METABOLISM

Daily energy expenditure through the human life course

Herman Pontzer[1,2]*†, Yosuke Yamada[3,4]*, Hiroyuki Sagayama[5]*, Philip N. Ainslie[6], Lene F. Andersen[7], Liam J. Anderson[6,8], Lenore Arab[9], Issaad Baddou[10], Kweku Bedu-Addo[11], Ellen E. Blaak[12], Stephane Blanc[13,14], Alberto G. Bonomi[15], Carlijn V. C. Bouten[12], Pascal Bovet[16], Maciej S. Buchowski[17], Nancy F. Butte[18], Stefan G. Camps[12], Graeme L. Close[6], Jamie A. Cooper[13], Richard Cooper[19], Sai Krupa Das[20], Lara R. Dugas[19], Ulf Ekelund[21], Sonja Entringer[22,23], Terrence Forrester[24], Barry W. Fudge[25], Annelies H Goris[12], Michael Gurven[26], Catherine Hambly[27], Asmaa El Hamdouchi[10], Marjije B. Hoos[12], Sumei Hu[28], Noorjehan Joonas[29], Annemiek M. Joosen[12], Peter Katzmarzyk[30], Kitty P. Kempen[12], Misaka Kimura[3], William E. Kraus[31], Robert F. Kushner[32], Estelle V. Lambert[33], William R. Leonard[34], Nader Lessan[35], Corby Martin[30], Anine C. Medin[7,36], Erwin P. Meijer[12], James C. Morehen[37,6], James P. Morton[6], Marian L. Neuhouser[38], Teresa A. Nicklas[18], Robert M. Ojiambo[39,40], Kirsi H. Pietiläinen[41], Yannis P. Pitsiladis[42], Jacob Plange-Rhule[43]‡, Guy Plasqui[44], Ross L. Prentice[38], Roberto A. Rabinovich[45], Susan B. Racette[46], David A. Raichlen[47], Eric Ravussin[30], Rebecca M. Reynolds[48], Susan B. Roberts[20], Albertine J. Schuit[49], Anders M. Sjödin[50], Eric Stice[51], Samuel S. Urlacher[52], Giulio Valenti[12,15], Ludo M. Van Etten[12], Edgar A. Van Mil[53], Jonathan C. K. Wells[54], George Wilson[6], Brian M. Wood[55,56], Jack Yanovski[57], Tsukasa Yoshida[4], Xueying Zhang[27,28], Alexia J. Murphy-Alford[58], Cornelia Loechl[58], Amy H. Luke[59]*, Jennifer Rood[30]*, Dale A. Schoeller[60]*, Klaas R. Westerterp[61]*, William W. Wong[18]*, John R. Speakman[62,27,28,63]*†, IAEA DLW Database Consortium§

Total daily energy expenditure ("total expenditure") reflects daily energy needs and is a critical variable in human health and physiology, but its trajectory over the life course is poorly studied. We analyzed a large, diverse database of total expenditure measured by the doubly labeled water method for males and females aged 8 days to 95 years. Total expenditure increased with fat-free mass in a power-law manner, with four distinct life stages. Fat-free mass–adjusted expenditure accelerates rapidly in neonates to ~50% above adult values at ~1 year; declines slowly to adult levels by ~20 years; remains stable in adulthood (20 to 60 years), even during pregnancy; then declines in older adults. These changes shed light on human development and aging and should help shape nutrition and health strategies across the life span.

All of life's essential tasks, from development and reproduction to maintenance and movement, require energy. Total daily energy expenditure (total expenditure; megajoules per day) is thus central to understanding both daily nutritional requirements and the body's investment among activities. Yet, we know surprisingly little about total expenditure in humans or how it changes over the life span. Most large (n > 1000 subjects) analyses of human energy expenditure have been limited to basal expenditure—the metabolic rate at rest (1), which accounts for only a portion (usually ~50 to 70%) of total expenditure—or have estimated total expenditure from basal expenditure and daily physical activity (2–5). Doubly labeled water studies provide measurements of total expenditure in free-living subjects but have been limited in sample size (n < 600 subjects), geographic and socioeconomic diversity, and/or age (6–9).

Body composition, size, and physical activity change over the life course, often in concert, making it difficult to parse the determinants of energy expenditure. Total and basal expenditures increase with age as children grow and mature (10, 11), but the relative effects of increasing physical activity and age-related changes in tissue-specific metabolic rates are unclear (12–16). Similarly, the decline in total expenditure beginning in older adults corresponds with declines in fat-free mass and physical activity but may also reflect age-related reductions in organ metabolism (9, 17–19).

