siberia had elevated size-adjusted TEE, on par with cohorts from the Gambia, Australia, and Switzerland. The high size-adjusted total expenditure of Tsimane horticulturalists in Bolivia and Yakut adults in rural Siberia was attributable to their elevated BEE rather than AEE or PAL, which were similar to High-HDI populations (Fig. 2).

Energy Expenditure and Obesity. The slopes of the regressions between TEE and both fat percentage and BMI differed between men and women (Fig. 3), and therefore we analyzed male and female cohorts separately. In women, total expenditure was positively associated with fat percentage ($P < 0.001$) in linear models that included age, but this relationship was not significant ($P > 0.05$) in men (*SI Appendix*, Table S4). When FFM and economy were included as covariates, total expenditure was not associated with body fat percentage among women ($P > 0.05$). Among men, this FFM-adjusted total expenditure was negatively associated with body fat percentage ($P < 0.001$), but the effect size was small. A 1-SD increase in FFM-adjusted TEE, equivalent to the largest differences between economic groups (*SI Appendix*, Table S1), was associated with a ~1% point decrement in body fat percentage. A similar pattern was evident in BMI. TEE was positively correlated with BMI in both men and women due to the covariation with FFM. When FFM, age, and economy were included in models, TEE was negatively

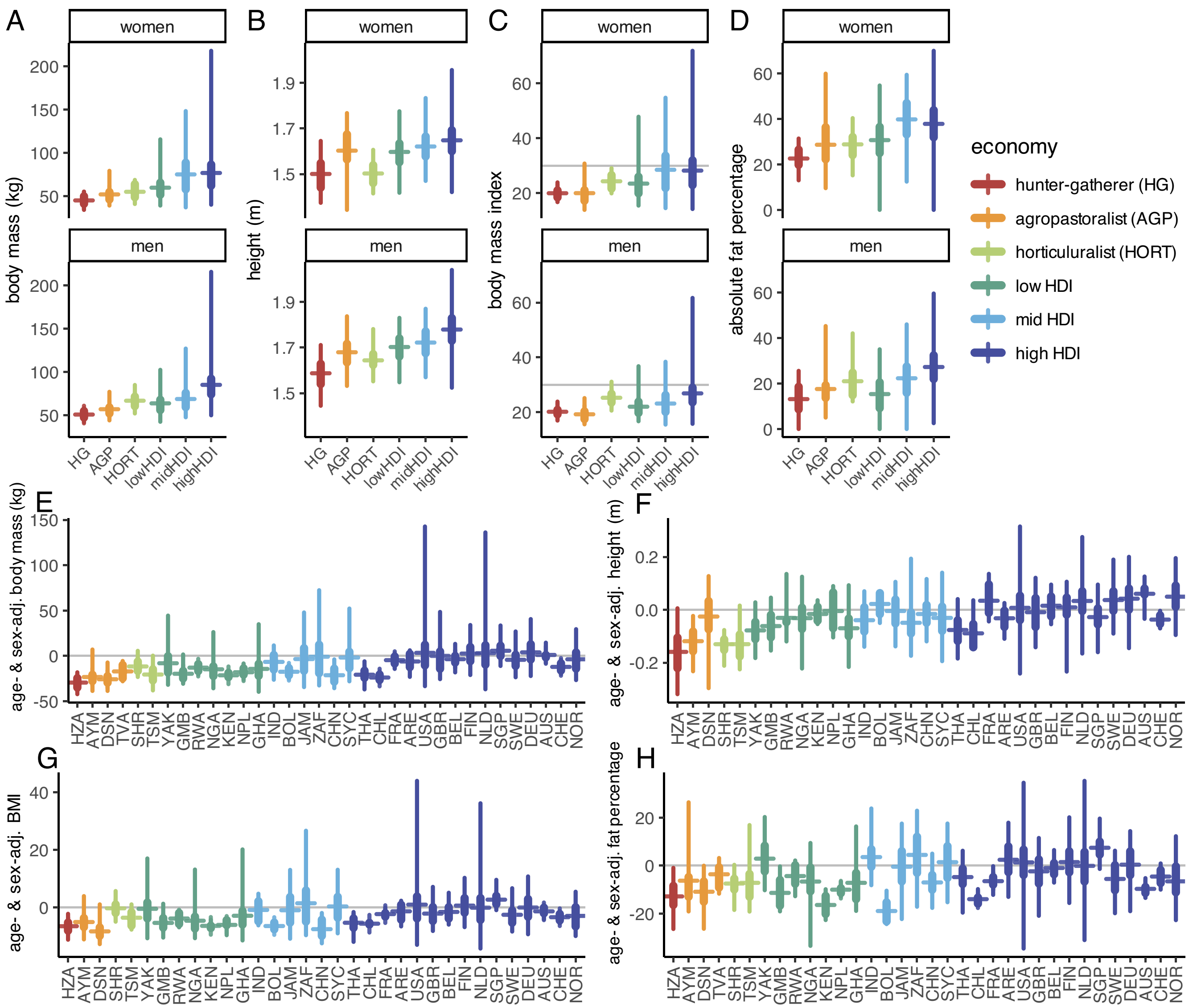

Fig. 1. Body size and composition across economies. Cohorts are ordered from lowest to highest HDI score. Bars indicate mean and quartiles. (*A*–*D*) Body mass, height, BMI, and body fat percentage increase with economic development in both women and men. Substantial portions of the BMI distribution fall above the criterion for obesity (BMI ≥ 30 kg/m^2) in Low, Mid, and High HDI populations. (*E*–*H*) There is considerable variability within and between populations in age- and sex-adjusted body mass, height, BMI, and body fat percentage. See *SI Appendix*, Table S8 for population measures and abbreviations.

associated with BMI in both men and women ($P < 0.05$), but the effect was small, with a 1-SD increase in TEE associated with a ~0.6 decrement in BMI for both men and women (*SI Appendix*, Table S5). The differences in body fat percentage and BMI among economic groups were approximately 10 times greater than those associated with a 1 SD increase in TEE (*SI Appendix*, Tables S4 and S5).

