The Exercise Paradox

EVOLUTION

Studies of how the human engine burns calories help to explain why physical activity does little to control weight—and how our species acquired some of its most distinctive traits

By Herman Pontzer

IN BRIEF

Conventional wisdom holds that physically active people burn more calories than less active people do.

But studies show that traditional hunter-gatherers, who lead physically hard lives, burn the same number of calories as people with access to modern conveniences.

The discovery that human energy expenditure is tightly constrained raises questions about how our large brain and other energetically demanding traits evolved.

Comparisons with energy expenditure in great apes suggest that the human metabolic engine has evolved to get more work done to support our costly features.

Illustration by Bomboland

Herman Pontzer is an anthropologist at Hunter College. He studies energy expenditure in humans and great apes to test hypotheses about the evolution of human physiology and anatomy.

Still no giraffe.

Four of us had been walking half the day, tracking a wounded giraffe that Mwasad, a Hadza man in his late 30s, shot the evening before. He hit it in the base of the neck from about 25 yards with a steel-tipped, wood arrow smeared with powerful, homemade poison. Hadza are traditional hunter-gatherers who live off of wild plants and animals in the dry savanna wilderness of northern Tanzania. They know the landscape and its residents better than you know your local Trader Joe's. Mwasad had let the giraffe run to give the poison time to work, hoping to find it dead in the morning. An animal that size would feed his family and his camp for a week—but only if he could locate it.

Mwasad led our party—Dave Raichlen from the University of Arizona, a 12-year-old Hadza boy named Neje and me—out of camp just after daybreak. Dave and I were of little use in this endeavor. Mwasad had invited us along as a friendly gesture and for the extra help to carry the butchered animal back to camp should our search effort succeed. As anthropologists who study human ecology and evolution, we jumped at the opportunity to tag along—Hadza men's tracking abilities are legendary. It certainly beat the prospect of a long day in camp spent fiddling with research equipment.

We walked hard for an hour through a pathless, rolling sea of golden, waist-high grass, dotted with brush and thorny acacia trees, directly to the bloody patch where the giraffe was struck. That bit of navigation in itself was quite a trick, like someone leading you to the middle of a 1,000-acre wheat field to show you where he had once dropped a toothpick and then nonchalantly reaching down to pick it up. Hour on hour, tracking the wounded animal under a relentless sun ensued as we followed ever more tenuous signs.

Still no giraffe. At least I had water. We sat in the shade of some bushes just after midday, taking a break while Mwasad pondered where the injured creature might head. I had a quart or so left—enough, I figured, to get through the heat of the afternoon. Mwasad, however, had not brought any water with him, as is typical of the Hadza. As we packed up to restart the search, I offered him a drink. Mwasad gave me a sideways look, smiled and proceeded to drink the entire bottle in one long pull. When he finished, he casually handed me the empty bottle.

It was karma. Dave and I, along with anthropologist Brian Wood from Yale University, had spent the past month living with the Hadza, conducting the first direct measurements of daily energy expenditure in a hunter-gatherer population. We enlisted a couple of dozen Hadza women and men, Mwasad among them, to drink small, incredibly expensive bottles of water enriched in two rare isotopes, deuterium and oxygen 18. Analyzing the concentration of those isotopes in urine samples from each participant would allow us to calculate their body's daily rate of carbon dioxide production and thus their daily energy expenditure. This approach, known as the doubly labeled water method, is the gold standard in public health for measuring the calories burned each day during normal daily life. It is straightforward, completely safe and accurate, but it requires that participants drink every last drop of the enriched water. We had taken pains to make clear that they must not spill, that they had to finish the dose completely. Mwasad seemed to have taken that message to heart.

Mwasad's sly joking aside, my colleagues and I have learned a lot about how the human body burns calories through our work with the Hadza. Together with findings from investigators who study other populations, our research has revealed some surprising insights into human metabolism. Our data indicate that, contrary to received wisdom, humans tend to burn the same number of calories regardless of how physically active they are. Yet we have evolved to burn considerably more calories than our primate cousins do. These results help to explain two puzzles that might seem disparate at first but are, in fact, related: first, why exercise generally fails to aid weight loss and, second, how some of humanity's unique traits arose.