We investigated the effects of age, body composition, and sex on total expenditure using a large (n = 6421 subjects; 64% female), diverse (n = 29 countries) database of doubly labeled water measurements for subjects aged 8 days to 95 years (20), calculating total expenditure from isotopic measurements by using a single, validated equation for all subjects (21). Basal expenditure, measured with indirect calorimetry, was available for n = 2008 subjects, and we augmented the dataset with additional published measures of basal expenditure in neonates and doubly labeled water–measured total expenditure in pregnant and postpartum women (supplementary materials, materials and methods, and table S1).

We found that both total and basal expenditure increased with fat-free mass in a power-law manner (Fig. 1, figs. S1 and S2, and table S1), requiring us to adjust for body size to isolate potential effects of age, sex, and other factors. Because of the power-law relation with size, the ratio of energy expenditure/mass does not adequately control for body size because the ratio trends lower for larger individuals (fig. S1). Instead, we used regression analysis to control for body size (22). We used a general linear model with log-transformed values of energy expenditure (total or basal), fat-free mass, and fat mass in adults 20 to 60 years (table S2) to calculate residual expenditures for each subject. We converted these residuals to "adjusted" expenditures for clarity in discussing age-related changes: 100% indicates an expenditure that matches the expected value given the subject's fat-free mass and fat mass, 120% indicates an expenditure 20% above expected, and so on. Using this approach, we also calculated the portion of adjusted total expenditure attributed to basal expenditure (Fig. 2D and materials and methods). Segmented regression analysis (materials and methods) revealed four distinct phases of adjusted total and basal expenditure over the life span.

The first phase is of neonates, up to 1 year of age. Neonates in the first month of life had size-adjusted energy expenditures similar to that of adults, with adjusted total expenditure of 99.0 ± 17.2% (n = 35 subjects) and adjusted basal expenditure of 78.1 ± 15.0% (n = 34 subjects) (Fig. 2). Both measures increased rapidly in the first year. In segmented regression analysis, adjusted total expenditure rose 84.7 ± 7.2% per year from birth to a break point at 0.7 years of age [95% confidence interval (CI): 0.6, 0.8]; a similar rise and break point were evident in adjusted basal expenditure (table S4). For subjects between 9 and 15 months of age, adjusted total and basal expenditures were nearly ~50% elevated compared with that of adults (Fig. 2).

