Feature Article

Physical Activity: The Present in the Context of the Past

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ABSTRACT In the broad sense, modern humans have lived in an environment in which physical activity and associated movement skills were central, especially in the context of physical competition with other animals. The physically active lifestyle of earlier human populations has been emphasized, especially the cardiovascular endurance component and energy expenditure, but less attention has been devoted to the gross and fine motor skills that are essential components of this lifestyle. Motor skills developed through practice are important determinants of success and survival in preindustrial societies. In industrial and postindustrial societies, on the other hand, the role of physical activity is different, with prowess in certain areas of physical expertise (e.g., accuracy with projectiles, muscular strength, among others) and prolonged exertion (i.e., cardiovascular endurance) less important for survival. The combined effects of the transition to a sedentary lifestyle and attendant dietary changes have resulted first an epidemic of coronary heart disease and more recently an epidemic of overweight/obesity in postindustrial societies. Although mortality associated with coronary heart disease has declined, due largely to biomedical advances, overweight and obesity have increased concomitantly with population reduction in physical activity (energy expenditure) and increased calorie (energy) consumption. The current scenario begs several questions which have implications for contemporary human biology related to sustaining the pace of cultural change on a biological base that is increasingly being compromised by physical inactivity, overweight, and obesity. Am. J. Hum. Biol. 20:373–391, 2008.

Physical activity is a topic of current discussion, specifically in terms of health promotion and disease prevention. Physical inactivity, on the other hand, is indicated as a major risk factor for morbidity and mortality in adults (American College of Sports Medicine, 2001; World Health Organization, 2005) and is increasingly being implicated as major risk factor for morbidity in children and adolescents (Strong et al., 2005). Physical inactivity is also implicated in the recent worldwide epidemic of obesity (Caballero, 2007; World Health Organization, 2000), which in turn is also an independent risk factor for morbidity and mortality in adults (World Health Organization, 2005) and also for metabolic morbidities in children and adolescents (Strong et al., 2005).

The lifestyles of earlier human populations included physical activity on a regular basis, a mixture of continuous and intermittent activities associated with hunting, gathering, and agriculture. Many discussions of earlier populations focus on the physically active lifestyles of hunter-gatherers (Bortz, 1985; Cordain et al., 1998; Eaton and Eaton, 2003; Hayes et al., 2005). The motivating factors for the physically active lifestyle were food (hunger) and in some instances water (thirst), not necessarily a desire for activity. Availability of food and water sources influences group migration, which of course involved men, women, and children walking while carrying limited possessions and young children. Given the active lifestyle and at times unpredictable diet, obesity was in all likelihood rare among earlier hunter-gatherers (Eaton et al., 1988). It is suggested that "... humans living today are Stone Age hunter-gatherers displaced through time to a world that differs from that for which our genetic constitution was selected" (Eaton et al., 1988, p 739).

Discussions of earlier populations seemingly focus on males more so than females, and rarely consider children and adolescents. Division of labor between males and females in earlier populations and contemporary hunter-gatherers is common. As such, focus is often on the physical activity of hunters (males) in contrast to gatherers (females). It is also reasonable to assume that children and adolescents are regularly active as they learn expected adult behaviors through modeling of and participation in adult behaviors during youth.

Many human behaviors and responses are probably rooted in our evolutionary past, both long term and short term. This review presents an overview of (1) the biocultural phylogeny of human physical activity; (2) trends in the physical activity of contemporary hunter-gatherers and agriculturalists relative to industrial populations; and (3) the secular decline in physical activity and fitness, on one hand, and the secular increase in obesity, on the other.

