# Physical Activity, Energy Expenditure and Fitness: An Evolutionary Perspective

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**The model for human physical activity patterns was established not in gymnasia, athletic fields, or exercise physiology laboratories, but by natural selection acting over eons of evolutionary experience. This paper examines how evolution has determined the potential for contemporary human performance, and advances the experience of recently-studied hunter-gatherers as the best available (although admittedly imperfect) indicator of the physical activity patterns for which our genetically determined biology was originally selected. From the emergence of the genus *Homo*, over 2 million years ago (MYA), until the agricultural revolution of roughly 10000 years ago our ancestors were hunter-gatherers, so the adaptive pressures inherent in that environmental niche have exerted defining influence on human genetic makeup. The portion of our genome that determines basic anatomy and physiology has remained relatively unchanged over the past 40000 years. Thus, the complex interrelationship between energy intake, energy expenditure and specific physical activity requirements for current humans remains very similar to that originally selected for Stone Age men and women who lived by gathering and hunting. Research investigating optimal physical activity for human health and performance can be guided by understanding the evolution of physical activity patterns in our species.**

**Key words: Exercise, evolution, fitness, anthropology, health, natural selection, Darwinian medicine.**

## Introduction

The model for human physical activity patterns was established not in gymnasia, athletic fields, or exercise physiology laboratories, but by natural selection acting over eons of evolutionary experience. This paper examines how evolution has determined the potential for contemporary human performance, and advances the experience of recently-studied hunter-gatherers as the best available (although admittedly imperfect) indicator of the physical activity patterns for which our genetically determined biology was originally selected. The information reviewed in this report is a result of an extensive literature search using Medline, Sport Discus, and Colorado Alliance of Research Libraries, as well as the bibliographies of original articles.

Virtually all biomedical literature regarding optimal frequency, intensity, duration, and mode of exercise (e.g. 36) addresses proximate mechanisms relating exercise to health and fitness; however, an evolutionary perspective focuses on the ultimate bases for these relationships (17). While there is substantial individual variation in exercise capacities because of differing developmental and biobehavioral factors and because of individual genetic diversity, the ultimate human functional range is genetically determined (17). Like all other organisms, our ancestors evolved species-specific physical capabilities, limitations, and requirements as they competed in their environmental niches and, for two million years until the appearance of agriculture just 10,000 years ago (Table 1), human ancestors were hunter-gatherers.[1] The occupational and environmental stresses of this lifestyle shaped the contemporary human gene pool.

Although anatomically modern humans first appeared perhaps 100,000 years ago, modern human behaviour first becomes recognizable in the fossil record of about 50,000 years ago. Comparisons of mitochondrial DNA from diverse human ethnic groups (58,62) indicate that the genetic constitution of contemporary men and women has changed relatively little over these 50 millennia despite the enormous societal changes associated with agriculture and industrialization. Hence the relationship between energy intake, energy expenditure, and specific motor activity is still that originally selected for Stone Agers living in a foraging environment. However, labor saving devices in the home and workplace, motorized transport, and increasingly sedentary recreational pursuits have reduced the amount of obligatory physical exertion much below the level obtained when the existing human genome was selected. In industrialized societies physical activity for most people has become an extraordinary activity largely separate from other daily tasks and engaged in specifically to improve fitness variables such as endurance, strength, and/or flexibility. In con-

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trast, daily physical exertion was an integral, obligatory aspect of our ancestors' existence: hunting, gathering, carrying, digging, and escape from predators were dependent upon individual muscular activity and physical fitness.