The second phase is of juveniles, 1 to 20 years of age. Total and basal expenditure continued to increase with age throughout childhood and adolescence along with fat-free mass (Fig. 1), but size-adjusted expenditures steadily declined. Adjusted total expenditure declined at a rate of –2.8 ± 0.1% per year from 147.8 ± 22.6% for subjects 1 to 2 years of age to 102.7 ± 18.1% for subjects 20 to 25 years of age (tables S2 and S4). Segmented regression analysis identified a break point in adjusted total expenditure at 20.5 years (95% CI: 19.8, 21.2), after which it plateaued at adult levels (Fig. 2); a similar decline and break point were evident in adjusted basal expenditure (Fig. 2 and table S4). No pubertal increases in adjusted total or basal expenditure were evident among subjects 10 to 15 years of age (Fig. 2 and table S3). In multivariate regression for subjects 1 to 20 years of age, males had a higher total expenditure and adjusted total expenditure (tables S2 and S3), but sex had no detectable effect on the rate of decline in
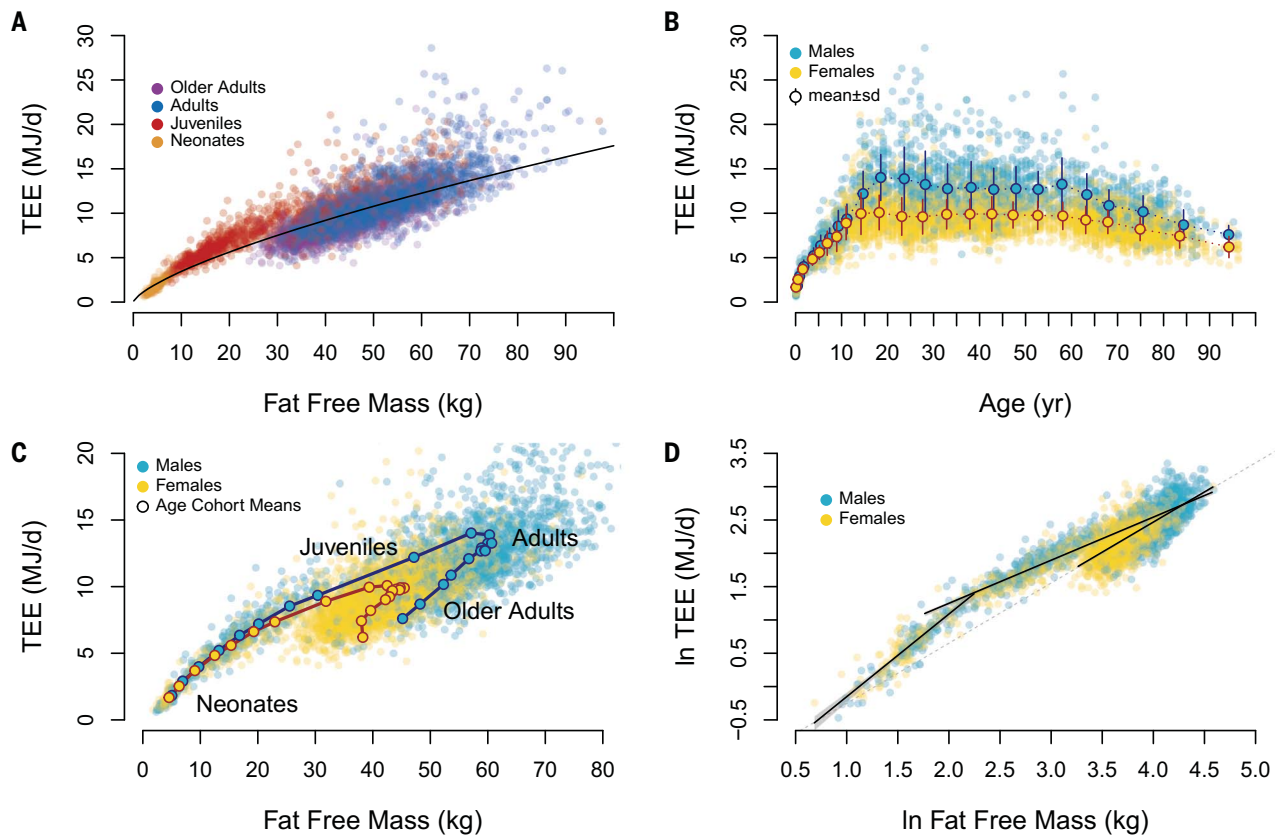
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Fig. 1. Total energy expenditure (TEE) through the human life course. (**A**) TEE increases with fat-free mass (FFM) in a power-law manner, but age groups cluster about the trend line differently. The black line indicates TEE = $0.677FFM^{0.708}$. Coefficient of determination (R^2) = 0.83; $P < 0.0001$ (table S2). (**B**) Total expenditure rises in childhood, is stable through adulthood, and declines in older adults. Means ± SD for age-sex cohorts are shown. (**C**) Age-sex cohort means show a distinct progression of total expenditure and fat-free mass over the life course. (**D**) Neonates, juveniles, and adults exhibit distinct relationships between fat-free mass and expenditure. The dashed line, extrapolated from the regression for adults, approximates the regression used to calculate adjusted total expenditure.