PHYSICAL ACTIVITY AND PHYSICAL FITNESS

Physical activity is a behavior or more appropriately a series of behaviors which involve bodily movements produced by skeletal muscles. Movement is the substrate of activity. Physical activities comprise a range of behaviors that can be viewed from several perspectives. Present day public health and biomedicine tend to view activity largely in terms of energy expenditure (physiological) and to a lesser extent in terms of the stresses and strains associated with weight bearing and ground reaction forces (bio-

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mechanical). The focus is largely health promotion and disease prevention. Physical activities also have major performance dimensions viewed in specific movement skills and physical fitness, traditional domains of the sport sciences. The settings and types of activities, i.e., contexts–subsistence, play, education, work, exercise, sport, training, among others, are additional but important dimensions. Contexts vary with culture, the system of meanings and associated feelings in which individuals and groups are embedded. The system of meanings is an amalgam of symbols, values, and behaviors that characterize a population (Kroeber et al., 1952). Meanings influence beliefs, sanctions and definitions, and ultimately human behaviors, including physical activity and inactivity in their many forms.

Physical fitness is often discussed with physical activity; it is a state or a condition which permits the individual to carry out her/his daily activities without undue fatigue and with sufficient reserve to enjoy active leisure pursuits. Physical fitness was historically viewed in terms of three components: muscular strength and endurance, cardiorespiratory endurance, and motor ability (Clarke, 1971). The concept has since evolved to place more emphasis on health-related physical fitness defined in terms of cardiorespiratory endurance; muscular strength and endurance; musculoskeletal function of the lower trunk and upper thighs, specifically flexibility; and body composition, specifically fatness (American Alliance for Health, Physical Education, Recreation and Dance, 1980). Morphological and metabolic components have since been added to the more traditional cardiovascular, muscular strength and endurance, and motor components (Bouchard and Shephard, 1994). Physical fitness is often an assumed correlate of physical activity though relationships are generally moderate during childhood and adolescence (Malina et al., 2004), but are stronger in adults, especially between habitual activity and cardiorespiratory fitness (Blair, 2007; Blair et al., 2001).

Features in the emergence of hominids/humans

The evolution of hominids/humans can be viewed in the context of four important features: bipedalism, expansion of the brain relative to body size, tool making, and language. Bipedalism is evident in the fossil record between ~8 and 5 million years before present (mybp) and adaptations associated with upright walking are postulated as central to subsequent biological and cultural evolution (Lovejoy, 1988). The expansion of the brain is a major feature in the evolution of hominids/humans. The brain is costly energetically (Leonard et al., 2003), and its size has increased proportionally more relative to the increase in body size especially since the Australopithecines and Homo habilis (McHenry and Coffing, 2000). Primitive tools are apparent in the fossil record since about 2.5 mybp (McHenry and Coffing, 2000; Plummer, 2004), while language is estimated to have been established about 50,000 years ago (Lewin 1993a,1993b).

The evolutionary development of bipedality, the brain, tool manufacture, and language highlight the concurrent progress of biological and cultural evolution. The neuromotor system is intimately involved in these evolutionary changes. The primacy of the neuromotor system is obvious in bipedal locomotion and proficiency in tool making and use, but it is also a major component of speech as evident in the movements of the lips and tongue and the relative dominance of these structures (and also the hands) in the sensory-motor cortex.

The dominance of the brain is reflected in the human growth curve. The human brain attains about 20% of adult size at birth and is characterized by rapid growth early in postnatal life so that about 95% of adult size is attained by 6–7 years (Malina et al., 2004; Scammon, 1930). In contrast, postnatal somatic growth and maturation are characterized by relatively slow progress compared with the brain and associated structures. The relative immaturity and lengthened period of postnatal somatic growth and maturation are important largely for cultural reasons. Slow somatic growth and prolonged immaturity have an important correlate in dependency with associated learning and cultural transmission: "Biologically, it takes more time to become human. Obviously, too, it is the human brain and human learning which gain particular advantages by this biological slow down" (La Barre, 1954, p 153).

Rapid growth and maturation of the brain and central nervous system, associated myelinization and cortical remodeling, and changes in electrical (EEG) activity during approximately the first 6–7 years of postnatal life are obviously important in the development of motor/movement competence and language. Focus of the present discussion is on movement, which is the substrate of physical activity. Independent walking from first steps to proficiency is the major motor development task during the first 2 years of life. With the refinement of the walking pattern, the development and control of a variety of locomotor (running, jumping, climbing, skipping, etc.) and manipulative (gross as in throwing and striking, fine as in pincer grasping) abilities improve. Basic movement patterns develop during these early postnatal ages and are the foundation upon which other movements and combinations of movements are developed and refined (Malina et al., 2004). Movement patterns are refined through appropriate modeling, instruction, and practice; performance quality improves; and the basic patterns are integrated into more complex movement sequences and skills required for specific cultural demands.

