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Review

Hunter-gatherers as models in public health

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Summary

Hunter-gatherer populations are remarkable for their excellent metabolic and cardiovascular health and thus are often used as models in public health, in an effort to understand the root, evolutionary causes of non-communicable diseases. Here, we review recent work on health, activity, energetics and diet among hunter-gatherers and other small-scale societies (e.g. subsistence farmers, horticulturalists and pastoralists), as well as recent fossil and archaeological discoveries, to provide a more comprehensive perspective on lifestyle and health in these populations. We supplement these analyses with new data from the Hadza, a hunter-gatherer population in northern Tanzania. Longevity among small-scale populations approaches that of industrialized populations, and metabolic and cardiovascular disease are rare. Obesity prevalence is very low ($<5\%$), and mean body fat percentage is modest (women: 24–28%, men: 9–18%). Activity levels are high, exceeding 100 min d^{-1} of moderate and vigorous physical activity, but daily energy expenditures are similar to industrialized populations. Diets in hunter-gatherer and other small-scale societies tend to be less energy dense and richer in fibre and micronutrients than modern diets but are not invariably low carbohydrate as sometimes argued. A more integrative understanding of hunter-gatherer health and lifestyle, including elements beyond diet and activity, will improve public health efforts in industrialized populations.

Keywords: Diet, longevity, obesity, physical activity.

> *The poets tell us it was gold and silver, but the philosophers assure us it was iron and corn, which first civilized man, and ruined human-kind*. Rousseau, 1755 (1)

Introduction

Life was better in the past is a foundational and reoccurring idea in Western thought. Origin stories, from the lost Garden of Eden in Genesis to the Golden Age of ancient Greece, describe a utopian past where humans lived in harmony with nature and were healthy and well nourished. Rousseau's ruminations on human origins, the Noble Savage of Enlightenment philosophy and Marx and Engels' nostalgic descriptions of early farming communities all paint pictures of healthful idyll prior to the corruption wrought by progress and industrialization (1).

Over the past 150 years, evolutionary anthropology, armed with an ever expanding fossil and ethnographic record of human evolution and diversity, has enabled us to move beyond mere speculation and to an evidence-based understanding of our species' past. Genetic and fossil evidence shows our hominin lineage diverged from our sister lineage, *Pan* (chimpanzees and bonobos), approximately 6–8 Ma (2). The hominin lineage is diverse and speciose, with dozens of species recognized in the fossil record, often living concurrently, all of them except ours now extinct. Roughly 2 Ma, we see the early beginnings of a suite of developments that mark the emergence of our genus, *Homo*: increased brain and body size, stone tools and an increasing proportion of meat in the diet, and expansion across Africa and Eurasia into a broad range of ecological zones (2). The reliance on a mix of wild (undomesticated) animal and plant foods defines the hunter-gatherer lifestyle and helps explain the adaptive suite of changes marking the emergence of our genus. Our species, *Homo sapiens*, emerged in Africa ~300,000 years ago (2), one of several species of our hunter-gatherer genus.

As epidemiology developed through the 20th century alongside a growing understanding of our species' evolution, it became common in public health to draw on our hunter-gatherer past to explain the rise of non-communicable diseases (diabetes, obesity, cancer and heart disease) in the developed world. By the 1980s and 1990s, this work had broadened into a focus on 'diseases of civilization' within a larger field of evolutionary medicine (3). The idea that modern, industrialized environments depart radically from the environments in which humans evolved and that these recent changes lead to disease is now well established and pervasive in public health. For example, the World Health Organization (WHO) (4) states that obesity is caused in part by 'an increase in physical inactivity due to the increasingly sedentary nature of many forms of work, changing modes of transportation, and increasing urbanization'.

There can be little doubt that an evolutionary perspective is important in understanding and mitigating disease (3). However, an evolutionary perspective is only as good as our understanding of the past. Without an accurate account of past diets, activity levels, disease profiles and other relevant characteristics, we will likely draw the wrong conclusions in diagnosing the root, evolutionary causes of 'diseases of civilization'. Notably, much of the foundational work in this area developed without detailed, quantitative measures of diet, activity or energetics in living hunter-gatherer or subsistence farming populations, much less those from the distant past. Can we be confident that conceptions of past employed in public health are not romanticized caricatures of some lost Eden?

Fieldwork among small-scale societies over the past few decades, as well as recent fossil discoveries, has greatly improved our understanding of our shared evolutionary past. Here, we review these studies, with a focus on health, physical activity, energy expenditure and diet. To supplement published data, we draw on previously unpublished measurements from our work with the Hadza, a hunter-gatherer population in northern Tanzania (5). We then synthesize what these data can tell us about preventing obesity and metabolic disease in industrialized populations.

Ethics statement

The previously unpublished data from the Hadza population discussed below were collected during studies of health and energy expenditure between 2009 and 2015 (6,7). Participants provided informed consent prior to participation. For participants younger than 18 years, parents also provided consent. Protocols were approved by US universities (Yale University, University Arizona, Washington University St. Louis and Hunter College) and Tanzanian institutions (National Institute of Medical Research, Commission for Science and Technology and local governments) prior to data collection.

Health

Lifespan

Due largely to high infant mortality from infectious disease, the expected lifespan at birth for hunter-gatherer populations is lower (typically 30s–40s) than developed countries today (8). A common misinterpretation of this observation is to assume that few hunter-gatherers (either today or in the past) live to older ages. If this were true, the near absence of chronic diseases in small-scale populations could be explained simply by a lack of adults living long enough to develop them. Further, if people in small-scale populations inevitably die young, they might not be useful models for public health.

In fact, demographic analyses of small-scale populations show that adult survivorship is similar in some ways to industrialized societies, with adults regularly living into their 60s and 70s and even beyond (5,8,9). Gurven and Kaplan (8), in a review of hunter-gatherer and subsistence farmer mortality data across 12 populations, report that ~60% of newborns in these populations survive to age 15 and ~40% to age 45. Those who survive to age 45 can expect to live another ~20 years (8). Indeed, the modal age at death for hunter-gatherer populations examined by Gurven and Kaplan (8) is ~72 years (range: 68–78 years), near the value for the US population (85 years) in 2002. Nevertheless, in wealthier nations, improvements in hygiene, diet and health care over the last hundred years have added several decades to life expectancies at birth, relative to those observed in hunter-gatherers (8).