[1]Department of Evolutionary Anthropology, Duke University, Durham, NC, USA. [2]Duke Global Health Institute, Duke University, Durham, NC, USA. [3]Institute for Active Health, Kyoto University of Advanced Science, Kyoto, Japan. [4]National Institute of Health and Nutrition, National Institutes of Biomedical Innovation, Health and Nutrition, Tokyo, Japan. [5]Faculty of Health and Sport Sciences, University of Tsukuba, Ibaraki, Japan. [6]Research Institute for Sport and Exercise Sciences, Liverpool John Moores University, Liverpool, UK. [7]Department of Nutrition, Institute of Basic Medical Sciences, University of Oslo, 0317 Oslo, Norway. [8]Crewe Alexandra Football Club, Crewe, UK. [9]David Geffen School of Medicine, University of California, Los Angeles. [10]Unité Mixte de Recherche en Nutrition et Alimentation, CNESTEN–Université Ibn Tofail URAC39, Regional Designated Center of Nutrition Associated with AFRA/IAEA, Rabat, Morocco. [11]Department of Physiology, Kwame Nkrumah University of Science and Technology, Kumasi, Ghana. [12]Maastricht University, Maastricht, Netherlands. [13]Department of Nutritional Sciences, University of Wisconsin, Madison, WI, USA. [14]Institut Pluridisciplinaire Hubert Curien, CNRS Université de Strasbourg, UMR7178, France. [15]Phillips Research, Eindoven, Netherlands. [16]Institute of Social and Preventive Medicine, Lausanne University Hospital, Lausanne, Switzerland. [17]Division of Gastroenterology, Hepatology, and Nutritiion, Department of Medicine, Vanderbilt University, Nashville, TN, USA [18]Department of Pediatrics, Baylor College of Medicine, USDA/ARS Children's Nutrition Research Center, Houston, TX, USA. [19]Department of Public Health Sciences, Parkinson School of Health Sciences and Public Health, Loyola University, Maywood, IL, USA. [20]Friedman School of Nutrition Science and Policy, Tufts University, Boston, MA, USA. [21]Department of Sport Medicine, Norwegian School of Sport Sciences, Oslo, Norway. [22]Charité–Universitätsmedizin Berlin, corporate member of Freie Universität Berlin, Humboldt-Universität zu Berlin, and Berlin Institute of Health (BIH), Institute of Medical Psychology, Berlin, Germany. [23]School of Medicine, University of California Irvine, Irvine, CA, USA. [24]Solutions for Developing Countries, University of the West Indies, Mona, Kingston, Jamaica. [25]Department of Biomedical and Life Sciences, University of Glasgow, Glasgow, UK. [26]Department of Anthropology, University of California Santa Barbara, Santa Barbara, CA, USA. [27]Institute of Biological and Environmental Sciences, University of Aberdeen, Aberdeen, UK. [28]State Key Laboratory of Molecular developmental Biology, Institute of Genetics and Developmental Biology, Chinese Academy of Sciences, Beijing, China. [29]Central Health Laboratory, Ministry of Health and Wellness, Candos, Mauritius. [30]Pennington Biomedical Research Center, Baton Rouge, LA, USA. [31]Department of Medicine, Duke University, Durham, NC, USA. [32]Feinberg School of Medicine, Northwestern University, Chicago, IL, USA. [33]Health through Physical Activity, Lifestyle and Sport Research Centre (HPALS), Division of Exercise Science and Sports Medicine (ESSM), FIMS International Collaborating Centre of Sports Medicine, Department of Human Biology, Faculty of Health Sciences, University of Cape Town, Cape Town, South Africa. [34]Department of Anthropology, Northwestern University, Evanston, IL, USA. [35]Imperial College London Diabetes Centre, Abu Dhabi, United Arab Emirates and Imperial College London, London, UK. [36]Department of Nutrition and Public Health, Faculty of Health and Sport Sciences, University of Agder, 4630 Kristiansand, Norway. [37]The FA Group, Burton-Upon-Trent, Staffordshire, UK. [38]Division of Public Health Sciences, Fred Hutchinson Cancer Research Center and School of Public Health, University of Washington, Seattle, WA, USA. [39]Kenya School of