Physical activity and biocultural evolution

Proficiency in gross and fine movements associated with tool manufacture and use and with hunting and gathering played an important role in the biocultural evolution of the genus Homo. Tools are an extension of the brain because they augment the ability to act upon the physical environment and facilitate expansion into a variety of ecological zones. With the emergence of early stone tool technologies about 2.5 mybp, the complexity of tool assemblages evolved from the relatively simple Olduwan (largely pebble tools and flakes) to the Acheulian (more variety, hand ax, cleaver, pick), and then increased markedly with archaic (60–70 different types) and then modern (especially blades and special purpose tools) Homo sapiens (Lewin, 1993a,1993b). Technological change also proceeds at rates that genetic change cannot match.

Our biocultural evolution can be characterized as a series of complex interactions between hominids/humans and their environments, and associated adaptive responses to the natural environment, human modifications of the environment, and the human or social environments. Over time the adaptive processes involved

TABLE 1. Indicators of cultural development and approximate chronology in the genus Homo (million years before present)

Oldowan tools	2.500 million ybp
Acheulian handaxe	1.700
Regular hunting	1.500
Use of fire/home base	0.500
Mastery of fire	0.250
Fishing harpoons	0.075–0.080
Arrow points (bow implied)	0.065–0.070
Language	0.050
Paleolithic art	0.035
Spear thrower	0.017
Bow	0.011
Agriculture	0.010
First cities	0.007
Earliest writing	0.0032
Industrial revolution	0.0002
Technological revolution	0.000025

Collated after Lewin (1993a,b), Marlowe (2005).

transitions from a relatively mobile to a more settled way of life, though the timing and tempo of transitions varied, and a variety of behavioral and biological responses to different environmental stresses. The transitions included the shift from hunting and gathering to agriculture about 10,000 years before present (ybp), the move from agriculture to settled communities and then early cities about 7,000 ybp, and more recently to the industrial (about 200 ybp) and technological (about 25 ybp and ongoing) revolutions. Each transition had major benefits but also had associated stresses. An approximate chronology of several major transitions and cultural developments is summarized in Table 1. It is reasonable to assume that biological and cultural evolution proceeded in concert for most of our existence as a species until relatively recently when the pace of cultural development has accelerated sharply.

The lifestyle of hominids/humans included physical activity on a regular basis throughout their evolutionary history except for the past two or three generations. The way of life associated with hunting, gathering, and agriculture probably included a mixture of continuous and intermittent activities which ranged from light to moderately vigorous with occasional periods of intense, vigorous activity. Periods of activity were balanced with periods of rest or inactivity. Quite recently this active lifestyle has been replaced by one that is considerably more sedentary. We thus may be biologically equipped for a physically active lifestyle, while cultural circumstances permit and reinforce an inactive alternative—at least for segments of populations resident in developed and also developing economies.

It is important to note that physical activity of earlier populations was not an isolated component of lifestyle as in many present industrialized populations. Rather, physical activity was an integral component of the nutritional ecology of hunter-gatherer populations: "... the interaction of diet, somatic maintenance, physical activity, and pathogenic agents as they relate to growth, body composition, development, and function ... (the) observed patterns of food intake, physical activity, growth, and health are viewed as the result of behaviorally and physiologically mediated trade-offs imposed by a constraining environment" (Jenike, 2001, p 207).

Insights into earlier populations

It is commonly asserted that our species has lived as hunter-gatherers for more than 99% of the past two million years (Lee and Devore, 1968). There is disagreement whether it was opportunistic scavenging or systematic hunting (Binford, 1985), although it has been suggested that effective scavenging goes hand-in-hand with effective hunting (O'Connell et al., 1988). These issues are beyond the scope of this discussion. Of relevance, it is generally inferred that the lifestyle of hunter-gatherers was physically active based on observations of skeletal remains of earlier hunter-gatherer populations (specifically anatomically modern humans) and contemporary hunter-gatherers (foragers).