TEE is strongly related to FFM (*SI Appendix*, Fig. S3), so to isolate and visualize the impact of TEE on body composition, we examined the relationship between FFM-adjusted total expenditure (i.e., residuals from the total expenditure-FFM regression) on body fat percentage. FFM-adjusted TEE was unrelated to body fat percentage for women ($P > 0.05$), and unrelated to BMI in both men and women ($P > 0.05$), in linear models including age and economy (*SI Appendix*, Tables S4 and S5). For men, FFM-adjusted TEE was negatively, but weakly associated with body fat percentage: 1-SD increase in FFM-adjusted TEE, equivalent to that between economic groups, was associated with a <1% point decrement in body fat percentage (*SI Appendix*, Table S4). By comparison, body fat percentage for the male High-HDI cohort was 12.5% points greater than the hunter-gatherer cohort (*SI Appendix*, Table S4). Further, the within-group relationships between FFM-adjusted TEE and both body fat percentage and BMI were highly variable among populations, with slopes distributed about 0 (Fig. 3).

Discussion

Economic Development and Energy Expenditure. Patterns of energy expenditure and obesity across this global sample challenge the hypothesis that decreased physical AEE contributes meaningfully to the rise in obesity with economic development. Absolute measures of TEE and AEE are greater in more economically developed populations (Fig. 2), consistent with their larger body size. Body size–adjusted TEE decreased marginally with greater development, but this effect was small, highly variable among populations, and attributableor PAL, mirrors the temporal patterns to the trend in size-adjusted BEE,

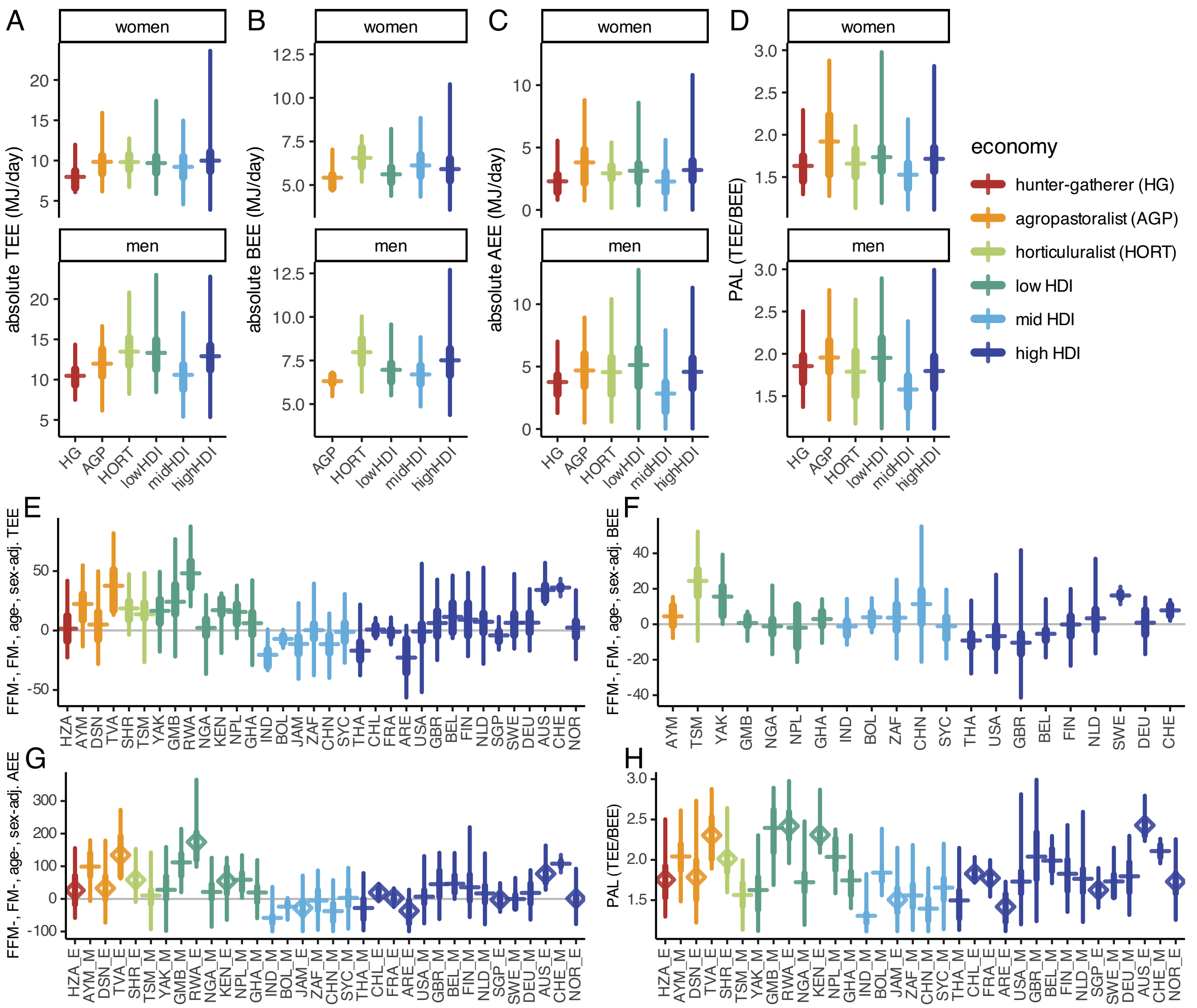

Fig. 2. Energy expenditure across economies. (*A*–*D*) TEE, BEE, and AEE increase with economic development. Bars indicate mean and quartiles. (*E*–*H*) Adjusted expenditures, calculated from residuals from multiple regression with FFM, FM, age, and sex varied considerably within and between populations. Size-adjusted TEE and BEE (residuals from regression with FFM, FM, sex, and age) decreased weakly with economic development. PAL and size-adjusted AEE were unrelated to economic development. Populations with measured basal expenditures are indicated with _M, estimated with _E.

not size-adjusted AEE or PAL. Unadjusted TEE was negatively associated with body fat percentage and BMI in some models, and size-adjusted TEE was negatively associated with body fat percentage in men, but these effects were universally small and variable (Fig. 3 and *SI Appendix*, Tables S4 and S5). At most, differences in TEE between economic groups could account for approximately one-tenth of the increase in BMI and body fat percentage associated with economic development.