Old age, like that recorded for recent hunter-gatherers, is not a recent phenomenon. Analysis of fossil evidence suggests the proportion of adults surviving to 40+ years has been stable since at least the Upper Palaeolithic, approximately 50,000 years ago (10). Comparison of mortality curves with chimpanzees indicates that humans have evolved much greater adult survivorship (9), but that in favourable ecological contexts, with lowered predation and increased food availability, chimpanzee life expectancy at birth can approach that of human hunter-gatherers (11). High rates of survival into the 60s, 70s and beyond are hypothesized to be an evolutionarily derived feature of human life history, driven by selection for grandparental investment in their grandchildren (9). Grandparents provide food and care to children, relieving mothers of some of the time and energy cost that they would otherwise bear. In hunter-gatherer and other small-scale populations, the presence of grandparents, particularly grandmothers, improves grandchild growth and survivorship (5).

Causes of death

Cause of death is notoriously difficult to ascertain for hunter-gatherers and other populations without regular access to hospitals with trained medical specialists. The leading cause of death across small-scale populations is acute infection (5,8). Gurven and Kaplan (8) report that ~70% of deaths are caused by acute illness (mostly infectious and gastrointestinal disease) and another ~20% by trauma, including accidents and violence. These ratios are fairly consistent across the lifespan, although total mortality rate is highest for young children (8). The percentage of deaths from chronic, non-communicable diseases common in developed countries (e.g. heart disease, metabolic disease and cancers) is very low in small-scale populations, <10% of deaths even for individuals over 60 years old (8).

Obesity and metabolic disease

As expected for populations with high levels of physical activity and limited access to processed, highly calorific foods, obesity and metabolic disease are rare among hunter-gatherers and subsistence farmers. Walker and colleagues (12) compiled body size and life history data for more than 20 small-scales societies. They report mean ± SD body mass indices (BMI) of 21.7 ± 2.9 for $n = 21$ adult female cohorts and 22.2 ± 2.7 for $n = 20$ male cohorts, mid-range within the WHO category for 'normal weight' (BMI: 18.5–24.9; WHO (4)). A paired *t*-test of male and female cohorts revealed no difference in mean BMI ($p = 0.17$).

Looking within the Hadza hunter-gatherer population, we find little evidence of overweight or obesity. BMI for both men (20.0 ± 1.7, $n = 84$) and women (20.3 ± 2.4, $n = 108$) 20 to 81 years remains essentially constant throughout adulthood and similar between sexes (Fig. 1). Fewer than 2% of Hadza adults qualify as overweight ($25 \le \text{BMI} < 30.0$). Of 192 Hadza adults in our sample, two would be classified as 'overweight', with BMI of 25.9 and 25.3, and one as 'obese' ($\text{BMI} \ge 30.0$) with a BMI of 30.1. Body composition changes markedly for women in their teenage years. Body fat percentage, as assessed via skin-folds, is similar for male and female children ~10 years old but increases thereafter for females, plateauing at 24.2 ± 5.8% for women. Men's body fat percentage is considerably lower, 8.6 ± 3.8% among adults ≥20 years (Fig. 1).

Other small-scale societies also have low prevalence of obesity. Gurven and colleagues (13) report BMI and body fat among Tsimane women (24.7 ± 3.9, 26.5 ± 7.4%, $n = 651$ age groups combined) and men (23.8 ± 2.9, 17.6 ± 5.6%, $n = 649$, ages combined) only marginally greater than among the Hadza. Yet despite modest body fat percentages, Tsimane adults exhibit obesity rates of 4.6% (women) and 1.2% (men), and many more qualify as overweight (women: 21.1%; men: 15.0%) using standard BMI criteria (14). Similarly, rural Shuar, hunter-gatherer/farmers in the rainforest of Ecuador (15), have mean BMI near 25 (women: 24.2 ± 2.5; men: 24.8 ± 3.1), indicating a considerable proportion would qualify as overweight, yet body fat is low (women: 28.8 ± 4.5%; men: 14.7 ± 4.8%). Bassett and colleagues (16) found similar BMI and body fat percentages among traditional Old Order Amish (women: 23.8 ± 3.9 BMI, 25.3 ± 6.7%; men: 23.4 ± 2.5, 9.4 ± 4.3%) who farm without machine assistance. As with the Shuar and Tsimane, few Old Order Amish in that study (16) were obese (women: 9%; men: 0%) but a considerable number qualified as overweight (women: 27%; men: 25%) despite their low body fat percentages. Thus, BMI may overestimate adiposity among some small-scale societies, presumably due to their relatively greater muscle mass.

Non-insulin dependent (type 2) diabetes is so rare among small-scale populations that it is difficult to find reports of its prevalence in these groups. Eaton and colleagues (3) compiled prevalence data from 11 populations of hunter-gatherers, subsistence farmers and pastoralists and found, on average, 1% prevalence reported (range: 0.0–2.0%). Our limited assessments among the Hadza ($n = 20$ adults) comport with this low prevalence; we have not encountered fasted blood glucose levels above 85 mg dL^{-1} (Table 1). Among the Tsimane (17) glucose levels are also low, with <1% of adults showing elevated morning fasted glucose levels (>126 mg dL^{-1} criterion). Fasted glucose levels among rural Shuar men (73.6 ± 13.2, $n = 32$) and women (82.1 ± 21.2 mg dL^{-1}, $n = 49$) indicate similarly low prevalence of adults with clinically elevated glucose levels (15).

Fossils do not preserve signals of adiposity, but the low prevalence of obesity among hunter-gatherers today and in the recent past suggest excess body fat was rare in our evolutionary history. Nonetheless, there is some evidence from the archaeological record that obesity was not unheard of in the deep past. Carved 'Venus' figurines recovered from Upper Palaeolithic sites up to 35,000 years old often depict overweight and obese women (18). While the cultural meaning of these figurines is the focus of much unresolved debate, it is notable that the pattern of fat deposition (abdomen, thighs and buttocks (18)) matches that observed in real-life cases of obesity. This accuracy suggests that the makers of these figurines had observed overweight women, and that, by extension, overweight and obesity were known (although most likely rare) in the Upper Palaeolithic prior to farming and perhaps even earlier.