### Evolutionary Changes in Hominid Anatomy and Physiology Influencing Exercise Capacities

Although mammalian origins extended ultimately to the beginnings of the Mesozoic Era, our prehuman (hominid) ancestors and those of today's great apes (pongids) diverged relatively recently, perhaps 5–7 million years ago (MYA). The evolutionary influences which make us uniquely human have operated chiefly during the period subsequent to this hominid/pongid split. The first known hominids – with an undisputed upright gait – were Australopithecines, who appear in the East African fossil record between 4.2 and 3.9 MYA (29). During the same time period, climatic changes reduced the extent of tropical forests and led to the formation of a drier, more open woodland/savanna mosaic environment (21). In this context an upright posture and bipedal gait conferred advantages: it aided visual location of food, water, and predators (50); it freed the hands for carrying, digging, and weapon use (35); and it minimized the body surface area exposed to the sun thereby partially offsetting the thermal load which resulted from daytime physical activity (14, 59, 61).

When humans and other primates run, their energy costs are roughly twice those of other mammals (55, 56), but human walking is at least as efficient as quadrupedal walking (45, 57). Human legs have a toggle-like structure which allows them to transfer potential and kinetic energy more efficiently than can the legs of quadrupedal mammals (12, 13). These considerations help explain why our Australopithecine ancestors could become bipedal; that they did had a profound impact on the physical characteristics and performance potential of their descendants, including ourselves.

The early Australopithecine, *A. afarensis*, retained many ape-like upper limb structural features (providing them continued access to trees for feeding, resting, and safety [53]) but analysis of both fossil footprints and pelvic/leg bone structure indicate they walked and ran with mechanical efficiency reasonably similar to that of contemporary humans (35). They were much smaller than we are: adult males stood about 1.5 m, weighed approximately 45 kg and their cranial capacities were only 400–500 ml (1) (Fig. 1). Like living pongids, they almost certainly had more body hair than current humans have, although body hair reduction to improve heat dissipation was probably underway. This adaptation acted synergistically with bipedalism to allow greater daytime phyiscal activity (60). Hairlessness can reduce the thermal load effectively only in conjunction with a substantial cutaneous sweat gland (or eccrine) system capable of evaporative cooling (40). Current human's sweat glands can produce more sweat per surface area than those of any other mammalian species (11, 40), a maximum heat dissipation rate in excess of 500 Watts/meter$^2$ (the maximum rate for modern hairy primates is 100 Watts/meter$^2$) (60). Hairlessness and an elaborate sweat gland system to facilitate heat dissipation would have had adaptive value chiefly if Australopithecines were more physically active in daytime than were their primate ancestors. This implies that walking, running, and other heat generating activtities became important aspects of their existence and, equally, that they were even possible for extended periods under the hot African sun.

**Table 1** The main events of human evolution.

| Million of Years Ago | Epoch | Development |
|---|---|---|
| 0.002 | | Industrial revolution |
| | Holocene | |
| 0.01 | | Agricultural revolution |
| | Latest Pleistocene | |
| 0.045 | | *Homo sapiens sapiens* (anatomically modern) appears |
| | Late Pleistocene | |
| 0.23 | | *H. sapiens neanderthalensis* appears |
| | Middle Pleistocene | |
| 0.400 | | Archaic *H. sapiens* appears |
| 1.7 | Early Pleistocene | *H. erectus* present |
| 2.0 | | *H. habilis* present |
| | Pliocene | Australopithecine divergence |
| 3.9 | | Bipedal *Australopithecus afarensis* present |
| | Late Miocene | |
| 7.5 | | Hominid-pongid divergence |