Medicine, Moi University, Eldoret, Kenya. [40]Rwanda Division of Basic Sciences, University of Global Health Equity, Rwanda. [41]Helsinki University Central Hospital, Helsinki, Finland. [42]School of Sport and Service Management, University of Brighton, Eastbourne, UK. [43]Department of Physiology, Kwame Nkrumah University of Science and Technology, Kumasi, Ghana. [44]Department of Nutrition and Movement Sciences, Maastricht University, Maastricht, Netherlands. [45]The Queen's Medical Research Institute, University of Edinburgh, Edinburgh, UK. [46]Program in Physical Therapy and Department of Medicine, Washington University School of Medicine, St. Louis, MO, USA. [47]Biological Sciences and Anthropology, University of Southern California, CA, USA. [48]Centre for Cardiovascular Sciences, Queen's Medical Research Institute, University of Edinburgh, Edinburgh, UK. [49]School of Social and Behavioral Sciences, University of Tilburg, Tilburg, Netherlands. [50]Department of Nutrition, Exercise and Sports, Copenhagen University, Copenhagen, Denmark. [51]Department of Psychiatry and Behavioral Sciences, Stanford University, Stanford CA, USA. [52]Department of Anthropology, Baylor University, Waco, TX, USA. [53]Maastricht University, Maastricht and Lifestyle Medicine Center for Children, Jeroen Bosch Hospital, Hertogenbosch, Netherlands. [54]Population, Policy, and Practice Research and Teaching Department, UCL Great Ormond Street Institute of Child Health, London, UK. [55]Department of Anthropology, University of California Los Angeles, Los Angeles, CA, USA. [56]Department of Human Behavior, Ecology, and Culture, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany. [57]Growth and Obesity, Division of Intramural Research, NIH, Bethesda, MD, USA. [58]Nutritional and Health Related Environmental Studies Section, Division of Human Health, International Atomic Energy Agency, Vienna, Austria. [59]Division of Epidemiology, Department of Public Health Sciences, Loyola University School of Medicine, Maywood, IL, USA. [60]Biotech Center and Nutritional Sciences University of Wisconsin, Madison, WI, USA. [61]Nutrition and Translational Research in Metabolism (NUTRIM), Maastricht University Medical Centre, Maastricht, Netherlands. [62]Center for Energy Metabolism and Reproduction, Shenzhen Institutes of Advanced Technology, Chinese Academy of Sciences, Shenzhen, China. [63]CAS Center of Excellence in Animal Evolution and Genetics, Kunming, China.
*Corresponding author. Email: herman.pontzer@duke.edu (H.P.); j.speakman@abdn.ac.uk (J.R.S.); yyamada831@gmail.com (Y.Y.); sagayama.hiroyuki.ka@u.tsukuba.ac.jp (H.S.); aluke@luc.edu (A.H.L.); jennifer.rood@pbrc.edu (J.R.); dschoell@nutrisci.wisc.edu (D.A.S.); k.westerterp@maastrichtuniversity.nl (K.R.W.); wwong@bcm.edu (W.W.W.)
†These authors contributed equally to this work. ‡Deceased. §IAEA DLW Database Consortium members are listed in the supplementary materials.
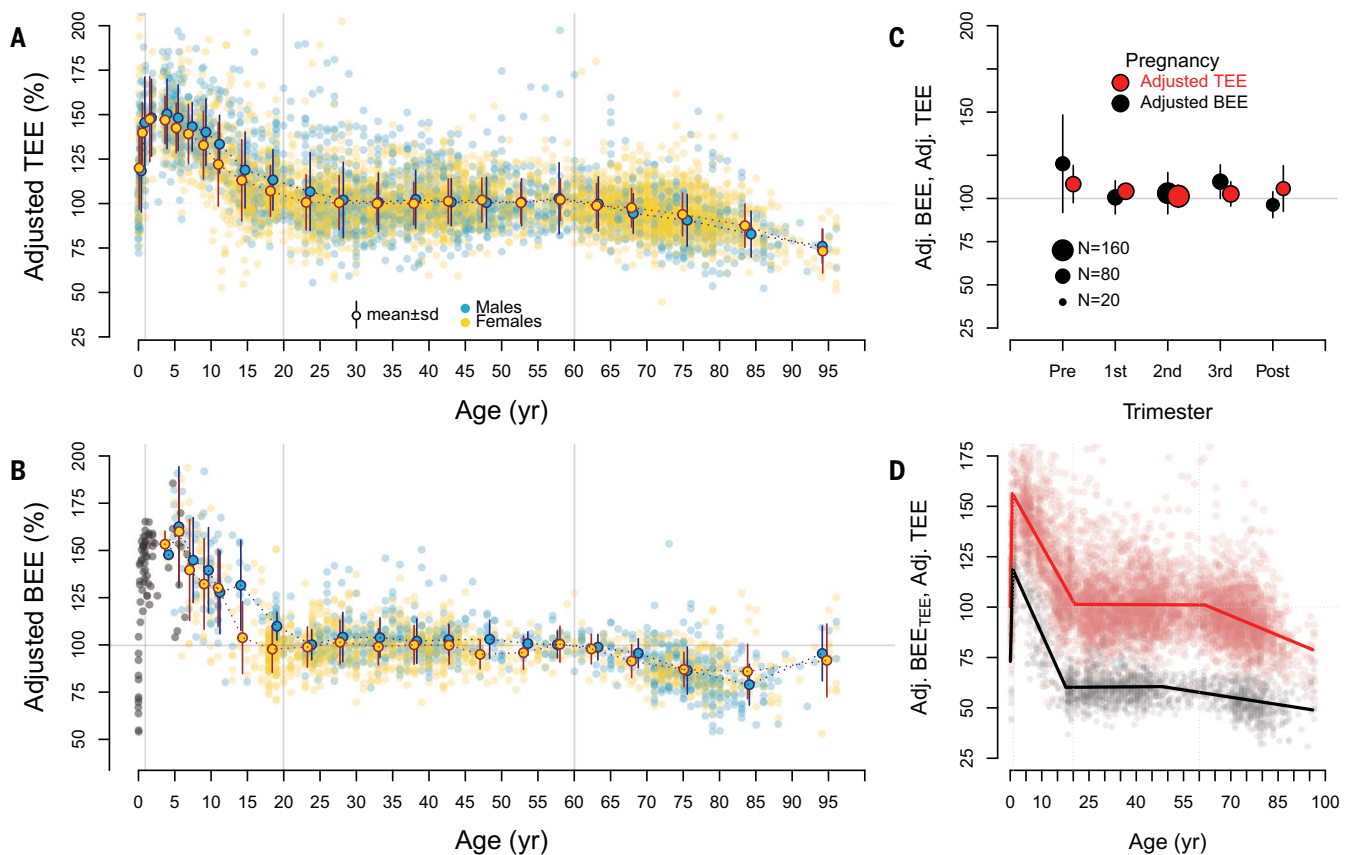
Fig. 2. Fat-free mass– and fat mass–adjusted expenditures over the life course. Individual subjects and age-sex cohort mean ± SD are shown. For both (**A**) total expenditure (adjusted TEE) and (**B**) basal expenditure (adjusted BEE), adjusted expenditures begin near adult levels (~100%) but quickly climb to ~150% in the first year. Adjusted expenditures decline to adult levels at ~20 years of age then decline again in older adults. Basal expenditures for infants and children not in the DLW Database are shown in gray. (**C**) Pregnant mothers exhibit adjusted total and basal expenditures similar to those of nonreproducing adults (Pre, before pregnancy; Post, 27 weeks postpartum). (**D**) Segmented regression analysis of adjusted total (red) and adjusted basal expenditure (black) (calculated as a portion of total, Adj. BEE_{TEE}) indicates a peak at ~1 year of age, adult levels at ~20 years of age, and decline at ~60 years of age.