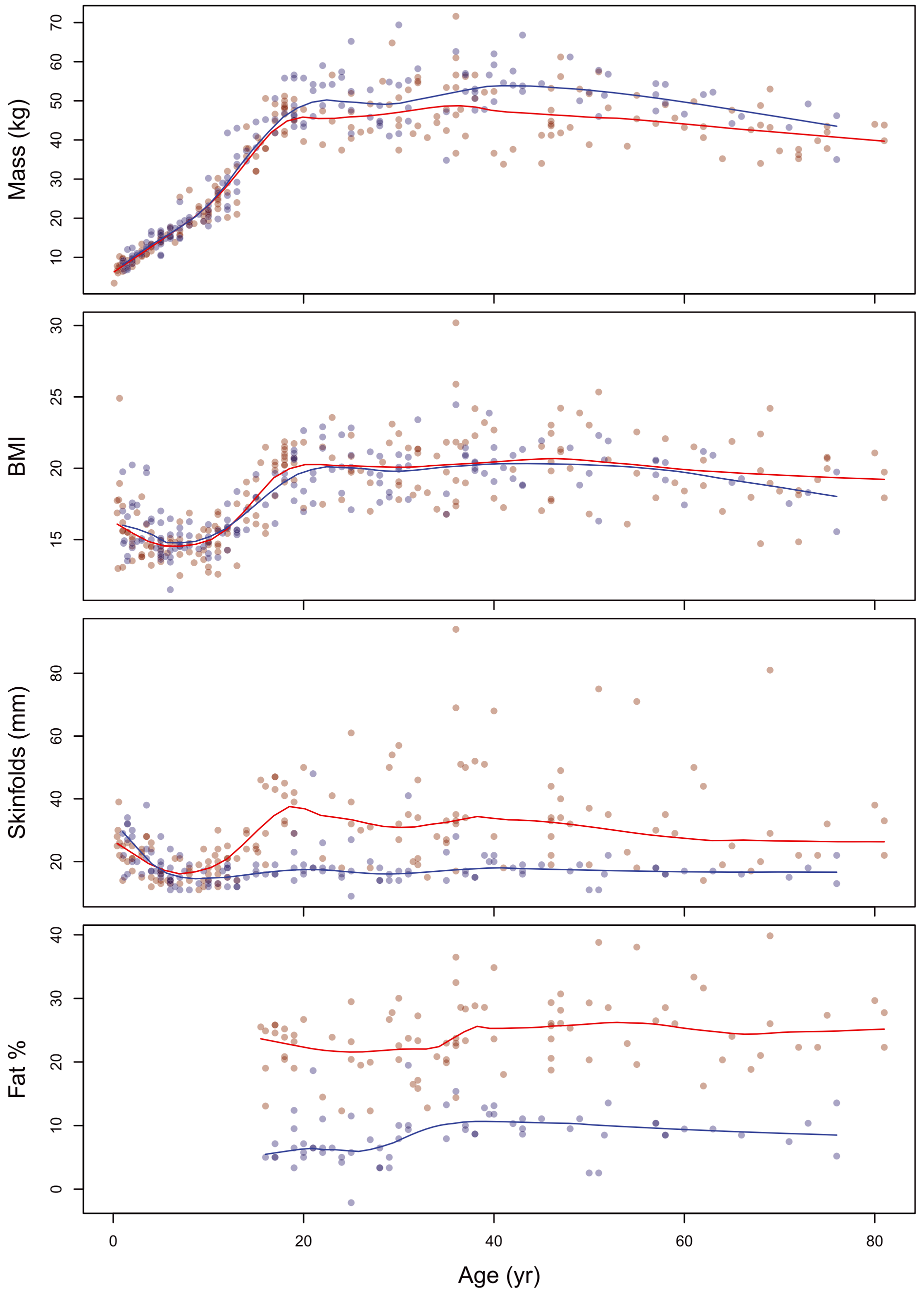

Figure 1 Hadza body size and composition across the lifespan. Red: female (*n* = 202), blue: male (*n* = 166). Skin-fold sums are from triceps, biceps, subscapular and suprailiac sites and converted to body fat % for subjects >15 years following calliper manufacturer instructions (Lange, Beta Technology). Lines are lowess curves. BMI, body mass index.

Cardiovascular disease

Hunter-gatherers and subsistence farming populations are notable for their remarkable cardiovascular health (3,7,17). Heart and vascular disease account for a negligible proportion of deaths in these populations, even among adults 60+ years (8). The difference between small-scale and industrialized populations is most stark at older ages. More than 60% of US adults 60+ years are hypertensive, while less than 30% of hunter-gatherers and subsistence farmers 60+ years show even mild hypertension (7,17). Cardiorespiratory fitness is also very high among small-scale societies. Eaton and colleagues (3) report mean maximal oxygen uptake, VO_2max, of 56.7 $mlO_2\ kg^{-1}\ min^{-1}$ (SD ±6.9) for men ~20–40 years old in seven global populations of hunter-gatherers, pastoralists and subsistence farmers, well above a reported value of 37.9 $mlO_2\ kg^{-1}\ min^{-1}$ for age-matched Canadian men.

Table 1 Diet composition, blood profile and blood pressure in hunter-gatherers and other small-scale societies

Population	Diet							Blood profile					Blood pressure (sys/dia)		
	Energy					Cholesterol (mg d^{-1})	Fibre (g d^{-1})	Cholesterol (mg dL^{-1})			Triglyc. (mg dL^{-1})	Glucose (mg dL^{-1})	Age (year)		
	(kcal g^{-1})‡‡	%Prot.	%Carb.	%Fat	FQ§§			Total	HDL	LDL			18–39	40–59	60+
Hadza†	1.46	24	65	11	0.92	–	80–150	115*	34*	62*	80*	67	116/70	123/75	126/70
Tsimane‡	–	14	72	14	0.93	–	–	153	39	93	106	–	–	115/73	119/74
Shuar§	–	–	–	–	–	–	–	153	41	89	131	78	113/77	113/77	113/77
USA††	1.78	12	46	42	0.85	300–500	20	211	55	135	105	92	114/69	114/69	–

*Mean was calculated assuming highest possible level for subjects who fell below sensitivity level of the instrument. For example, if total cholesterol was reported as <100 mg dL^{-1}, subject was assigned a value of 99.