THE CALORIE ECONOMY

RESEARCHERS WHO ARE INTERESTED in human evolution and ecology often focus on energy expenditure because energy is central to everything in biology. One can learn a lot about any species by measuring its metabolism: life is essentially a game of turning energy into kids, and every trait is tuned by natural selection to maximize the evolutionary return on each calorie spent. Ideally, the study population lives in the same environments in which the species originally evolved, where the same ecological pressures that shaped its biology are still at work. That is difficult to achieve with human subjects because most people are divorced from the daily work of acquiring food from a wild landscape. For nearly all the past two million years, humans and our ancestors have been living and evolving as hunter-gatherers. Farming only got going about 10,000 years ago; industrialized cities and modern technology are only a few generations old. Populations such as the Hadza, one of the last hunter-gatherer populations left in the world, are key to understanding how our bodies evolved and functioned before cows, cars and computers.

Life for the Hadza is physically demanding. Each morning the women leave the grass huts of camp in small groups, some carrying infants on their back in a wrap, foraging for wild berries or other edibles. Wild tubers are a staple of the Hadza diet, and women can spend hours digging them out of the rocky ground with sticks. Men cover miles each day hunting with bows and arrows they make themselves. When game is scarce, they use simple hatchets to chop into tree limbs, often 40 feet up in the canopy, to harvest wild honey. Even the children contribute, hauling buckets of water back from the nearest watering hole, sometimes a mile or more from camp. In the late afternoon, folks wend their way back to camp, sitting on the ground and talking around small cooking fires, sharing the day's returns and tending to the kids. Days roll along like this through dry and wet seasons, ad millennium.

But forget any romantic notions of some lost Eden. Hunting and gathering is cerebral and risky, a high-stakes game in which the currency is calories and going bust means death. Men such as Mwasad spend hundreds of calories a day hunting and tracking, a gamble that they hope will pay off in game. Savvy is just as critical as stamina. Whereas other predators can rely on their speed and strength to obtain prey, humans have to outthink their quarry, considering their behavioral tendencies and scouring the landscape for signs of game. Still, Hadza men land big game like giraffes only about once a month. They would starve if Hadza women were not executing an equally sophisticated, complementary strategy, using their encyclopedic knowledge of local plant life to bring home a reliable bounty every day. This complex, cooperative foraging is what made humans so incredibly successful and is the core of what makes us unique.

Researchers in public health and human evolution have long assumed that our hunter-gatherer ancestors burned more calories than people in cities and towns do today. Given how physically hard folks such as the Hadza work, it seems impossible to imagine otherwise. Many in public health go so far as to argue that this reduction in daily energy expenditure is behind the global obesity pandemic in the developed world, with all those unburned calories slowly accumulating as fat. One of our motivations for measuring Hadza metabolism was to determine the size of this energy shortfall and see just how deficient we Westerners were in our daily expenditure. Back home in the U.S. after a hot and dusty field season, I lovingly packed the vials of Hadza urine on dry ice and sent them away to the Baylor College of Medicine, home of one of the best doubly labeled water laboratories in the country, imagining the whopping calorie totals they would reveal.

But a funny thing happened on the way to the isotope ratio mass spectrometer. When the analyses came back from Baylor, the Hadza looked like everyone else. Hadza men ate and burned about 2,600 calories a day, Hadza women about 1,900 calories a day—the same as adults in the U.S. or Europe. We looked at the data every way imaginable, accounting for effects of body size, fat percentage, age and sex. No difference. How was it possible? What were we missing? What else were we getting wrong about human biology and evolution?