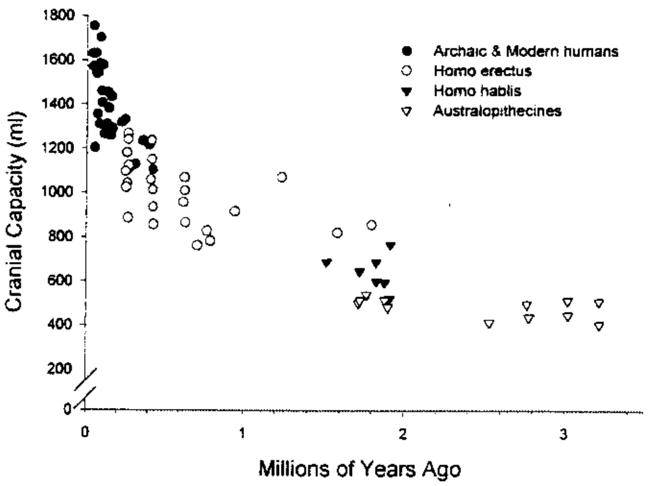


**Fig. 1** Increase in absolute hominid cranial capacity over time. (Adapted from [1]).

Early Australopithecines were capable of walking upright and likely had the beginnings of an efficient thermoregulatory system. Their body proportions were ape-like with relatively longer arms and shorter legs than those of their descendants – early humans (53) in whom the forearm bones (radius and ulna) became shorter and the femur longer (26). Evolutionary adaptations subsequent to *A. afarensis* therefore favored more energetically efficient walking: relative reduction of superacetabular mass via arm length shortening improved balance while a relatively longer femur facilitated transfer of potential and kinetic energy thereby increasing recovery of mechanical energy during locomotion (11). On the other hand, decreased forearm length had the undesirable effect of reducing maximum upper limb strength because it diminished the arm's biomechanical lever action (4,19,26).

Chimpanzees eat chiefly plant foods (94%), especially fruits; the remainder of their diet consists of insects and small vertebrates (37). Paleoanthropologists assume that pre-Australopithecine hominoids[2] and early Australopithecines had a similar subsistence pattern. However, towards the end of the Pliocene era, as the tropical forest gave way to more open woodland and savanna, fruit availability became more seasonal. Those Australopithecines who were human ancestors responded by including more animal material in their diets (37); other hominids (e.g. *A. robustus*) reacted to the same environmental challenge by utilizing lower quality plant foods, developing massive jaws and molars to process the tougher vegetation. These masticatorily robust species of Australopithecines eventually became extinct, but the protohuman line, now consuming more animal foods, gradually evolved into the first species of our genus, *Homo habilis*, which was similar in body size to *A. afarensis* but with a significantly larger brain (Fig. 1). *Homo habilis* was probably the first hominid to make stone tools and is consequently believed to have increased reliance on hunting and/or scavenging. The resulting increase in animal food availability was an important factor in the evolution of a larger brain and increased biobehavioral complexity (1).

Evolution of an expanded, more metabolically active brain required an increase in dietary quality (i.e. caloric density) (1, 33). Humans expend 20–25% of their resting metabolic requirement (RMR) to fuel the brain, whereas nonhuman primates need only about 8% and other mammals only 3–4% (32). However, increased brain metabolism in encephalized primates, and especially humans, evolved without increases in RMR (1), a development which required a balancing decrease in the metabolism of other body organs. Increased dietary quality permitted reduction in the size and metabolic activity of the gut, thereby largely offsetting increased brain metabolism (32,33,37).

Encephalization proceeded together with increasing behavioral complexity (47), an expanded daily range (32), greater daily total energy expenditures (TEE) (Table **2**), and increasing height: by 1.7 MYA *H. habilis* had evolved into *Homo erectus*, a species as tall as contemporary humans (10,46). The cortical thickness and overall diameter of their bony remains (Fig. **2**) indicate that *H. erectus* was heavily muscled (47); on average they must surely have been stronger than most contemporary humans. Their stone implements were much less sophisticated than those of later humans. They did not use hafted tools, or compound levers to multiply force, thus muscular loading for these early human ancestors must have been high. In addition to muscular extremities, *H. erectus* almost certainly had cardi-