adjusted total expenditure with age (sex:age interaction, $P = 0.30$).

The third phase is adulthood, from 20 to 60 years of age. Total and basal expenditure and fat-free mass were all stable from ages 20 to 60 years (Figs. 1 and 2 and tables S1 and S2). Sex had no effect on total expenditure in multivariate models with fat-free mass and fat mass, nor in analyses of adjusted total expenditure (tables S2 and S4). Adjusted total and basal expenditures were stable even during pregnancy; the elevation in unadjusted expenditures matched those expected from the gain in mothers' fat-free mass and fat mass (Fig. 2C). Segmented regression analysis identified a break point at 63.0 years of age (95% CI: 60.1, 65.9), after which adjusted total expenditure begins to decline. This break point was somewhat earlier for adjusted basal expenditure (46.5, 95% CI: 40.6, 52.4), but the relatively small number of basal measures for 45 to 65 years of age (Fig. 2D) reduces our precision in determining this break point.

The fourth phase is of older adults, >60 years of age. At ~60 years of age, total and basal expenditure begin to decline, along with fat-free mass and fat mass (Fig. 1, fig. S3, and table S1). Declines in expenditure are not only a function of reduced fat-free mass and fat mass, however. Adjusted total expenditure declined by –0.7 ± 0.1% per year, and adjusted basal expendiure fell at a similar rate (Fig. 2, fig. S3, supplementary text S1, and table S4). For subjects 90+ years of age, adjusted total expenditure was ~26% below that of middle-aged adults.

Our analyses provide empirical measures and predictive equations for total and basal expenditure from infancy to old age (tables S1 and S2) and bring to light major metabolic changes across the life course. To begin, we can infer fetal metabolic rates from maternal measures during pregnancy: If body size–adjusted expenditures were elevated in the fetus, then adjusted expendiures for pregnant mothers—particularly late in pregnancy, when the fetus accounts for a substantial portion of a

mother's weight—would be likewise elevated. Instead, the stability of adjusted total and basal expenditures at ~100% during pregnancy (Fig. 2B) indicates that the growing fetus maintains a fat-free mass– and fat mass–adjusted metabolic rate similar to that of adults, which is consistent with adjusted expenditures of neonates (both ~100%) (Fig. 2) in the first weeks after birth. Total and basal expenditures, both absolute and size-adjusted values, then accelerate rapidly over the first year. This early period of metabolic acceleration corresponds to a critical period in early development in which growth often falters in nutritionally stressed populations (23). Increasing energy demands could be a contributing factor.