The decrease in BEE with economic development, but not AEE or PAL, mirrors the temporal patterns observed in the United States and Europe over the past three decades (11). One hypothesis is that economic development is associated with reduced pathogen burden, which in turn reduces immune activity and BEE. Previous studies with the Tsimane (21) and Shuar (22) horticulturalist populations in South America have reported associations between elevated BEE and measures of immune activity (e.g., serum immunoglobulin levels, the presence of helminths, white blood cell count). Others have argued that the decrease in BEE in the United States and Europe may be driven by dietary changes, particularly changes in saturated fat relative to unsaturated fat intake or decreases in fiber intake (11). Additional measures of immune function and diet across a broad set of populations are needed to test these hypotheses.

Economic Development and Obesity. Comparisons of energy expenditure across populations strongly suggest that increased energy intake (i.e., caloric consumption and absorption) is the primary factor promoting overweight and obesity with economic development. This view is supported by measures of total expenditure and weight change, which together provide an estimate of energy intake (23). Participants in this study were relatively weight stable during the 7- to 14-d energy expenditure measurement period (mean weight change = −0.04 kg; SD = 0.97 kg across all individuals; see *SI Appendix*, Table S6 for weight change by economy and sex), suggesting that the greater absolute TEEs evident in more economically developed populations (Fig. 1) were accompanied by greater caloric intake. Our analyses suggest that increased energy intake has been roughly 10 times

 https://doi.org/10.1073/pnas.2420902122

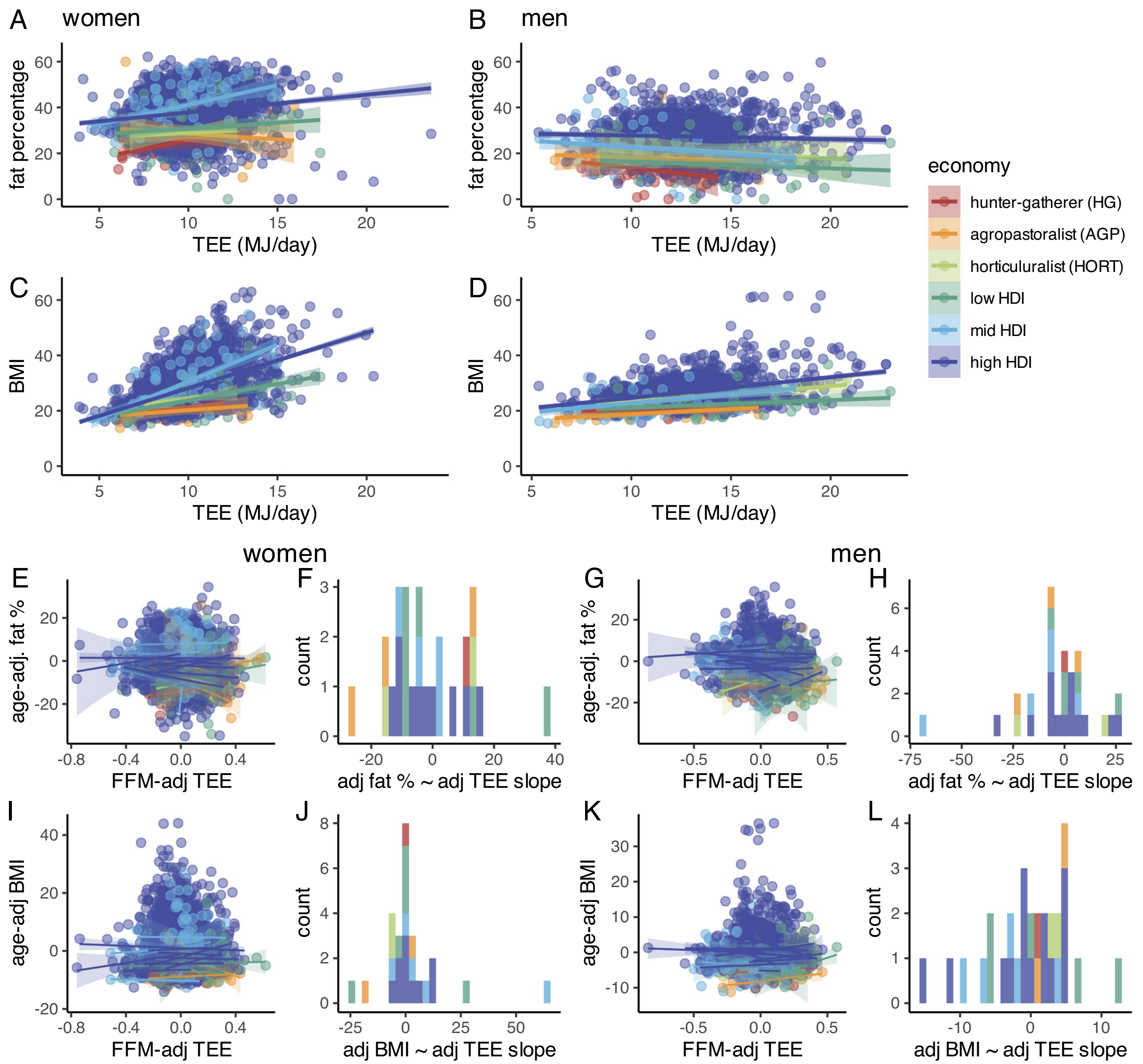

Fig. 3. The relationship between energy expenditure, adiposity, and BMI. The relationship between TEE and body fat percentage (*A* and *B*) and BMI (*C* and *D*) differed between women and men. The relationship between FFM-adjusted TEE and body fat percentage (*E*–*H*) and BMI (*I*–*L*) was weak, highly variable, and distributed about 0 among populations (*SI Appendix*, Tables S4 and S5).

more important than declining TEE in driving the modern obesity crisis.