**Table 2** Primate energy expenditure.

| Species | Sex | Weight (kg) | RMR (kJ) | TEE (kJ) | TEE RMR | PA (kJ) | Day Range (km) | PA/kg/d (kJ/kg/d) |
|---|---|---|---|---|---|---|---|---|
| Nonhuman Primates[1] | | | | | | | | |
| *H. lar* (gibbon) | M/F | 6.0 | 1222 | 1432 | 1.17 | 209 | 0.74 | 39 |
| *P. pygmaeus* | M | 83.6 | 8154 | 10879 | 1.33 | 2725 | 0.30 | 33 |
| (orang-utan) | F | 37.8 | 4496 | 6275 | 1.39 | 1779 | 0.30 | 47 |
| *P. troglodytes* | M | 39.5 | 4337 | 6321 | 1.46 | 1984 | 4.80 | 50 |
| (chimpanzee) | F | 29.8 | 3512 | 4789 | 1.36 | 1277 | 3.00 | 43 |
| Fossil Hominids[1] | | | | | | | | |
| *A. afarensis* | M/F | 37.1 | 4810 | 7635 | 1.6 | 2826 | - | 76 |
| *A. africanis* | M/F | 35.3 | 4630 | 7409 | 1.6 | 2780 | - | 79 |
| *A. robustus* | M/F | 44.4 | 5534 | 8853 | 1.6 | 3319 | - | 75 |
| *H. habilis* | M/F | 48.0 | 5877 | 9992 | 1.7 | 4115 | - | 86 |
| *H. erectus* | M/F | 53.0 | 6350 | 11432 | 1.8 | 5082 | - | 96 |
| *H. sapiens* (early) | M/F | 57.0 | 6719 | 12093 | 1.8 | 5375 | - | 94 |
| Recent Foragers[1] | | | | | | | | |
| !Kung | M | 46.0 | 5337 | 9117 | 1.71 | 3780 | 14.9 | 82 |
| | F | 41.0 | 4898 | 7409 | 1.51 | 2512 | 9.1 | 61 |
| Ache | M | 59.6 | 6484 | 13927 | 2.15 | 7443 | 19.2 | 125 |
| | F | 51.8 | 5647 | 10992 | 1.88 | 5346 | 9.2 | 103 |
| Current Westerners[2] | | | | | | | | |
| Office worker | M | 70.0 | 6869 | 9444 | 1.37 | 2574 | - | 37 |
| | F | 58.0 | 5584 | 7677 | 1.37 | 2093 | - | 36 |
| Fitness Enthusiast | M | 70.0 | 6869 | 12642 | 1.84 | 5772 | 12 | 82 |

[1] From (32)
[2] Derived from National Research Council Recommended Daily Allowances Tables 3–1 and 3–3 (39). Fitness enthusiast exercising equivalent of running 7.5 mph, 60 min/day (25).
RMR, resting metabolic rate; TEE, total energy expenditure; PA, physical activity (ignoring the thermic effect of food). 1 kJ = 0.238 kcal.

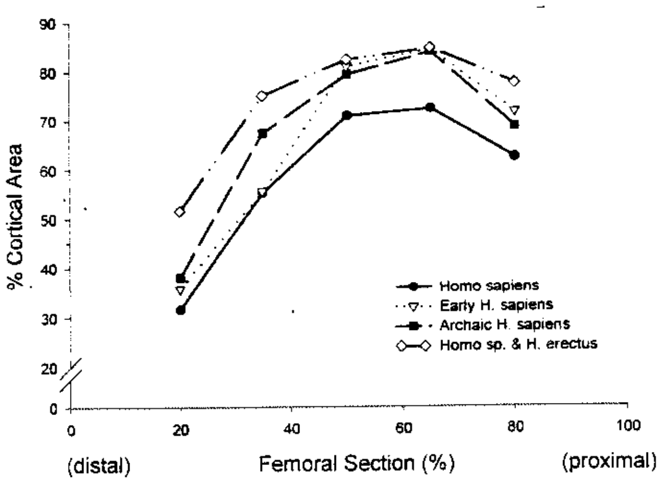


**Fig. 2** Differences in percent cortical area ([cortical area/periosteal area] × 100) along the length of the femoral shaft in early and recent *Homo* (from 47).

ovascular, metabolic, and thermoregulatory systems capable of sustaining high level aerobic exertion (1,46), physiological adaptations necessary for diurnal hominids who traveled considerable distances as they hunted, scavenged, gathered, and carried in hot equatorial climates.