LIES MY FITBIT TOLD ME

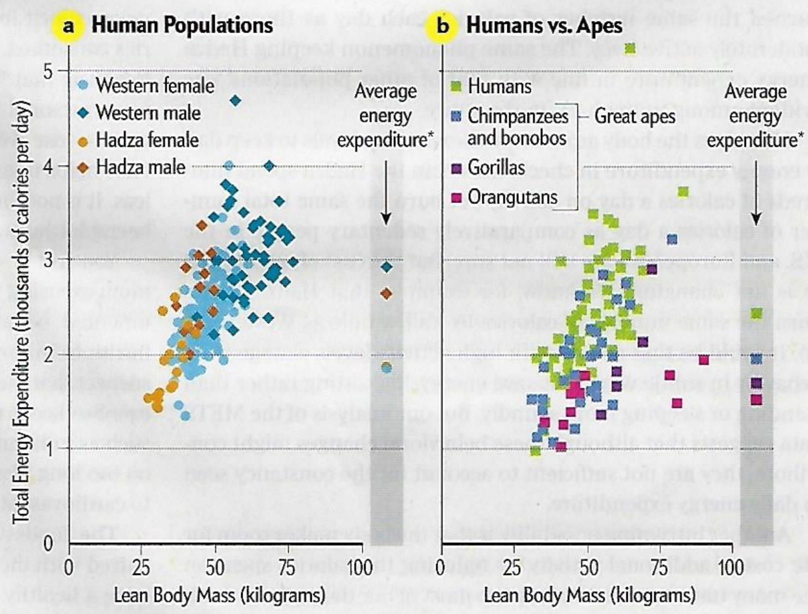
IT SEEMS SO OBVIOUS and inescapable that physically active people burn more calories that we accept this paradigm without much critical reflection or experimental evidence. But since the 1980s and 1990s, with the advent of the doubly labeled water method, the empirical data have often challenged the conventional wisdom in public health and nutrition. The Hadza result, strange as it seemed, was not some thunderbolt from the blue but more like the first cold drop of water down your neck from a rain that had been building, ignored, for years.

The earliest doubly labeled water studies among traditional farmers in Guatemala, the Gambia and Bolivia showed their energy expenditures were broadly similar to those of city dwell-

FINDINGS

Gas Guzzlers

Experts have assumed that physically active people burn more calories than less active folks. But direct measurements of energy expenditure in modern-day hunter-gatherers in the developing world and comparatively sedentary populations in the U.S. and Europe reveal similar results (a). If human metabolism is so tightly constrained, how did our big brain, long life span and other energetically costly features that distinguish us from our primate relatives evolve? Humans consume and expend hundreds of calories a day more than great apes (b), suggesting that our metabolic engine changed to burn energy faster, thus powering our expensive traits.



*To account for differences in energy expenditure arising from body size, Western averages are calculated at Hadza body sizes, and great ape averages are calculated at average human body size.

BRAIN SIZE AND LIFE HISTORY," BY HERMAN PONTZER ET AL., IN NATURE, VOL. 533; MAY 19, 2016 (right)

Graphic by Jen Christiansen

ers. In a study published in 2008, Amy Luke, a researcher in public health at Loyola University Chicago, took this work a step further, comparing energy expenditure and physical activity in rural Nigerian women with that in African-American women in Chicago. Like the Hadza study, hers found no differences in daily energy expenditure between populations, despite large differences in activity levels. Following up on that work, Lara Dugas, also at Loyola, along with Luke and others, analyzed data from 98 studies around the globe and showed that populations coddled by the modern conveniences of the developed world have similar energy expenditures to those in less developed countries, with more physically demanding lives.

Humans are not the only species with a fixed rate of energy expenditure. On the heels of the Hadza study, I piloted a large collaborative effort to measure daily energy expenditure among primates, the group of mammals that includes monkeys, apes, lemurs and us. We found that captive primates living in labs and zoos expend the same number of calories each day as those in the wild, despite obvious differences in physical activity. In 2013 Australian researchers found similar energy expenditures in sheep and kangaroos kept penned or allowed to roam free. And in 2015 a Chinese team reported similar energy expenditures for giant pandas in zoos and in the wild.

For a more granular look, comparing individuals instead of population averages, I recently joined Luke and her team, including Dugas, to examine activity and energy expenditure in a large, multiyear analysis known as the Modeling the Epidemiological Transition Study (METS). More than 300 participants wore accelerometers similar to a Fitbit or other fitness tracker 24 hours a day for an entire week while their daily energy expenditure was measured with doubly labeled water. We found that daily physical activity, tracked by the accelerometers, was only weakly related to metabolism. On average, couch potatoes tended to spend about 200 fewer calories each day than people who were moderately active: the kind of folks who get some exercise during the week and make a point to take the stairs. But more important, energy expenditure plateaued at higher activity levels: people with the most intensely active daily lives burned the same number of calories each day as those with moderately active lives. The same phenomenon keeping Hadza energy expenditure in line with that of other populations was evident among individuals in the study.