The data in this study are cross-sectional and we lack detailed dietary data for most of the populations in this dataset. We therefore cannot establish causality in the relationships between economic development, body fat percentage, and dietary intake. We also cannot resolve the environmental, societal, and physiological factors promoting increased caloric intake and absorption. One possibility is that greater physical activity in less-developed populations helps to regulate hunger and satiety (24). Another hypothesis is that environmental contaminants in industrialized settings promote fat storage and obesity (25). Differences in the quality or quantity of food available in developed populations are also likely factors (12). For example, industrially produced foods common in developed countries may be more easily digested, reducing fecal energy loss and increasing the proportion of consumed calories that are absorbed (26). Others have argued that modern foods may promote the partitioning of calories to fat storage rather than expenditure, leading to increased hunger and overconsumption (27). We do not have the dietary nutrient data needed to test this hypothesis, but we note that diets in hunter-gatherer and horticulturalist populations, including some in the present analysis, often have different macronutrient profiles than those of more industrialized populations, including more carbohydrate and less fat than the average US diet (4, 28).

One recent change in global food systems is access to ultraprocessed foods (UPF) [i.e., industrial formulations of five or more ingredients (29)] among populations that traditionally had minimal exposure. While intake of UPF has been associated with risk of obesity and obesity-related outcomes (30–32), the mechanisms involved are not clear. The low cost and long shelf lives of these foods may contribute to increased

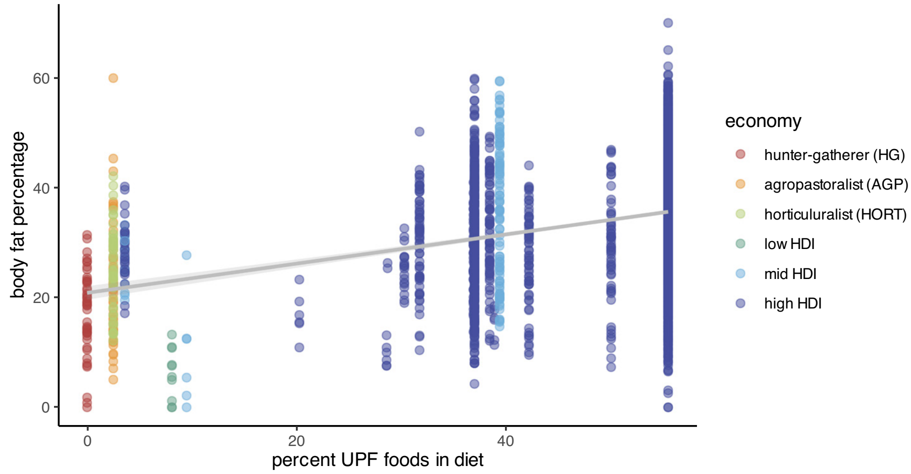

Fig. 4. UPF and adiposity. The percentage of daily calorie intake from UPF was positively associated with body fat percentage in bivariate analyses and in multiple regression including FFM-adjusted total expenditure, age, sex, and HDI rank (*SI Appendix*, Table S5).

availability of calories. The hyperpalatability, energy density, nutrient composition, and appearance of UPF might disrupt satiety signaling and encourage overconsumption (33). Processing has also been shown to increase the percentage of calories consumed that are absorbed into the body rather than excreted (34). We found some support for an obesogenic role of UPF in the current dataset. For the 25 populations in this sample for whom dietary data (e.g., percent UPF in the diet, per capita meat consumption) were available (*SI Appendix*, Table S8), the percent of UPF in the diet was positively correlated with body fat percentage, both in bivariate analyses and in multivariate regression controlling for age, sex, energy expenditure, and HDI rank (Fig. 4 and *SI Appendix*, Tables S7). By contrast, per capita meat consumption, another dietary change associated with development, was not significantly associated with fat percentage when added to models including percent UPF (*SI Appendix*, Table S7).

The central role of diet in the global obesity crisis does not mean that efforts to promote physical activity should be minimized. Daily physical activity has a broad range of well-documented health benefits, from reducing all-cause and cardiovascular mortality to improving mental health, and is an essential component of a healthy lifestyle (35). Time spent sedentary and the prevalence of insufficient daily physical activity are both higher in wealthy countries and have been increasing globally in recent decades (36), and cardiovascular disease is now a leading cause of mortality globally (37). Rather than advocating for diet over exercise in public health, data from this study join an emerging consensus that both must prioritized. Diet and physical activity should be viewed as essential and complementary, rather than interchangeable.

Results here highlight the need to identify the factors that make foods in developed countries obesogenic. Not all impacts of economic development and the adoption of the modern food system have been negative. Current global networks of production and supply ensure that affordable foods and food components are available to almost every population on earth (38). Much of the additional energy provided by modern food systems appears to be channeled into healthy growth, as both adult stature and FFM are considerably greater among industrialized populations (Fig. 1 and *SI Appendix*, Tables S1 and S2). Indeed, in the present sample, the increase in BMI with economic development was largely attributable to greater FFM (*SI Appendix*, Table S2). Efforts to track and prevent obesity will be improved by utilizing measures of body fat rather than BMI, and by focusing on dietary intake rather than expenditure. Regulating food environments to maximize the benefits of increased calorie availability without promoting a nutrient-poor, obesogenic diet remains a crucial challenge in public health that will only become more acute as economic development continues globally.