After rapid acceleration in total and basal expenditure during the first year, adjusted expenditures progressively decline thereafter, reaching adult levels at ~20 years of age. Elevated adjusted expenditures in this life stage may reflect the metabolic demands

Fig. 3. Modeling the contribution of physical activity and tissue-specific metabolism to daily expenditures. (**A**) Observed total expenditure (TEE; red), basal expenditure (BEE; black), and activity expenditure (AEE; gray) (table S1) show age-related variation with respect to fat-free mass (Fig. 1C) that is also evident in adjusted values (Fig. 2D and table S3). (**B**) These age effects do not emerge in models that assume constant physical activity (PA; green) and tissue-specific metabolic rate (TM; black) across the life course. (**C**) When physical activity and tissue-specific metabolism follow the life course trajectories evident from accelerometry and adjusted basal expenditure, respectively, model output is similar to observed expenditures.
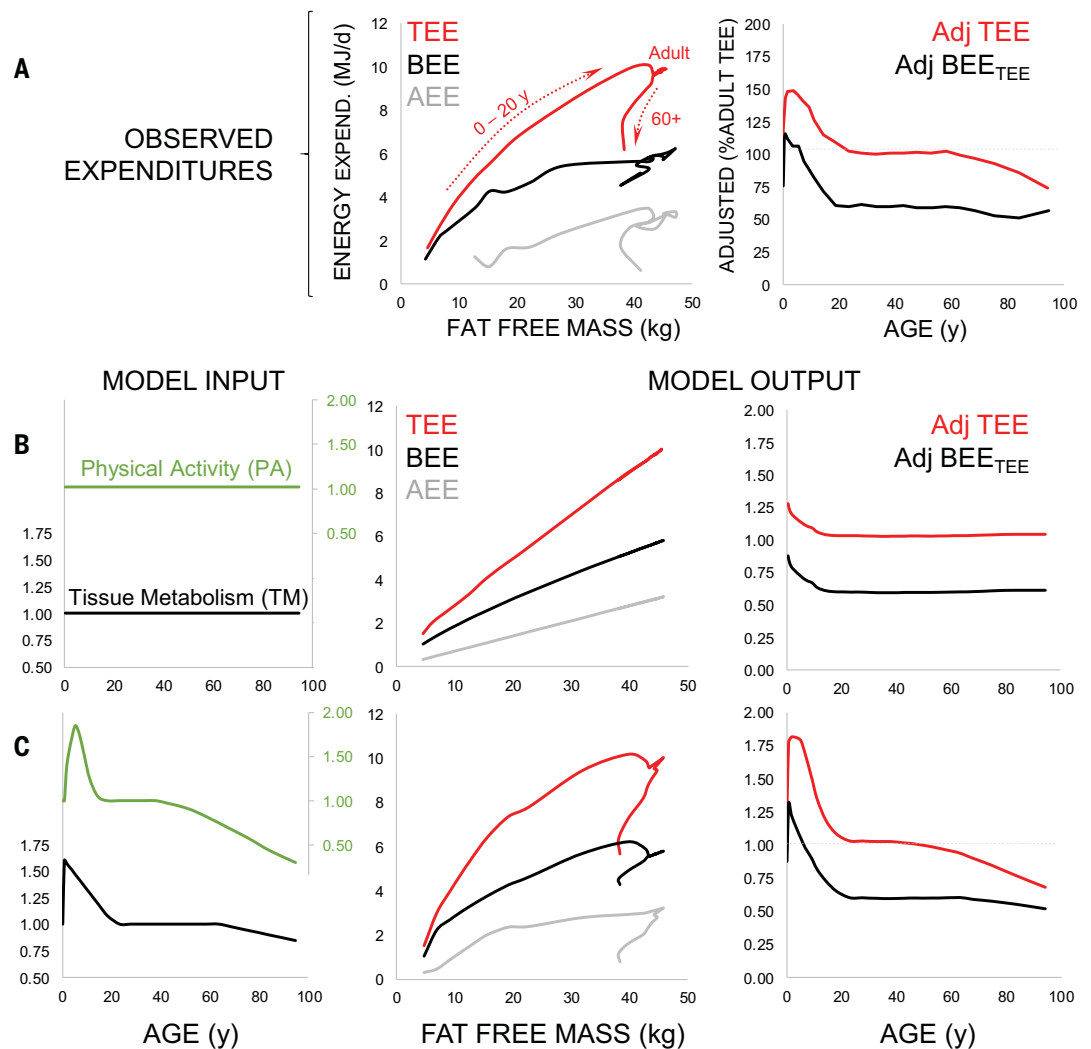
of growth and development. Adult expenditures, adjusted for body size and composition, are remarkably stable, even during pregnancy and postpartum. Declining metabolic rates in older adults could increase the risk of weight gain. However, neither fat mass nor percentage increased in this period (fig. S3), which is consistent with the hypothesis that energy intake is coupled to expenditure (*24*).