The relevance of contemporary hunter-gatherers for inferences on earlier populations is often questioned on the grounds that they tend to live in marginal habitats (Binford, 2001; Eaton and Eaton, 2003; Lee and Devore, 1968). Recent evaluation of habitats based upon global remote sensing data suggests, however, negligible differences between the habitats of ethnographic samples of foragers and agriculturalists (Porter and Marlowe, 2007). It is also suggested that hunter-gatherers live close to the edge of subsistence (Binford, 2001). Limited data for contemporary hunter-gatherers indicate low heights and weights of children, often below the 5th and 3rd percentiles, e.g., Dobe !Kung (Truswell and Hansen, 1976) and Ache (Walker and Hill, 2003). Growth status suggests nutritional stress associated with marginal energy and nutrient intake which is commonly associated with elevated infant and preschool mortality (Bengoa, 1972; Gordon et al., 1967). Adult heights of contemporary hunter-gatherers are, on average, quite short compared with the western reference values (Binford, 2001; Jenike, 2001), perhaps reflecting nutritional and disease stresses early in life and uncertainties associated with the foraging lifestyle (Froment, 2001). Adult heights are also shorter than estimates for earlier Homo specimens (McHenry, 1992; McHenry and Coffing, 2000).

Hunter-gatherers: cardiorespiratory endurance

Discussions of the physical activity habits of hunter-gatherers often focus on cardiorespiratory endurance. Early hunters have been described as endurance specialists, specifically endurance running in a hot environment (Bortz, 1985; Bramble and Lieberman, 2004; Carrier, 1984). Accordingly, endurance running, presumably by males, over long distances in hot, midday temperatures facilitated tracking and chasing of prey was an adaptive advantage which "... may have provided early hominids with a reliable mechanism for increasing their intake of animal protein" (Carrier, 1984, p 492), or endurance running as in scavenging and hunting "... may have made possible a diet rich in fats and proteins thought to account for the unique human combination of large bodies, small guts, big brains, and small teeth" (Bramble and Lieberman, 2004, p 351).

On the other hand, others have maintained that early human hunters were adapted to long distance walking and not to running (Leonard and Robertson, 1997a; Lovejoy, 1988). Walking of course required cardiorespiratory endurance though not at the extreme as required for running. This is consistent with observational data for modern foraging groups, e.g., !Kung, Ache, and Efe, which indicate that walking at moderate speeds is the primary movement strategy during hunting (Astrand, 1994; Bailey, 1991; Hill and Hurtado, 1989; Hill et al., 1985). This is likely because relative to other mammals of the same size, human bipedal locomotion is energetically economical at walking speeds but is quite expensive while running (Leonard, 2002; Leonard and Robertson, 1997a, 1997b). Mobility of groups is also related to walking. Although mobility varies widely among hunter-gatherers, greater distances are generally traveled in the most difficult foraging environments (Kelly, 1995).

Proponents of the running hypothesis suggest that endurance running capacity was under strong selective pressure: "... the best hunter, the alpha runner, had survival and reproductive advantage" (Bortz, 1985, p 148). Emphasis on the selective advantage of endurance capacity in evolution of late Paleolithic populations (50,000–10,000 ybp) was also placed in the context of the "thrifty gene" hypothesis (Neel, 1962), which relates to the more efficient storage of fuel (glycogen) during cyclical feast and famine conditions (and perhaps during unsuccessful hunts). The hypothesis was extended to more efficient oxidation of stored fuel during famine and physical activity (Booth et al., 2002; Chakravarthy and Booth, 2004). Given the more efficient use of muscle glycogen stores with endurance training, thrifty genes related to endurance activity have been hypothesized and have been suggested as consistent with "... Darwin's 'survival of the fittest' hypothesis because of the advantage given to the hunter-gatherer by improved physical endurance" (Chakravarthy and Booth, 2004, p 6, see Note). It should be noted, perhaps, that ethnographic data for contemporary foragers and agriculturalists suggest inconsistencies in the assumptions of Neel's (1962) "thrifty gene" hypothesis (Benyshek and Watson, 2006).