*Homo erectus* began spreading from Africa at least a million years ago, colonizing the warmer regions of southern Asia. Forms intermediate between *H. erectus* and *H. sapiens* appeared perhaps 500,000 to 400,000 years ago. In Europe these evolved into the Neanderthals. In Africa they gave rise to anatomically modern *Homo sapiens*, who appear in the fossil record there somewhat before 100,000 BP (Before Present). At first this anatomic modernity was not associated with archaeologically recognizable cultural advances; *H. sapiens* lived much like his predecessors. However, between 50,000 and 40,000 years ago their creativity and technological innovation increased dramatically (54), so that the efficiency of hunting, gathering, food processing and many other necessary activities was improved. During this period skeletal robusticity decreased somewhat, suggesting that less muscular force was required for daily tasks (47). Still, the Cro-Magnons and other anatomically modern humans of this era continued to be hunter-gatherers – vigorous physical activity remained an essential feature of their existence. A gathering and hunting lifestyle remains the fundamental link between the Stone Agers of 25,000 years ago and foragers studied in this century. Circumstances in the late Paleolithic (35,000 to 15,000 BP) differed in important ways from the experience of recent hunter-gatherers. For example the latter now inhabit areas with marginal resource availability, the likely cause for their short stature (which contrasts with that of Late Paleolithic humans). Nevertheless foragers like the Ache, !Kung, Agta, Hadza, and Inuit provide a window into the lives of our preagricultural ancestors – including insight into the physical activity patterns for which our species is genetically constituted.

## Energy Expenditure, Physical Activity and Fitness

Daily energy intake is expended for physical exertion, growth, reproduction, RMR, and to offset the thermic effects of food (mastication, increased peristalsis, digestion, etc.). Any excess is stored as fat. At present, for average humans in affluent nations, RMR comprises about 70% of TEE and the thermic effect of food 5 – 10%; most of the remainder of TEE is attributable to physical activity (9). RMR is closely related to body size across mammalian species, often being estimated as 70 times body mass (in kg) to the 3/4 th power (27).

### *Physical activity patterns*

Prior to this century, human/prehuman activity patterns and daily ranges were largely dictated by food procurement. Like most other primates, Australopithecines lived in habitats dominated by woodlands and forests. In these areas, foods were readily available and a limited range was sufficient for subsistence (Table **2**). However, between 2.5 and 1.5 MYA, forestation in eastern and southern Africa decreased markedly due to a prolonged drying period (5,15). This environmental shift from woodland to open savanna altered the abundance and distribution of food resources (22) and required early members of the genus *Homo* to extend their daily range (20). *H. erectus* may have transported tools, weapons and game over 15 km (23,28), similar to recent foragers who have substantial daily ranges (Table **2**).

The weekly activity pattern of gatherer-hunters in this century follows what has been called a Paleolithic rhythm: men commonly hunt from one to four nonconsecutive days a week with intervening days of rest and women routinely gather every two or three days (48). Other common physically taxing activities include tool making, child care (an average child is carried 1500 km during its first two years of life [30]), butchering and other food preparation, clothing preparation, carrying firewood and water and moving to new campsites. Dances (which can last for hours) are a major recreational activity of many cultures, often taking place several nights a week. Overall, the Paleolithic rhythm involves days of fairly intense physical exertion which alternate with days of rest and light activity (48).

### *Total energy expenditure*

Because their daily ranges were almost certainly greater, *H. habilis* and *H. erectus* probably had greater TEE than did Australopithecines. To account for differences in body size, it is useful to discuss TEE/RMR rather than absolute TEE. This ratio has been estimated at 1.6 for Australopithecines, 1.7 for *H. habilis*, and 1.8 for *H. erectus* and early *H. sapiens* (32) (Table **2**). The measured TEE/RMR of recently studied foragers approaches 2.0 (for contemporary rural agriculturists it can exceed 2.0), but in striking contrast, TEE/RMR for modern, sedentary humans in affluent societies is below 1.4 (Table **2**)!