How does the body adjust to higher activity levels to keep daily energy expenditure in check? How can the Hadza spend hundreds of calories a day on activity yet burn the same total number of calories a day as comparatively sedentary people in the U.S. and Europe? We are still not sure, but the cost of activity per se is not changing: we know, for example, that Hadza adults burn the same number of calories to walk a mile as Westerners do. It could be that people with high activity levels change their behavior in subtle ways that save energy, like sitting rather than standing or sleeping more soundly. But our analysis of the METS data suggests that although these behavioral changes might contribute, they are not sufficient to account for the constancy seen in daily energy expenditure.

Another intriguing possibility is that the body makes room for the cost of additional activity by reducing the calories spent on the many unseen tasks that take up most of our daily energy budget: the housekeeping work that our cells and organs do to keep

HADZA HUNTER-GATHERERS in Tanzania spend hundreds of calories a day on activity yet burn the same total number of calories as city dwellers in the U.S.

us alive. Saving energy on these processes could make room in our daily energy budget, allowing us to spend more on physical activity without increasing total calories spent per day. For example, exercise often reduces inflammatory activity that the immune system mounts as well as levels of reproductive hormones such as estrogen. In lab animals, increased daily exercise has no effect on daily energy expenditure but instead results in fewer ovulatory cycles and slower tissue repair. And extremes may lead some animals to eat their own nursing infants. Humans and other creatures seem to have several evolved strategies for keeping daily energy expenditure constrained.

All of this evidence points toward obesity being a disease of gluttony rather than sloth. People gain weight when the calories they eat exceed the calories they expend. If daily energy expenditure has not changed over the course of human history, the primary culprit in the modern obesity pandemic must be the calories consumed. This should not be news. The old adage in public health is that "you can't outrun a bad diet," and experts know from personal experience and lots of data that just hitting the gym to lose weight is frustratingly ineffective. But the new science helps to explain why exercise is such a poor tool for weight loss. It is not that we are not trying hard enough. Our bodies have been plotting against us from the start.

You still have to exercise. This article is not a note from your mom excusing you from gym class. Exercise has tons of well-documented benefits, from increased heart and immune system health to improved brain function and healthier aging. In fact, I suspect that metabolic adaptation to activity is one of the reasons exercise keeps us healthy, diverting energy away from activities, such as inflammation, that have negative consequences if they go on too long. For example, chronic inflammation has been linked to cardiovascular disease and autoimmune disorders.

The foods we eat certainly affect our health, and exercise paired with dietary changes can help keep off unwanted pounds once a healthy weight has been reached, but evidence indicates that it is best to think of diet and exercise as different tools with

HARRY HOOK *Getty Images*

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different strengths. Exercise to stay healthy and vital; focus on diet to look after your weight.

ENERGY BUDGETS AND EVOLUTION

EVEN AS THE RECENT SCIENCE in metabolic adaptation helps to clarify the relation between exercise and obesity, a constrained, adaptive metabolism leaves researchers with larger, existential questions. If daily energy expenditure is virtually immobile, how could humans evolve to be so radically different from our ape relatives? Nothing in life is free. Resources are limited, and investing more in one trait inevitably means investing less in another. It is no coincidence that rabbits reproduce prodigiously but die young; all that energy plowed into offspring means less for bodily maintenance and longevity. *Tyrannosaurus rex* can thank its big head of nasty teeth and powerful hind limbs for its puny arms and hands. Even dinosaurs couldn't have it all.

Humans flout this bedrock evolutionary principle of austerity. Our brains are so large that, as you sit reading this article, the oxygen from every fourth breath you take is needed just to feed your brain. Yet humans have bigger babies, reproduce more often, live longer and are more physically active than any of our ape relatives. Hadza camps are full of cheerfully chaotic children and hale, hearty men and women in their 60s and 70s. Our energetic extravagance presents an evolutionary puzzle. Humans are so genetically and biologically similar to other apes that researchers have long assumed that our metabolisms are similar, too. But if energy expenditures are as constrained as our Hadza study and others suggest, how could an inflexible, apelike metabolism process all the calories needed to support our costly human traits?