Materials and Methods

Sample. Data were compiled from the International Atomic Energy Agency Doubly Labelled Water Database (39) version 3.9. The doubly labeled water method uses the rate of isotope depletion (^{2}H and ^{18}O) from the body water pool to calculate the rate of CO_2 production and thus energy expenditure (MJ/d) over a 7- to 14-d period (40). Isotope depletion rates for Doubly Labelled Water Database entries were used to calculate TEE using a single, validated equation (40). The doubly labeled water method also provides a measure of body composition via deuterium dilution, which was used to calculate FFM, FM, and body fat percentage for each subject in the Doubly Labelled Water Database. Age, sex, body weight, and height were reported for each entry in the database. BMI was calculated as mass/height^2, where mass is in kg and height is in meters.

To further expand the geographic and economic diversity of the populations represented, we included published doubly labeled water measures of TEE from three pastoralist populations, the Aymara community in Bolivia (41), the Tuvan community in Siberia (42), and the Daasanach community in northern Kenya (43). Adding these populations to the Doubly Labelled Water Database sample resulted in an initial sample of 10,590 individuals. From that initial sample, we excluded subjects with missing data for sex or with reported health conditions (obesity excepted). We also excluded those listed as "athletes" in the database and those with TEEs greater than 25 MJ/d (all of these excluded individuals were from High HDI populations). Finally, to minimize the impact of age in our analyses (19), we excluded individuals younger than 18 y or older than 60 y.

BEE measurements from indirect calorimetry were available for 1,300 subjects in the sample. These measurements were used for analyses of BEE, AEE, and PAL. For populations in which no measures of BEE were available, we estimated BEE via a predictive equation determined from the 1,300 subjects with BEE. This equation had the form [$\ln(\text{BEE}) = \ln(\text{FFM}) \times 0.703804 + \ln(\text{FM}) \times 0.02424 - 0.963250$; $r^2 = 0.64$; $P < 0.001$]. Following previous work (44), we estimated AEE by modeling TEE as being composed of three components: BEE, the thermic effect of food (i.e., energy expended digesting and metabolizing food), and AEE (i.e., physical activity). Since the thermic effect of food is ~10% of TEE for people in energy balance (45), AEE can be estimated using this approach as [0.9(TEE) − BEE] (44). In addition to estimating activity energy expenditure, because PAL is commonly used as a body size–adjusted measure of physical activity expenditure (46), we also calculated PAL using the equation PAL = [TEE/BEE].

Methodological differences in measuring TEE and BEE can affect results. To minimize the impact of these effects for TEE, the DLW Database applies the same, validated equations to measures of isotope depletion and dilution, eliminating variation that can arise from using different equations to calculate energy expenditure from isotope data (40). Protocols for measuring TEE and BEE were similar for populations regardless of economic development (see for example refs. 8 and 47), and are not expected to result in systematic biases that would affect comparisons with economic development in this study.

Economic development scores for industrialized populations were assigned using the HDI, following previous work (14). The HDI is designed to be a holistic measure of development that incorporates population metrics for life expectancy, education, and income. HDI scores were obtained from the United Nations Development Programme's Human Development Report (18); we followed the UN's thresholds used for low (<0.550), medium (0.550 to 0.699), and high-very high (≥0.700) HDI. HDI scores were converted to rank-order, with the highest HDI assigned a rank of 1. Based on assessments of market integration for nonindustrialized populations, we assigned HDI rank of 206 to hunter-gatherers (Hadza), 203 to 205 to pastoralists (Daasanach, Tuvan, and Aymara), 201 to 202 to horticulturalists (Shuar and Tsimane), and 200 to Yakut, who supplement subsistence pastoralism, fishing, and hunting with market participation. We note that, because economic development was used as a rank-order variable in our analyses, it is the relative HDI value among populations, not the precise, absolute HDI score, that is relevant for analyses and results in this paper.

Analyses. The scaling of TEE and BEE with body size follows a power-law curve (19), and therefore size measures (mass, FFM, and FM) and expenditure measures (TEE, BEE, and AEE) were *ln*-transformed prior to multiple linear regression analysis. All analyses were conducted in R version 4.3.1 for Mac (48). We used general linear models to assess the effects of economic development, as well as the associations between TEE and dietary measures with body fat% and BMI (Figs. 1–4 and *SI Appendix*, Tables S2–S5). Regression-based approaches with *ln*-transformed measures of expenditure and body size are the preferred approach for assessing these relationships because they do not rely on simple ratios of energy/mass, which themselves are related to body size (19, 49). We examined economic development as both a categorical variable (hunter-gatherer, pastoralist, horticulturalist, low-HDI, mid-HDI, high-HDI) and as a rank-order variable using the HDI score.

To calculate "adjusted" values of energy expenditure for visualization in Fig. 2 *E*–*G*, we calculated residual values of *ln*-transformed expenditure (TEE, AEE, and BEE, depending on the analysis) for each subject using the general linear model regression with *ln*(FFM), *ln*(FM), age, and sex. We used a similar approach for visualizing adjusted TEE for Fig. 3 *E*, *G*, *I*, and *K*, calculating residual ln-transformed TEE using the regression with *ln*(FFM).

Data on the percentage of ultraprocessed food (%UPF) were collected from the literature (see *SI Appendix*, Table S8 for sources); data on meat consumption were collected from a recent analysis of 175 global populations (50) and supplemented with additional data from the literature (see *SI Appendix*, Table S8 for sources). To evaluate the relationship between body composition and diet, body fat percentage was modeled as a function of %UPF, per capita meat consumption, HDI rank, age, sex, and/or FFM-adjusted TEE using general linear models.

Data, Materials, and Software Availability. Some study data available [All data were collected from published sources or the IAEA DLW Database, which is publicly accessible but requires a research proposal (https://www.iaea.org/resources/hhc/nutrition/databases/double-labelled-water-dlw/how-to-request)] (39).

ACKNOWLEDGMENTS. The Doubly Labeled Water Database is supported bythe International Atomic Energy Agency. This project was funded by the US NSF Grant BCS-1824466 (H.P.), Chinese Academy of Sciences Grant CAS 153E11KYSB20190045 (J.R.), Taiyo Nippon Sanso (DLW Database), and Sercon Group (DLW Database).