†Dietary values calculated by combining proportions of foods in the diet reported by Marlowe and Berbesque (36) with nutritional values for Hadza foods (37,38); values for meat from Eaton and Konner (39). Fibre intake calculated assuming daily caloric intakes match TEE values discussed in text to calculate grams per day intake of different foods. Further, we calculated a low estimate of fibre intake assuming 80% of fibre from tubers is spit out as a quid rather than ingested, and a high value assuming all fibre from tubers is ingested. Blood profile and blood pressure data from Raichlen and colleagues (8).

‡Dietary data from Gurven and colleagues (13). Blood profiles and blood pressure data from Kaplan and colleagues (17). Blood pressures are weighted means for younger (40–64 years) and older (65+) cohorts.

§Blood profile and blood pressure data from Liebert and colleagues (15). Blood pressures are for all adults, not reported by age category.

††Dietary energy density from $n = 7$ lean cohorts reported by Karl and Roberts (40), includes non-US populations. Other dietary data from Eaton and colleagues (3). Blood profile data from NHANES dataset, reported by van der Velde and colleagues (47) for $n = 543$ US adults age 18 to 49 without elevated glucose levels.

‡‡Dietary energy density calculated from wet weight of food (excludes beverages).

§§Food quotient (FQ) calculated from % energy values as FQ = 0.7 × %Fat + 0.8 × %Protein + 1 × %Carbohydrate.

The Tsimane, a population with a mixed hunter-gatherer and subsistence farming economy living in the Amazon rainforest (13,14,17), offers a useful case study in heart health. Cardiovascular disease has been intensively studied among the Tsimane for over two decades (17). Despite relative high levels of C-reactive protein, a marker of inflammation associated with increased risk of cardiovascular disease, Tsimane adults show very low rates of hypertension with age and almost no evidence of peripheral artery disease (17), even for individuals over 60. Indeed, the Tsimane have the lowest prevalence of coronary artery disease, assessed by coronary artery calcium, ever reported (17).

Fewer cardiovascular measures are available for other small-scale societies, but, like the Tsimane, many show little or no increase in blood pressure with age and low prevalence of hypertension (3,7) (Table 1). Heart health in these populations is consistent with their high levels of daily physical activity and salutary serum cholesterol and triglyceride profiles, discussed below.

Other non-communicable disease

Other ‘diseases of civilization’ have received relatively little attention in studies of hunter-gatherer and subsistence farmer health. A small number of cancer deaths are reported in well-studied small-scale populations with large samples, particularly among the elderly, but cancers are often difficult to detect without modern medical screening, and thus, cancer prevalence is largely unknown (9). Cognitive decline and dementia are a recent focus in some groups, and early studies there are intriguing. For example, the apolipoprotein E4 allele, associated with earlier age-related cognitive decline and Alzheimer’s disease in industrialized populations, is associated with better cognitive function among elderly Tsimane (19). Additional work among small-scale populations is needed to understand the environmental and genetic influences on non-communicable diseases beyond cardiovascular and metabolic health.

Physical activity and energy expenditure

Daily physical activity

Hunter-gatherers and subsistence farmers have high levels of physical activity throughout their lives. Much of the ecological research among these populations has measured activity through time-budgets or distance travelled. Leonard and Robertson (20) report ~6–9 h of walking and other physical activity per day for two hunter-gatherer populations, the San of southern Africa and the Ache of Paraguay. Adults among the Old Order Amish community studied by Bassett and colleagues (16) self-reported ~8 h d^{-1} of moderate and vigorous activity, including walking. Marlowe (21), in a thorough review of hunter-gatherer ecology, reported that women walk an average of 9.5 km d^{-1} ($n = 8$ populations) and men walk 14.1 km d^{-1} ($n = 6$) in these populations. We reported similar daily walking distances for the Hadza adults (women: 6.2 ± 1.7 km d^{-1}, $n = 26$; men: 12.2 ± 2.7, $n = 15$) and found a small but detectable decrease (−0.4 km d^{-1} per decade) with age (6).

The advent of accelerometry and heart rate monitoring has added to our understanding of activity levels and improved comparisons across populations. Accelerometry based assessments of the Tsimane and other small-scale societies indicate high levels of low-intensity and moderate-intensity physical activity (14). Our heart rate measures of Hadza adults indicate remarkably high levels of daily physical activity, again mostly at low and moderate intensities (7). Hadza adults accumulate over ~135 min of moderate and vigorous physical activity (MVPA) per day, several times more than adults in the USA and Europe (7) (Fig. 2). Objectively measured MVPA among Hadza men and women remains high throughout adulthood, with no apparent age-related decline (7).

These high levels of physical activity are not offset by increased time resting, at least as measured by sleep patterns. Despite the lack of electricity and artificial light, the Hadza, Tsimane, San and other hunter-gatherer and subsistence farming groups sleep the same amount (5.9–7.1 h per night) as adults in industrialized populations (22). Nonetheless, it