Fig. **3** expresses estimated energy expenditure as a function of body mass and suggests that RMR and TEE, expressed per kg body weight, remained relatively consistent for human ancestors over a period of 3.5 million years until contemporary *H. sapiens* became affluent and sedentary. Typical current Westerners have TEE/kg/d values barely equaling the RMR/kg/d of recent hunter-gatherers and of that estimated for our preagricultural ancestors. The RMR/kg/d reduction for modern humans probably reflects altered body composition (more fat, less muscle), a result of sedentary living (43). The TEE/kg/d of typical contemporary humans is about 65% that of late Paleo-

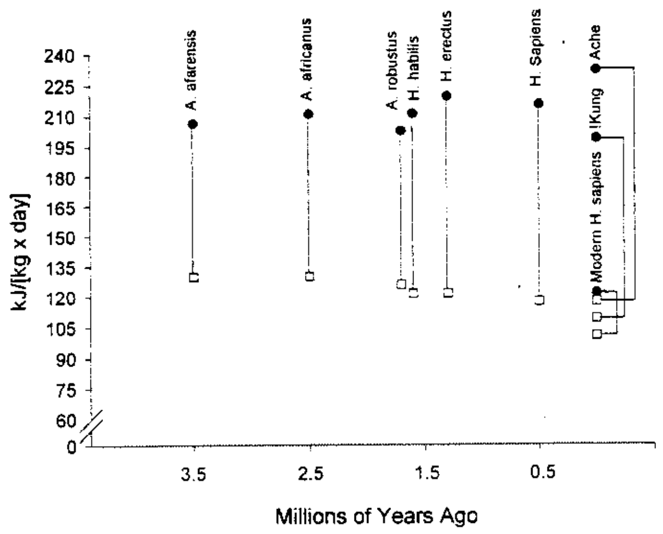


**Fig. 3** Estimates of Hominid daily energy expenditures over the past 3.5 million years (adapted from [32] and Table 2). Open squares are resting metabolic rates; filled circles are total energy expenditures. Values for Mexican Indians are exaggerated by the ritual running of the Tarahumara runners.

lithic Stone Agers (assuming their TEE/kg/d was similar to that of recent foragers; 134 kJ/kg/d for contemporary humans compared to the average of 206 kJ/kg/d for !Kung and Ache). Subtracting RMR from TEE provides a rough measure of the energy expenditure due to physical activity (PA) (although it disregards the thermal effects of food). The energy expenditure per unit body mass of PA for contemporary Westerners is about 38% that of our human ancestors, a discrepancy even more startling than that for TEE. For typical Americans to approximate the TEE/kg/d of recently-studied gatherer-hunters it would require adding ~72 kJ/kg/d (~17 kcal/kg/d), the equivalent of a 19 km (12 mile) walk for a 70 kg man, to each day's current activity level!

### *Aerobic fitness levels*

It should not be surprising that the limited physical activity typical of modern affluent humans generates mediocre aerobic fitness nor that the aerobic fitness levels of recently-studied foragers are superior to those of North Americans. Hunter-gatherers and other traditional populations have aerobic fitness levels ranging from good to excellent when plotted against fitness norms derived from studies of Amercians (49, 51) (Fig. 4). The effects of modernization are also predictable. Between 1970 and 1990 a community of Canadian Inuit acculturated from a partially traditional (hunting/fishing) lifestyle to a largely Western way of living – including extensive use of ski mobiles, outboard motors and labor-saving household appliances (44). During the 20-year period the Inuit became fatter as a group while they lost muscular strength and aerobic fitness. In 1970, before acculturation, both Inuit men and women were more aerobically fit than age-matched men in industrialized nations, but by 1990, the Inuit physical superiority had become much less pronounced (Fig. 5).

### *Modern guidelines for fitness and health*

There has been much interest in the amount of physical activity that should be recommended by health professionals. Physical activity/training improves both athletic performance and overall health, benefits which are not mutually exclusive. Performance exercise characteristics have been clearly defined: the 1995 American College of Sports Medicine (ACSM) guidelines (2) recommend participating in physical activity 3–5 days/week, at 50–85% maximum intensity, continuously for 20–60 minutes. For health promotion, however, the ACSM suggests individuals accumulate 30 minutes of physical activity over most days of the week (2). Activity need not be continuous, and can be of moderate intensity (equivalent to walking 4.83 kilometers per hour, or 3 miles per hour). On the other hand, several recent reports have emphasized the dose-response nature of physical activity and related health outcomes (6, 8, 24, 42).