Author affiliations: [a]Department of Evolutionary Anthropology, Duke University, Durham, NC 27708; [b]Department of Biology, Elon University, Elon, NC 27244; [c]Department of Public Health Sciences, Parkinson School of Health Sciences and Public Health, Loyola University, Maywood, IL 60153; [d]David Geffen School of Medicine, University of California, Los Angeles, CA 90095; [e]Department of Physiology, Kwame Nkrumah University of Science and Technology, KNUST-Kumasi, Ghana; [f]Phillips Research, Eindhoven 5656 AE, The Netherlands; [g]University Center for Primary Care and Public Health (Unisanté), University of Lausanne, Lausanne 1011, Switzerland; [h]Medical Research Council Epidemiology Unit, University of Cambridge, Cambridge CB2 0QQ, United Kingdom; [i]Division of Gastroenterology, Hepatology and Nutrition, Department of Medicine, Vanderbilt University, Nashville, TN 37232; [j]Department of Pediatrics, Baylor College of Medicine, Houston, TX 77030; [k]Clinical Nutrition Research Center, Singapore Institute for Clinical Sciences, Agency for Science, Technology, and Research and National University Health System, Singapore 138669, Singapore; [l]Psychiatry and Behavioral Sciences, Stanford University, Stanford, CA 94305-5723; [m]Economic Science Institute, Chapman University, Orange, CA 92866; [n]Jean Mayer US Department of Agriculture Human Nutrition Research Center on Aging, Tufts University, Boston, MA 02111; [o]Cambridge Centre for Sport and Exercise Sciences, Anglia Ruskin University, Cambridge CB1 1PT, United Kingdom; [p]Division of Epidemiology and Biostatistics, School of Public Health, Faculty of Health Science, University of Cape Town, Cape Town 7925, South Africa; [q]Department of Sport Medicine, Norwegian School of Sport Sciences, Oslo 0806, Norway; [r]Solutions for Developing Countries, University of the West Indies, Mona, Kingston 7, Jamaica; [s]University of Glasgow, Glasgow G12 8QQ, United Kingdom; [t]Department of Molecular and Medical Genetics, Oregon Health and Science University, Portland, OR 97239; [u]OnePlanet Research Center, Wageningen 6708 WE, The Netherlands; [v]Department of Anthropology, University of California, Santa Barbara, CA 93106; [w]Institute of Biological and Environmental Sciences, University of Aberdeen, Aberdeen AB24 3FX, United Kingdom; [x]Nutrition and Translational Research in Metabolism, Maastricht University Medical Centre, Maastricht 6200 MD, The Netherlands; [y]Pennington Biomedical Research Center, Baton Rouge, LA 70808; [z]Department of Medicine, Duke University, Durham, NC 27710; [aa]Institute of Nutrition, Mahidol University, Nakhon Pathom 73170, Thailand; [bb]Division of Nutrition, St. John's Research Institute, Bangalore 560034, India; [cc]Department of Medicine and Medical Education, Feinberg School of Medicine, Northwestern University, Chicago, IL 60611; [dd]Health through Physical Activity, Lifestyle and Sport Research Centre, Division of Exercise Science and Sports Medicine, Faculty of Health Sciences, University of Cape Town, Cape Town 7700, South Africa; [ee]Department of Food and Nutrition and Sport Science, University of Gothenburg, Gothenburg 40530, Sweden; [ff]Imperial College London Diabetes Centre, PO Box 48338, Abu Dhabi, United Arab Emirates; [gg]Imperial College London, London SW7 2AZ, United Kingdom; [hh]Department of Medicine, Karolinska Institutet 141 83, Huddinge, Sweden; [ii]Department of Nutrition, Institute of Basic Medical Sciences, University of Oslo, Oslo 0317, Norway; [jj]Department of Nutrition and Public Health, Faculty of Health and Sport Sciences, University of Agder, Kristiansand 4630, Norway; [kk]Division of Public Health Sciences, Fred Hutchinson Cancer Center and School of Public Health, University of Washington, Seattle, WA 98109; [ll]Healthy Weight Hub, Helsinki University Central Hospital, Helsinki 00280, Finland; [mm]Department of Nutrition and Movement Sciences, Maastricht University, Maastricht 6200 MD, The Netherlands; [nn]College of Health Solutions, Arizona State University, Phoenix, AZ 85004; [oo]Biological Sciences and Anthropology, University of Southern California, Los Angeles, CA 90089; [pp]Centre for Cardiovascular Science, Queen's Medical Research Institute, University of Edinburgh, Edinburgh EH16 4TJ, United Kingdom; [qq]Department of Epidemiology, Harvard T.H. Chan School of Public Health, Harvard University, Boston, MA 02115; [rr]Geisel School of Medicine, Dartmouth College, Hanover, NH 03755; [ss]Department of Biobehavioral Health, Pennsylvania State University, University Park, PA 16802; [tt]Department of Anthropology, Pennsylvania State University, University Park, PA 16802; [uu]Division of Endocrinology, Diabetes and Clinical Nutrition, Oregon Health and Science University, Portland, OR 97239; [vv]Department of Anthropology, University of Oregon, Eugene, OR 97403; [ww]Institute of Nutrition and Food Technology, University of Chile, Santiago 7830490, Chile; [xx]Department of Anthropology, Baylor University, Waco, TX 76798; [yy]Oregon Health and Science University, Portland, OR 97239; [zz]Department of Anthropology, University of California, Los Angeles, CA 90095; [aaa]Department of Human Behavior, Ecology, and Culture, Max Planck Institute for Evolutionary Anthropology, Leipzig 04103, Germany; [bbb]Center for Energy Metabolism and Reproduction, Shenzhen Institutes of Advanced Technology, Chinese Academy of Sciences, Shenzhen, Guangdong 518055, China; [ccc]Nutritional and Health-Related Environmental Studies Section, Division of Human Health, International Atomic Energy Agency, Vienna A-1400, Austria; [ddd]Faculty of Health and Sport Sciences, University of Tsukuba, Ibaraki 305-8577, Japan; [eee]Biotech Center and Nutritional Sciences, University of Wisconsin, Madison, WI 53706; [fff]Department of Sports and Health Sciences, Graduate School of Biomedical Engineering, Tohoku University, Sendai, Miyagi 980-8579, Japan; [ggg]Department of Medicine and Science in Sports and Exercise, Graduate School of Medicine, Tohoku University, Sendai, Miyagi 980-8575, Japan; and [hhh]Duke Global Health Institute, Duke University, Durham, NC 27710