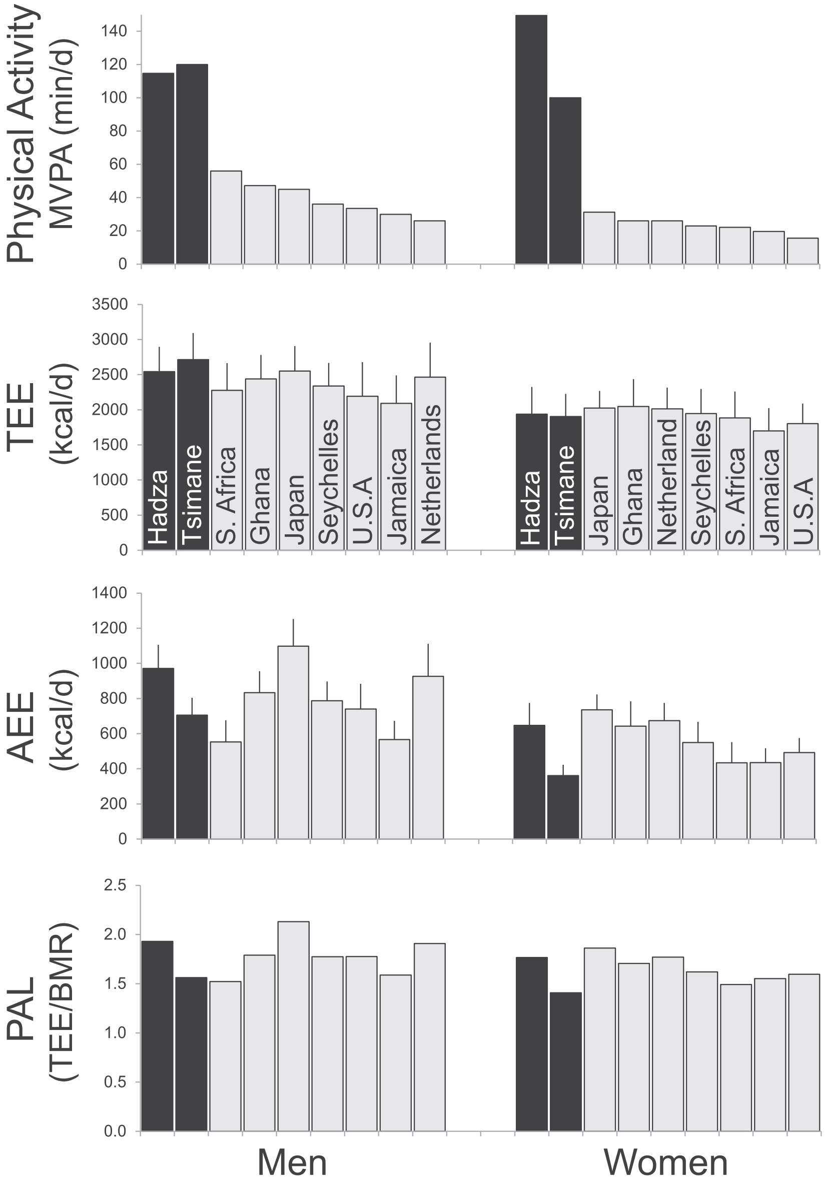

Figure 2 Daily moderate and vigorous physical activity (MVPA) (measured via heart rate or accelerometry), total energy expenditure (TEE) (kcal d^{-1}), activity energy expenditure (AEE) (kcal d^{-1}) and physical activity level (PAL) (TEE/BMR) for the Hadza, Tsimane and seven industrialized populations. TEE and AEE are adjusted to Hadza fat free mass; see text. Error bars for TEE and AEE are standard deviations, calculated from reported coefficients of variation in TEE (13,27–30). MVPA for South Africa, USA, Ghana, Jamaica and Seychelles cohorts from Dugas and colleagues (51). MVPA for Netherlands cohorts from baseline measures in van der Meij and colleagues (52). Note that MVPA is reported using three different measures by Gurven and colleagues (14); for comparison here, conservative values of 120 min (men) and 100 min (women) are shown.

is notable that *inactivity* and sedentary behaviour, which has been linked to disease risk in industrialized populations (23), is largely unstudied among small-scale populations.

The fossil and archaeological records suggest that high levels of physical activity are ancient in the human lineage, evolving ~2 Ma with the genus *Homo* and the emergence of the hunter-gatherer lifestyle (24). Increased activity is argued to have played an essential role in the evolution of our larger brains, derived life history and diet (24). Indeed, humans have remarkable endurance capabilities compared with other primates, and running prey to exhaustion is a documented hunting strategy among some hunter-gatherer groups that may have been even more common in the ancient past (24). However, among hunter-gatherers and subsistence farmers today, running is rare, as indicated by accelerometry and GPS recording (7). While endurance running may have been a common hunting strategy among past hunter-gatherer populations, its frequency likely varied widely in response to local ecology and lifestyle.

Daily energy expenditure

Remarkably, despite high levels of physical activity, total energy expenditures (TEE) (kcal d^{-1}) are not necessarily elevated in small-scale societies compared with industrialized populations (6,7,25,26). This metabolic similarity was first noted in comparisons among rural Nigerian women (many of them physically active farmers) and African–American women in the USA (25). Even activity energy expenditure (AEE) (kcal d^{-1}), the portion of TEE not attributable to basal metabolic rate (BMR) (kcal d^{-1}) or the cost of digestion, was found to be similar among these groups despite clear differences in daily physical activity.

Our own studies of Hadza adults have shown that TEE among these traditional hunter-gatherers is similar to that of adults in the USA, Europe and other industrialized populations (6,7). Since those first studies, we have expanded the sample to measure TEE in other seasons, years and camps. Results from this larger sample (n = 22 women, age: 39.0 ± 18.5 years, mass: 44.0 ± 6.3 kg; n = 24 men, age: 36.6 ± 14.8, mass: 50.4 ± 5.0) are similar to previous analyses. Using doubly labelled water methods described previously (6), with an updated food quotient for the Hadza population (0.92; see below, Table 1), men's TEE (2,542 ± 355 kcal d^{-1}) was greater than women's (1,939 ± 384; $p < 0.001$, Student's *t*-test). However, this difference in TEE was largely explained by differences in fat free mass (FFM) (women: 34.4 ± 4.5 kg; men: 43.7 ± 4.3). In multiple linear regression with FFM and sex as covariates, FFM was strongly correlated with TEE ($t(45) = 3.98$, $\beta = 41.4 \pm 10.4$ kcal kg^{-1}, $p < 0.001$, model adj. $r^2 = 0.58$), and men had marginally greater TEE ($t(45) = 1.87$, β (male) = 244 ± 130, $p = 0.07$). Neither age ($p = 0.35$) nor fat mass ($p = 0.47$) were significant factors when added to the model, while FFM ($t(45) = 3.52$, $\beta = 38.4 \pm 10.9$ kcal kg^{-1}, $p < 0.001$, model adj. $r^2 = 0.57$) and sex ($t(45) = 2.11$, β (male) = 290 ± 138, $p = 0.04$) remained significant. We note that TEE for Hadza men and women in this larger sample are similar to those reported previously for a subset of these data (6) and that calibrated heart rate measures of Hadza TEE provide similar results (6,7).