Comparing minimum physical activity requirements for health promotion as proposed by the ACSM (2) with estimates of ancestral physical exertion reveals a striking discrepancy. A 70 kg man who walks 4.83 km per hour for 30 min (1.5 mi) expends an additional ~628 kJ (~150 kcal). Adding these 628 kJ to the ~2574 kJ (615 kcal) a typical male office worker expends in daily activities (Table 2) totals 3202 kJ/d (45.7 kJ/kg/d, or 11 kcal/kg/d), a value which satisfies ACSM recommendations. However, this expenditure falls far short of the !Kung male's 82 kJ/kg/d (19.6 kcal/kg/d) or the Ache male's 125 kJ/kg/d (24.7 kcal/kg/d). The ACSM guidelines are roughly 44% of the level of energy expended by PA observed among hunter-gatherers[3], almost surely far below those of our preargricultural ancestors, and, very likely, below the level of physical exertion for which our genetically-determined physiology and biochemistry have been programmed through evolution.

Total energy expenditure from physical activity may be the key component for health benefits (7, 31). Weekly activity-related energy expenditures of 4,186 to 12,558 kJ (1,000 to 3,000 kcal) have been proprosed as necessary for significant health benefits (38, 41, 52). For a 70 kg man this implies 63 to 179 kJ/kg/week (15 to 45 kcal/kg/week), far below the expenditure of modern foragers – !Kung males expend 573 kJ/kg/week (137 kcal/kg/week) and Ache males 724 kJ/kg/week (173 kcal/kg/week) – and also much below estimates for preagricultural human ancestors.

If the level of physical activity suggested by the ACSM for health promotion can be considered a minimum, what level is necessary for optimizing health benefits? The answer may lie in the experience of our ancestors and, if so, could be PA energy expenditures in the range of 377 kJ/kg/week (90 kcal/kg/week); the equivalent of walking 406 kilometers (252 miles) per month in addition to current physical activities. While this seems extreme, the daily range of the !Kung male is about 15 kilometers (9 miles) per day, a figure close to that for William Wordsworth, whose experience can serve as an exemplar of activity levels just before the Industrial era began and who is estimated to have walked 289,800 kilometers (180,000 miles) during his life (about 15 kilometers/d for 60 of his 70 years) (16)! In evolutionary perspective it is the sedentary existence characterizing life in contemporary affluent nations which represents the extreme, not the lifestyle which prevailed gener-

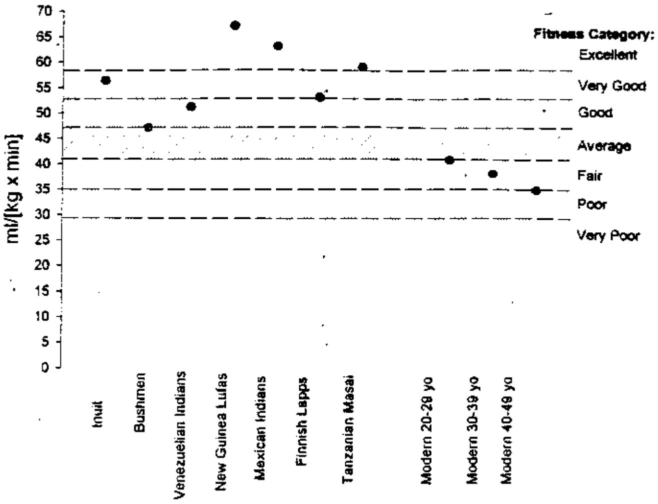


**Fig. 4** Comparisons of maximal aerobic capacities (maximal oxygen consumption) between unacculturated and acculturated (industrialized) societies (adapted from [18]). Fitness categories based upon (51) for modern, acculturated societies.