Author contributions: A.L. and H.P. designed research; A.M. and H.P. performed research; A.M., A.L., and H.P. analyzed data; A.M., A.L., L.A., K.B.-A., A.G.B., P.B., S.B., M.S.B., N.B., S.G.C., R.C., D.K.C., S.K.D., S.D., T.F., B.W.F., M. Gillingham, A.H.G., M. Gurven, C.H., A.J., P.T.K., K.P.K., W.E.K., W.K., R.K., R.F.K., E.V.L., W.R.L., N.L., C.K.M., A.C.M, M.L.N., K.H.P., G.P., R.L.P., S.B.R., D.A.R., E.R., L.R., R.M.R., E.B.R., S.R., A.Y.R., M.H.S., S.S., J.J.S., E.S., R.U., S.S.U., J.A.V., B. Wolfe, B. Wood, X.Z., A.J.M.-A., C.J.L., H.S., K.R.W., Y.Y., J.R.S., H.P., and I.D.D.C. contributed data; A.M., A.L., and H.P. wrote the paper with input from all authors; and A.M., A.L., L.R.D., U.E., M. Gurven, C.L.L., M.L., A.C.M., M.L.N., R.L.P., S.B.R., E.R., A.Y.R., E.S., B. Wolfe, H.S., K.R.W., W.W.W., Y.Y., J.R.S., and H.P. edited the paper.

1. J. D. Stanaway *et al.*, Global, regional, and national comparative risk assessment of 84 behavioural, environmental and occupational, and metabolic risks or clusters of risks for 195 countries and territories, 1990–2017: A systematic analysis for the Global Burden of Disease Study 2017. *Lancet* **392**, 1923–1994 (2018).
2. B. Caballero, The global epidemic of obesity: An overview. *Epidemiol. Rev.* **29**, 1–5 (2007).
3. J. Komlos, M. Brabec, The trend of mean BMI values of US adults, birth cohorts 1882–1986 indicates that the obesity epidemic began earlier than hitherto thought. *Am. J. Hum. Biol.* **22**, 631–638 (2010).
4. H. Pontzer, B. M. Wood, D. A. Raichlen, Hunter-gatherers as models in public health. *Obes. Rev.* **19**, 24–35 (2018).
5. L. M. Jaacks *et al.*, The obesity transition: Stages of the global epidemic. *Lancet Diabetes Endocrinol.* **7**, 231–240 (2019).
6. T. S. Church *et al.*, Trends over 5 decades in U.S. occupation-related physical activity and their associations with obesity. *PLoS ONE* **6**, e19657 (2011).
7. U. Ladabaum, A. Mannalithara, P. A. Myer, G. Singh, Obesity, abdominal obesity, physical activity, and caloric intake in US adults: 1988 to 2010. *Am. J. Med.* **127**, 717–727.e12 (2014).