To compare Hadza expenditures with other populations, we adjusted TEE reported for those cohorts to match FFM and (where possible) other characteristics of the Hadza sample (FFM is by far the strongest anthropometric predictor of TEE in humans (6,13,27)). For USA, South Africa, Ghana, Seychelles and Jamaica cohorts, the relationship between FFM, age, height, body mass and sex is reported (27), allowing us to calculate TEE for these groups matched to the body size, body composition and age of the male and female Hadza cohorts. For Tsimane adults (13), the relationship between FFM and TEE is reported (52 kcal d^{-1} per kilogram of FFM), and this ratio was used to reduce mean TEE reported for Tsimane men and women to match the FFM of the Hadza. For Dutch adults (28) and Japanese men (29), we used the ratio of 42 kcal d^{-1} per kilogram of FFM from a large recent study (27) to reduce reported TEE to match the FFM of the Hadza samples. A study of Japanese women (30) reported low BMI cohorts that matched Hadza women for FFM (1st and 2nd BMI quartiles FFM: 35.9 kg), allowing direct comparison of TEE without size adjustment.

Hadza TEE in the expanded sample confirms previous analyses. When TEE for industrialized populations from America, Europe, Africa and Asia are adjusted for differences in FFM, Hadza TEE is similar to the others despite large differences in daily physical activity (Fig. 2). For both male and female cohorts, mean size-adjusted TEE for every industrialized population except Jamaican men falls within 1 SD of the Hadza means. Mean TEE for both male and female Japanese cohorts exceed that of the Hadza, as do female cohorts from Netherlands, Seychelles and Ghana (Fig. 2). Notably, the pattern of variation in daily physical activity measured with accelerometry is not reflected in TEE among populations (Fig. 2).

To examine the relationship between activity and expenditure further, we calculated and compared AEE. For the Hadza, we first calculated BMR from body mass and height (women: 148.5 ± 8.4 cm; men: 158.5 ± 7.0) using equations from Henry (31). We then calculated AEE following the standard approach (27) as AEE = 0.9 × TEE − BMR. We also did this for the Jamaican population as BMR data were not available for them. For all other cohorts, we used their reported physical activity level (PAL) (the ratio of TEE/BMR) to calculate size-adjusted BMR and AEE from their size-adjusted TEE values.

As with TEE, neither reported PAL values nor size-adjusted AEE reflect the pattern of variation in daily physical activity measured using accelerometry. Despite very high levels of daily physical activity, Tsimane AEE and PAL are very low (Fig. 2) due to their elevated resting metabolic rate, which is in turn related to high levels of pathogen burden and immune activity (13). Several of the industrialized population cohorts have reported PAL values and size-adjusted AEE values near or greater than the Hadza (Fig. 2).

The similarity in TEE, AEE and PAL suggests that the body adjusts to variation in physical activity to maintain TEE within a narrow physiological range. This 'Constrained TEE' hypothesis is consistent with other studies showing no correspondence between activity levels and TEE, AEE and PAL among human populations, similar TEE in captive and wild mammal populations, and limited or no effect of increased activity on TEE in controlled laboratory studies of birds and rodents (6,25–27). The suggestion that TEE, AEE and PAL may be largely unrelated to lifestyle and daily physical activity has broad implications in obesity research (6,25–27). In regard to evolutionary perspectives in public health, results from the Hadza show that our hunter-gatherer past need not have been marked by higher energy expenditures than today, even if (as was surely the case) our ancestors were far more physically active. Some other implications for metabolic health and obesity are discussed below.

Diet

Dietary diversity among hunter-gatherers is so vast that dietary universals are few. All human groups cook their food and appear to have done so for at least the past ~250,000 years and likely much longer (32). And nearly all hunter-gatherers populations today and in the recent past are known to have a mix of both meat and plant foods in their diet; of 265 such populations compiled by Murdock (33), only one was reported to subsist on no fish or game. Beyond these broad strokes, dietary diversity is the rule (Fig. 3). Across the globe, the human diet is dictated by geography and local ecology.

It has been suggested (34) that modern, processed diets are more energy dense (kcal g^{-1}) than those of our Palaeolithic past. Available measures of dietary energy density among living and recent hunter-gatherer populations lend limited support to this view (Fig. 4). Simmen and colleagues (35) report mean dietary energy density of 1.65 ± 0.38 kcal g^{-1} for eight small-scale populations. We calculated dietary energy densities for the Hadza, combining long-term data on estimated monthly dietary intake (grams per day of foods brought into camp) from Marlowe and Berbesque (36) with energy densities for these foods

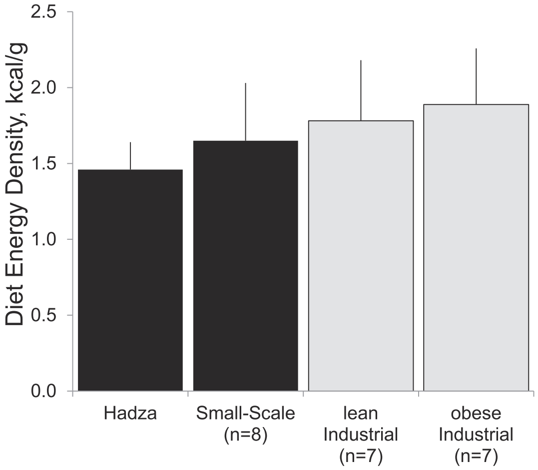

Figure 4 Energy density (kcal g^{-1}) calculated for the Hadza, by Simmen and colleagues for eight small-scale societies (35) and for seven lean and obese cohorts in industrialized populations reported by Karl and Roberts (40). For the Hadza sample, error bars represent standard deviation across 12 months (36). For others, error bars represent standard deviations across populations.