In the wake of our broad, comparative primate energetics study, my colleagues and I began to wonder whether humans' adaptive suite of energetically costly traits was fueled by a wholesale evolutionary change in metabolic physiology. We had found in that study that primates burn only half as many calories a day as other mammals do. The reduced metabolic rates of primates correspond with their slow rates of growth and reproduction. Perhaps, conversely, the faster reproduction and other expensive traits of humans were linked to the evolution of an increased metabolic rate. All that was needed to test this idea was getting a bunch of frenetic chimpanzees, wily bonobos, phlegmatic orangutans and skittish silverback gorillas to carefully drink doses of doubly labeled water without spilling and to provide a few urine samples. In a scientific tour de force, my colleagues Steve Ross and Mary Brown, both at Lincoln Park Zoo in Chicago, worked with caretakers and veterinarians from more than a dozen zoos across the U.S. to pull that off. It took a couple of years, but they accumulated enough data on great ape energy expenditure to provide a solid comparison with humans.

Sure enough, humans burn more calories each day than any of our great ape relatives. Even after accounting for effects of body size, activity level and other factors, humans consume and expend about 400 more calories a day than chimpanzees and bonobos do; differences with gorillas and orangutans are larger still. Those extra calories represent the extra work our bodies do to support larger brains, produce more babies and maintain our bodies so we live longer. It is not simply that we eat more than other apes (although we do that, too); as we know all too well, piling extra calories into a body that is not equipped to use them only results in obesity. Our bodies, right down to the cellular level, have evolved to burn energy faster and get more done than our ape relatives. Human evolution was not entirely without trade-offs: our digestive tract is smaller and less costly than other apes, which need a large, energetically expensive gut to digest their fibrous, plant-based diets. But the critical changes that make us human were fueled by an evolutionary shift in our metabolic engine.

SHARED FORTUNES

AT SOME POINT in the late afternoon, our path bent toward camp, Mwasad looking ahead instead of searching the ground. We were heading home sans giraffe. Here was the fundamental danger in the high-energy human strategy: coming home empty-handed was both more likely and more consequential. Many of the energy-rich foods we need to fuel our faster metabolisms are inherently difficult to obtain in the wild, increasing the energy cost of finding food and heightening the risk of starvation for the men and women out foraging and their kids back at camp.

Happily for Mwasad, humans have evolved a few tricks to keep starvation at bay. We are the only species that has learned to cook, which increases the caloric value of many foods and makes them more efficient to digest. Our mastery of fire converts otherwise inedible root vegetables—from Trader Joe's yams to wild Hadza tubers—into veritable starch bombs. We have also evolved to be fat. We know this all too well from the obesity crisis in the West, but even Hadza adults, lean by any human standard, carry twice as much fat as chimpanzees idling away in zoos. Problematic though it may be in our modern era, our propensity to store fat most likely coevolved with our faster metabolism as a critical energy buffer to survive lean times.

As the sun sat heavy and orange just above the trees, we melted back into camp, Dave and I toward our tents, Mwasad and Neje to their families' huts, each one of us glad to be home. Despite the lost giraffe, no one went hungry that evening. Instead, with little fanfare or conscious effort, the camp deployed our species' most ingenious and powerful weapon against starvation: sharing. Sharing food is so fundamental to the human experience, the common thread of every barbecue, birthday, bar mitzvah, that we take it for granted, but it is a unique and essential part of our evolutionary inheritance. Other apes do not share.

Beyond our nutritional requirements and fixation with fat, perhaps the most profound impact of our increased energy expenditure is this human imperative to work together. Evolving a faster metabolism bound our fortunes to one another, requiring that we cooperate or die. As I sat with Dave and Brian, recounting the day's adventures over tinned sardines and potato chips, I realized I would not have had it any other way. No giraffe, no problem. SA

MORE TO EXPLORE

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