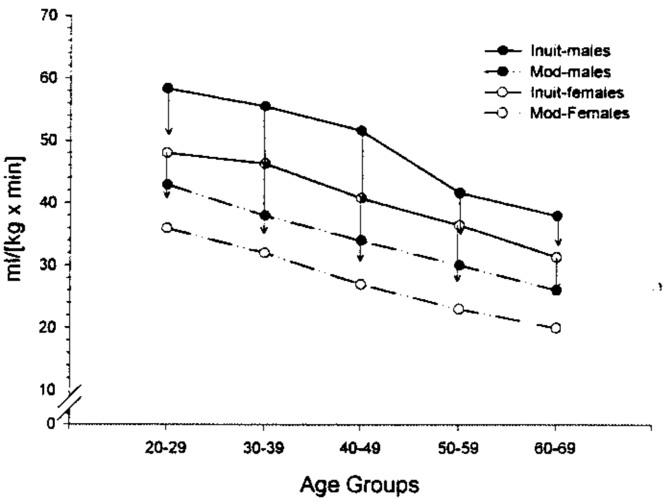


**Fig. 5** Comparisons of maximal aerobic capacities (maximal oxygen consumption) between Inuit and acculturated populations by age groups (adapted from [44]) for the Inuit, and from [51] for acculturated populations). Mod = modern acculturated population. Dropped arrows represent the change in Inuit fitness over 20 years of acculturation from 1970 to 1990 (44).

ally for humans from the origin of our genus until well after industrialization appeared 200 years ago.

## Conclusions

With the exception of *Homo sapiens*, mammals have to work in order to eat: food procurement depends directly upon energy expenditure. However, technological achievement and social organization have disrupted this basic relationship for contemporary humans. In today's affluent nations there is no longer an obligatory link between the food we eat and the energy we expend. Food energy has become more affordable and accessible, while mechanization has reduced work-related physical exertion and recreational pursuits have become more sedentary. The result is a relative energy surplus, increased body weight, sarcopenia, and distorted body composition with an excess of adipose tissue relative to bone and muscle (18, 34). Evolution has endowed humans with exceptional adaptability, but our capacity in this regard has limits and current circumstances, novel in evolutionary and comparative zoological experience, appear to have exceeded our threshold. Human biology has become so disordered that physiological and biochemical risk factors affecting the cardiovascular system, the skeleton, and our carbohydrate metabolism are now unprecendentedly common. In each case, departure from exercise patterns which prevailed during evolution plays a fundamental role (18).

Per-Olof Åstrand stated that, "Through the centuries humans have chosen a food intake sufficient to provide an energy intake of 12,000 kJ (about 3000 kcal) or more" (3). This contention matches paleoanthropological data which indicate that a TEE of 209 kJ/kg/d (50 kcal/kg/d) or 14.651 kJ/d (3500 kcal) for a 70 kg human was typical for human ancestors from the appearance of *A. afarensis* until the late 19th Century. The circumstances of life in today's affluent, industrialized nations are hardly conductive to adding physical exercise with another 4,186 – 6279 kJ (1000 – 1500 kcal) to each day's already hectic schedule. However, the activities of our ancestors, while demanding, lacked the efficiency of physical exercise conducted according to the tenets of modern exercise physiology. It might be possible to attain similar physiological effects with less time expenditure: investigations designed to explore this possibility are needed. To emulate the essential physiological and metabolic benefits of physical exertion as experienced throughout the evolution of humanity is a logical and attractive goal, on which accomplishment might advance health promotion, disease prevention and general well-being. The most efficient methods for its achievement and a fuller understanding of its impact on human health merit the best investigative efforts of exercise scientists.

## Footnotes

[1] We use the terms hunter-gatherers, gatherer-hunters, and foragers interchangeably.
[2] Hominoids: common ancestors of Hominids and Pongids.
[3] Average of !Kung and Ache (104 kJ/kg/d).

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