Following previous studies (*15, 16, 19, 25, 26*), we calculated the effect of organ size on basal expenditure over the life span (materials and methods). Organs with a high tissue-specific metabolic rate, particularly the brain and liver, account for a greater proportion of fat-free mass in young individuals. Thus, organ-based basal expenditure, estimated from organ size and tissue-specific metabolic rate, follows a power-law relationship with fat-free mass that is roughly consistent with observed basal expenditures (materials and methods, and fig. S6). Still, observed basal expenditure exceeded organ-based estimates

by ~30% in early life (1 to 20 years of age) and was ~20% lower than organ-based estimates in subjects over 60 years of age (fig. S6), which is consistent with studies indicating that tissue-specific metabolic rates are elevated in juveniles (*15, 16*) and reduced in older adults (*19, 25, 26*).

We investigated the contributions of daily physical activity and changes in tissue-specific metabolic rate to total and basal expenditure using a simple model with two components: activity and basal expenditure (Fig. 3 and materials and methods). Activity expenditure was modeled as a function of physical activity and body mass, assuming that activity costs are proportional to weight, and could either remain constant over the life span or follow the trajectory of daily physical activity measured with accelerometry, peaking at 5 to 10 years of age and declining thereafter (Fig. 3) (*12, 17, 18*). Similarly, basal expenditure was modeled as a power function of fat-free mass (consistent with organ-based basal expenditure estimates) (materials and methods) multiplied by a "tissue-

specific metabolism" term, which could either remain constant at adult levels across the life span or follow the trajectory observed in adjusted basal expenditure (Fig. 2). For each scenario, total expenditure was modeled as the sum of activity and basal expenditure (materials and methods).

Models that hold physical activity or tissue-specific metabolic rates constant over the life span do not reproduce the observed patterns of age-related change in absolute or adjusted measures of total or basal expenditure (Fig. 3). Only when age-related changes in physical activity and tissue-specific metabolism are included does model output match observed expenditures, indicating that variation in both physical activity and tissue-specific metabolism contribute to total expenditure and its components across the life span. Elevated tissue-specific metabolism in early life may be related to growth or development (*15, 16*). Conversely, reduced expenditures in later life may reflect a decline in organ-level metabolism (*25–27*).

Metabolic models of life history commonly assume continuity in tissue-specific metabolism over the life course, with metabolic rates increasing in a stable, power-law manner (28, 29). Measures of humans here challenge this view, with deviations from the power-law relationships for total and basal expenditure in childhood and old age (Figs. 1 and 2). These changes present a potential target for investigating the kinetics of disease, drug activity, and healing, processes that are intimately related to metabolic rate. Further, interindividual variation in expenditure is considerable even when controlling for fat-free mass, fat mass, sex, and age (Figs. 1 and 2 and table S2). Elucidating the processes underlying metabolic changes across the life course and variation among individuals may help reveal the roles of metabolic variation in health and disease.

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A lifetime of change

Measurements of total and basal energy in a large cohort of subjects at ages spanning from before birth to old age document distinct changes that occur during a human lifetime. Pontzer *et al.* report that energy expenditure (adjusted for weight) in neonates was like that of adults but increased substantially in the first year of life (see the Perspective by Rhoads and Anderson). It then gradually declined until young individuals reached adult characteristics, which were maintained from age 20 to 60 years. Older individuals showed reduced energy expenditure. Tissue metabolism thus appears not to be constant but rather to undergo transitions at critical junctures.

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