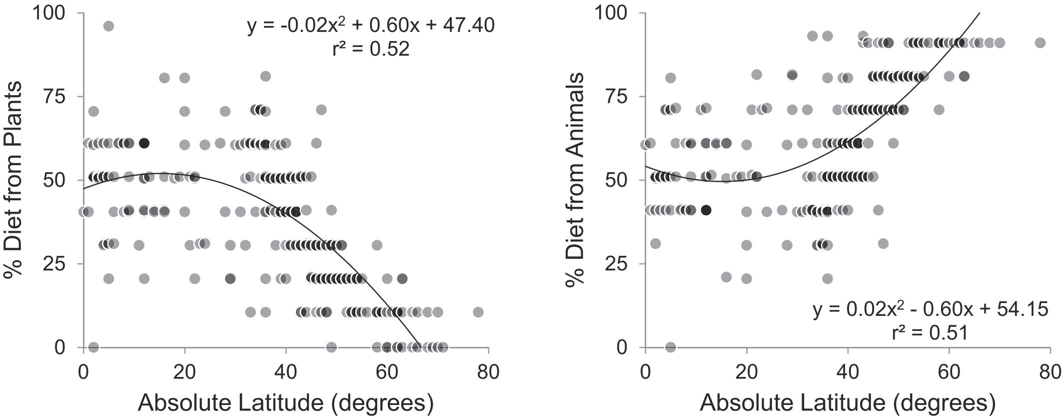

Figure 3 Proportions of the diet from plant and animal foods plotted against absolute latitude for n = 265 hunter-gatherer and mixed hunter-gatherer/farmer populations reported in Murdock's *Ethnographic Atlas* (33).

(kcal g^{-1}) from Schoeninger and colleagues (37,38); for meat, we used a value of 1.41 kcal g^{-1} reported for lean, wild game by Eaton and Konner (39). This approach yields a mean Hadza dietary energy density of 1.46 ± 0.19 kcal g^{-1} averaged over the year. These values are somewhat lower than those from a recent review comparing dietary energy density in lean and obese cohorts among seven industrialized populations in the USA, Europe and China (40). Energy densities from table 2 from Karl and Roberts (40) give a mean of 1.78 ± 0.40 and 1.89 ± 0.37 kcal g^{-1} among lean and obese cohorts, respectively. While these results suggest a trend towards increased energy density in modern diets, the range of densities among industrialized populations even in Karl and Roberts' sample (1.40–2.57 kcal g^{-1}) overlaps hunter-gatherer diets.

Eaton, Cordain and colleagues have modelled the nutritional profiles of Palaeolithic diets extensively in several thorough studies over the past three decades (3,39,41). These analyses rely heavily on Murdock's *Ethnographic Atlas* (33), a compendium of ethnographic information for hundreds of hunter-gatherer and other small-scale populations, for information on the proportion of the diet in each population obtained from animals and plants (Fig. 3). Among other findings, these studies have argued that most hunter-gatherer groups obtain ≥50% of their calories from meat and that, therefore, modern starch-heavy and sugar-heavy diets have a much higher proportion of carbohydrate and lower proportion of protein than was typical in the past (3,41). These analyses have become the foundation of the Palaeodiet movement (42), which advocates for (among other lifestyle adjustments) a high-fat, high-protein diet and the avoidance of cereals and sugars to protect against cardiovascular and metabolic disease.

These dietary assessments, which rely on rough and often methodologically opaque approximations of food intake from Murdock (33) and additional estimates of macronutrient content for plant and animal foods, are difficult to reconcile with more detailed ethnographic and nutritional studies of hunter-gatherer diets. First, the Murdock entries do not include information on honey consumption. This oversight is important, because honey accounts for a substantial portion of the diet for many hunter-gatherer groups (43) (*contra* Cordain and colleagues (41)). For example, among the Hadza, Marlowe and colleagues have estimated that honey accounts for ~15% of energy, ranging monthly from 1% to 50% (36,43). Even these values, which rely on measurements of foods brought back to camp, are likely underestimates of honey intake. Our detailed focal follow observations have shown that men eat substantial amounts of honey out of camp while foraging, which leads us to estimate that 16–20% of the annual diet of foraging Hadza is derived from honey and bee larvae (44). Second, many well-studied small-scale populations obtain considerably less than 50% of their calories from fish and game. For example, Kaplan and colleagues (9) report the proportion of dietary energy from game and other foods for eight populations of hunter-gatherers (data for a ninth are incomplete). Half of these populations (4/8) obtain less than 50% of their calories from game (9). Indeed, the data from Murdock suggest that populations below ~45° absolute latitude subsist on a wide range of diets with most populations subsisting on roughly equal proportions of plant and animal foods (Fig. 3). Third, macronutrient proportions for many small-scale societies used as models in public health, including the Hadza and Tsimane, are much more carbohydrate-heavy than recommended by Palaeodiet proponents. Our estimated food quotient for the Hadza, based on dietary analyses described earlier, is 0.92, more carbohydrate-rich than the average US diet (Table 1). Our limited tests ($n = 19$ adults) for urinary ketones among the Hadza have yet to produce a positive test. The Tsimane also have a food quotient >0.90 (Table 1), and the same is likely true for most small-scale societies that depend on a carbohydrate-rich staple food (e.g. tubers, manioc, plantains and rice). Meat-heavy, low-carbohydrate diets may have been the norm for some hunter-gatherer populations in the past, but many small-scale societies, including those with excellent metabolic and cardiovascular health, eat diets that are relatively rich in carbohydrates and (via honey) simple sugars.

While the macronutrient content of hunter-gatherer diets can be debated, it seems clear that they are micronutrient-rich and likely more healthful than diets in industrialized populations (41). Wild plant foods tend to have a lower glycaemic index than processed foods and very little salt (41). Hunter-gatherer diets also contain a higher proportion of dietary fibre than typical modern diets. Eaton and colleagues (3) estimate fibre intake of 100–150 g d^{-1} for Palaeolithic populations, far greater than the ~20 g d^{-1} typical intake in the USA. Our assessments of the Hadza diet support this view. Combining daily food intakes (36) (g d^{-1}) with nutritional analyses of fibre content for Hadza foods (37,38), we estimate daily fibre intakes of 80–150 g d^{-1} for Hadza adults (Table 1). Finally, hunter-gatherer diets are thought to be base-yielding, in contrast to the acid-yielding foods common in Western diets (41).