8. K. E. Ebersole *et al.*, Energy expenditure and adiposity in Nigerian and African-American women. *Obesity* **16**, 2148–2154 (2008).
9. H. Pontzer *et al.*, Hunter-gatherer energetics and human obesity. *PLoS ONE* **7**, e40503 (2012).
10. V. Careau *et al.*, Energy compensation and adiposity in humans. *Curr. Biol.* **31**, 4659–4666.e2 (2021).
11. J. R. Speakman *et al.*, Total daily energy expenditure has declined over the past three decades due to declining basal expenditure, not reduced activity expenditure. *Nat. Metab.* **5**, 579–588 (2023).
12. J. R. Speakman, T. I. A. Sørensen, K. D. Hall, D. B. Allison, Unanswered questions about the causes of obesity. *Science* **381**, 944–946 (2023).
13. S. S. Urlacher *et al.*, Childhood daily energy expenditure does not decrease with market integration and is not related to adiposity in Amazonia. *J. Nutr.* **151**, 695–704 (2021).
14. L. R. Dugas *et al.*, Energy expenditure in adults living in developing compared with industrialized countries: A meta-analysis of doubly labeled water studies. *Am. J. Clin. Nutr.* **93**, 427–441 (2011).
15. R. Micha *et al.*, Global, regional and national consumption of major food groups in 1990 and 2010: A systematic analysis including 266 country-specific nutrition surveys worldwide. *BMJ Open* **5**, e008705 (2015).
16. B. A. Swinburn *et al.*, The global obesity pandemic: Shaped by global drivers and local environments. *Lancet* **378**, 804–814 (2011).
17. L. Orcholski *et al.*, Under-reporting of dietary energy intake in five populations of the African diaspora. *Br. J. Nutr.* **113**, 464–472 (2015).
18. United Nations Development Programme, *Human Development Report* (United Nations Development Programme, 2024).
19. H. Pontzer *et al.*, Daily energy expenditure through the human life course. *Science* **373**, 808–812 (2021).
20. R. Rimbach *et al.*, Total energy expenditure is repeatable in adults but not associated with short-term changes in body composition. *Nat. Commun.* **13**, 99 (2022).
21. M. D. Gurven *et al.*, High resting metabolic rate among Amazonian forager-horticulturalists experiencing high pathogen burden. *Am. J. Phys. Anthropol.* **161**, 414–425 (2016).
22. S. S. Urlacher *et al.*, Constraint and trade-offs regulate energy expenditure during childhood. *Sci. Adv.* **5**, eaax1065 (2019).
23. E. Tasali, K. Wroblewski, E. Kahn, J. Kilkus, D. A. Schoeller, Effect of sleep extension on objectively assessed energy intake among adults with overweight in real-life settings: A randomized clinical trial. *JAMA Intern. Med.* **182**, 365–374 (2022).
24. J. E. Blundell, K. Beaulieu, The complex pattern of the effects of prolonged frequent exercise on appetite control, and implications for obesity. *Appetite* **183**, 106482 (2023).
25. B. E. Corkey, Reactive oxygen species: Role in obesity and mitochondrial energy efficiency. *Philos. Trans. R. Soc. Lond. B, Biol. Sci.* **378**, 20220210 (2023).
26. J. Lund, Z. Gerhart-Hines, C. Clemmensen, Role of energy excretion in human body weight regulation. *Trends Endocrinol. Metab.* **31**, 705–708 (2020).
27. M. I. Friedman, T. I. A. Sørensen, G. Taubes, J. Lund, D. S. Ludwig, Trapped fat: Obesity pathogenesis as an intrinsic disorder in metabolic fuel partitioning. *Obes. Rev.* **25**, e13795 (2024).
28. H. Pontzer, B. M. Wood, Effects of evolution, ecology, and economy on human diet: Insights from hunter-gatherers and other small-scale societies. *Annu. Rev. Nutr.* **41**, 363–385 (2021).
29. M. J. Gibney, Ultra-processed foods: Definitions and policy issues. *Nutrition* **3**, nzy077 (2019).
30. S. J. Dicken, R. L. Batterham, The role of diet quality in mediating the association between ultra-processed food intake, obesity and health-related outcomes: A review of prospective cohort studies. *Nutrients* **14**, 23 (2022).
31. V. M. Valicente *et al.*, Ultraprocessed foods and obesity risk: A critical review of reported mechanisms. *Adv. Nutr.* **14**, 718–738 (2023).
32. K. D. Hall *et al.*, Ultra-processed diets cause excess calorie intake and weight gain: An inpatient randomized controlled trial of ad libitum food intake. *Cell Metab.* **30**, 67–77.e3 (2019).
33. M. Askari, J. Heshmati, H. Shahinfar, N. Tripathi, E. Daneshzad, Ultra-processed food and the risk of overweight and obesity: A systematic review and meta-analysis of observational studies. *Int. J. Obes.* **44**, 2080–2091 (2020).
34. K. D. Corbin *et al.*, Host-diet-gut microbiome interactions influence human energy balance: A randomized clinical trial. *Nat. Commun.* **14**, 3161 (2023).
35. F. C. Bull *et al.*, World Health Organization 2020 guidelines on physical activity and sedentary behaviour. *Br. J. Sports Med.* **54**, 1451–1462 (2020).
36. T. Strain *et al.*, National, regional, and global trends in insufficient physical activity among adults from 2000 to 2022: A pooled analysis of 507 population-based surveys with 5·7 million participants. *Lancet Glob. Health* **12**, e1232–e1243 (2024).
37. M. Naghavi *et al.*, Global burden of 288 causes of death and life expectancy decomposition in 204 countries and territories and 811 subnational locations, 1990–2021: A systematic analysis for the Global Burden of Disease Study 2021. *Lancet* **403**, 2100–2132 (2024).
38. Institute of Medicine (US), *Improving Food Safety Through a One Health Approach: Workshop Summary* (National Academies Press (US), 2012).
39. J. R. Speakman *et al.*, International Atomic Energy Agency. Doubly Labelled Water (DLW) Database. https://www.iaea.org/resources/hhc/nutrition/databases/double-labelled-water-dlw. Accessed 30 September 2023.
40. J. R. Speakman *et al.*, A standard calculation methodology for human doubly labeled water studies. *Cell Rep. Med.* **2**, 100203 (2021).
41. H. Kashiwazaki *et al.*, Year-round high physical activity levels in agropastoralists of Bolivian Andes: Results from repeated measurements of DLW method in peak and slack seasons of agricultural activities. *Am. J. Hum. Biol.* **21**, 337–345 (2009).
42. A. J. Sellers, D. Khovalyg, G. Plasqui, W. van Marken Lichtenbelt, High daily energy expenditure of Tuvan nomadic pastoralists living in an extreme cold environment. *Sci. Rep.* **12**, 20127 (2022).
43. A. McGrosky *et al.*, Total daily energy expenditure and elevated water turnover in a small-scale semi-nomadic pastoralist society from northern Kenya. *Ann. Hum. Biol.* **51**, 2310724 (2024).
44. K. R. Westerterp, Physical activity and physical activity induced energy expenditure in humans: Measurement, determinants, and effects. *Front. Physiol.* **4**, 90 (2013).
45. K. R. Westerterp, Diet induced thermogenesis. *Nutr. Metab. (Lond.)* **1**, 5 (2004).
46. K. R. Westerterp *et al.*, Physical activity and fat-free mass during growth and in later life. *Am. J. Clin. Nutr.* **114**, 1583–1589 (2021).
47. A. Luke *et al.*, Protocol for the modeling the epidemiologic transition study: A longitudinal observational study of energy balance and change in body weight, diabetes and cardiovascular disease risk. *BMC Public Health* **11**, 927 (2011).
48. R Core Team, *R: A Language and Environment for Statistical Computing* (2023).
49. D. B. Allison, F. Paultre, M. I. Goran, E. T. Poehlman, S. B. Heymsfield, Statistical considerations regarding the use of ratios to adjust data. *Int. J. Obes. Relat. Metab. Disord.* **19**, 644–652 (1995).
50. W. You, R. Henneberg, A. Saniotis, Y. Ge, M. Henneberg, Total meat intake is associated with life expectancy: A cross-sectional data analysis of 175 contemporary populations. *IJGM* **15**, 1833–1851 (2022).