Diets in small-scale societies are generally associated with favourable blood profiles. Eaton and colleagues (3) report total cholesterols of 134 ± 20 mg dL^{-1} for $n = 19$ populations of hunter-gatherers, subsistence farmers and pastoralists. More recent reports of cholesterol and triglyceride levels among the Hadza (7), Tsimane (17) and Shuar (15) are similarly low (Table 1). Kaplan and colleagues (17) report less than 1% prevalence of high total cholesterol and 4% prevalence of high triglycerides among Tsimane adults 40+ years ($n = 705$). Fasted glucose levels are also low among these populations as discussed earlier.

The fossil and archaeological record shows that hominin diets have been diverse and adaptable since the Lower

Palaeolithic. Stone tools and preserved butchery marks on animal fossils indicate that meat has been an important component of the hominin diet for over 2 Myr (2). Dietary flexibility is evident in the repeated expansion of these hominins throughout Africa and into Eurasia, occupying a broad range of habitats and climates, beginning with *Homo erectus* ~1.8 Ma (2). More recent discoveries have emphasized the importance of plant foods in the Palaeolithic diet. Microfossils trapped in the dental calculus and stone tool surfaces of Neanderthals and Palaeolithic humans show they were eating cooked, processed grains from wild grasses as well as starchy roots in addition to other plant foods and game (45). The broad range of foods and macronutrient profiles evident in living and recent hunter-gatherers reflects a deep history of hominin dietary diversity.

What do hunter-gatherers teach us in public health?

The remarkable metabolic and cardiovascular health of hunter-gatherers and other small-scale populations has long made them attractive models in public health. Given the similarity in health profiles across ethnic groups, it is clearly their environments, rather than genetics, that keep people within small-scale societies so healthy. Indeed, from Australia to the Americas, these populations develop the same metabolic and cardiovascular ‘diseases of civilization’ when they move away from traditional lifestyles and adopt Western diets and activity levels (46). Yet the diversity of traditional lifestyles and diets makes it difficult to draw simple lessons to apply in industrialized populations. Contemporary hunter-gatherers and industrialized populations differ along many dimensions, including cultural history, geography and state provisioning of education, health care and other services. Hunter-gatherer life expectancies at birth are lower than those measured in any national level health survey, but hunter-gatherers also have extremely low obesity and diabetes rates and high levels of physical activity.

One common element of traditional lifestyles that clearly seems to be protective against non-communicable disease is a high level of daily physical activity. Hunter-gatherers and subsistence farmers accumulate several times as much physical activity each day as people in developed countries (Fig. 2). The health benefits of exercise are well established, and increasing daily activity is already a common focus in public health worldwide (4). Measures of the volume and intensity of daily activity in small-scale societies might aid in shaping these efforts. For example, the US Centers for Disease Control recommend $\geq$150 min week^{-1} of MVPA, a goal that fewer than 10% of American adults achieve (8,47). Data from small-scale societies suggest even this goal (150 min/week^{-1}) is too modest and that optimal levels of activity might be much greater. However, data from small-scale societies also show a high proportion of low-intensity and moderate-intensity activity, which may be easier to incorporate into public health strategies than higher intensity exercise.

The surprising discovery that high levels of physical activity do not invariably result in elevated TEE and PAL (6,7,25–27) (Fig. 2) forces us to rethink the mechanisms by which exercise promotes health. The hypothesis that industrialized populations are prone to metabolic disease because they are less active and therefore expend fewer calories per day is not supported by metabolic measurements from hunter-gatherers and other small-scale societies (6,7,25,26) (Fig. 2). Rather than changing the amount of energy expended each day, exercise may improve health by affecting the allocation of energy among physiological tasks. For example, increased physical activity expenditure might reduce energy expended on inflammation and other deleterious activity (26). Exercise may also help to regulate appetite, improving the balance between energy expenditure and intake (34,48), and exercise has been shown to help maintain weight loss (34). The regulatory effects of exercise warrant further attention.

The lack of correspondence between objectively measured physical activity and TEE, AEE or PAL (Fig. 2) suggests caution is warranted when interpreting these metabolic measures. Conversely, converting objective measures of physical activity to estimates of TEE, AEE or PAL should be performed with an understanding of the weak and sometimes non-intuitive relationships among these measures. As noted by Pontzer and colleagues (27), there is typically a significant but weak ($r^2 \approx 0.10$) relationship between accelerometer measurements of physical activity and TEE or AEE in large human samples, with far more TEE variation within quantiles of activity than between them. Among populations, there is no clear correspondence between objectively measured activity and daily expenditure (Fig. 2).

The constancy of TEE among a diverse range of lifestyles, including living hunter-gatherers and other small-scale societies, strongly suggests that the modern obesity pandemic stems from increased energy intake rather than decreased energy expenditure. But other than reducing calorie consumption, it is not immediately clear what aspects of traditional diets are most important to emulate to promote health. The idea that there is one true, natural human diet to which we might all aspire is negated by the incredible variety of hunter-gatherer diets recorded by early ethnographers and researchers today. Specifically, the suggestion that Palaeolithic cultures invariably had low-carbohydrate diets is strongly challenged by detailed dietary assessments among living groups and in the fossil record (45). Traditional diets do seem to be more nutrient dense, higher in fibre and lower in glycaemic index than foods in industrialized cultures (3,41). Many modern processed foods are also engineered to optimize flavour and encourage consumption, and the combination of fat and carbohydrate in modern processed foods may encourage overconsumption (49). These aspects of diet and the interactions between diet and physical activity (34,47) warrant more attention.

Finally, it is worth considering what other aspects of traditional lifestyles, in addition to diet and physical activity, might contribute to the remarkable health of hunter-gatherers. Close friendships and family bonds, low levels of social and economic inequality and lots of time spent outdoors are typical in hunter-gatherer populations and other small-scale societies. The absence of these in modern societies is associated with chronic social stress and a range of non-communicable diseases, including metabolic disease and obesity (50). As we work to understand the evolutionary roots of modern disease, we should strive for a more integrative and holistic understanding of lifestyle and health among hunter-gatherers today and in our collective past.

Conflict of interest statement

The authors declare no conflict of interest.

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