Selective advantage and Darwinian or biological fitness refer to survival and reproductive efficiency and fertility. It is generally defined in terms of the average reproductive success of an individual. According to Dobzhansky (1962, p 125), "... the genetic fitness of a phenotype, and by extension of an individual, is measured by the contribution it makes, relative to other genotypes or individuals, to the gene pool of the succeeding generations. The biologically fittest parent is the parent with the greatest number of surviving children." Components of Darwinian fitness include mate selection, mating success, social status, age at marriage, fecundity, rate of reproduction, progeny survival to maturity and longevity. Characteristics of an individual, including cultural context, which influence survival to reproductive age and subsequent reproduction affect their genetic fitness.

Ethnographic observations of contemporary hunter-gatherers suggest that foraging patterns are more complex than running or other physical activities imply; it has been suggested that foraging patterns are part of an overall reproductive strategy that varies with age, sex, reproductive status, stage of life and local ecology (Hawkes et al., 1997). Endurance capacity may have been or may be a component of mate selection and reproductive success among hunter-gatherers, but data relating endurance capacity to reproductive success are lacking. A number of genes and markers associated with endurance phenotypes have been identified (see, for example, Rankinen et al., 2006; Wolfarth et al., 2005). However, research into the role of DNA sequence variation in contributing to individual differences in endurance (and other performance related phenotypes) is quite limited (Rankinen et al., 2006).

Hunter-gatherers: intermittent activity

Other considerations of the physical activity patterns of Paleolithic hunter-gatherers suggest habitual and largely intermittent activity except for long range walking, which varies in type and intensity from light to moderate but periodically vigorous (Cordain et al., 1998; Eaton and Eaton, 2003). Activities of late Paleolithic hunter-gatherers included walking (gathering, hunting, migrating), running (after wounded prey, flight), carrying (game meat, children, plants), flint knapping, tool making, meat butchering, digging (roots, tubers), dancing (recreational, ritual), playing, and others (Eaton and Eaton, 2003). The pattern suggests "cross-training" (Eaton and Eaton, 2003), in contrast to the aerobic (endurance) and resistance (strength) training models of exercise physiology and the sport sciences. The pattern also includes motor skills as in flint knapping, tool making and butchering, and presumably in activities specific to hunting and gathering (see Sahlins, 2005).

Hunter-gatherers: motor skills

The acquisition and refinement of requisite motor skills for hunting and gathering behaviors—cognitive, motor, and social—are not often considered. It seems logical that the foundations for these skills and behaviors are developed and learned during childhood and adolescence and subsequently refined in adulthood.

Data dealing with the development of movement skills related to hunting and gathering in children and adolescents of contemporary hunter-gathers are limited. Inferences may be gleaned from general discussions or depictions of childhood activities (e.g., Draper, 1976; Gardner and Heider, 1968; Smole, 1976; Sorenson, 1976), but specific studies are few. Foraging patterns and return rates of Hadza children provide insights into general behaviors, but specific movement patterns and skills are not considered (Hawkes et al., 1995). On the other hand, !Kung children apparently do not forage with adults as they progress too slowly; it is suggested that children do not handle the walk in high temperatures during the dry season very well (Blurton Jones et al., 2002). This is an interesting insight of the !Kung because children have a higher surface area-to-mass ratio which is related to heat transfer; in addition, children have a lower sweating rate than adolescents and adults (Malina et al., 2004). The growth pattern of grip strength, upper body muscular strength and endurance, running speed and estimated aerobic capacity among Ache youth is similar to that described for Western youth, though the timing of the adolescent inflection in males appears later. In girls, the dash (running speed) and upper body muscular strength and endurance show negligible change between 9- to 14- and 15- to 19-year age groups (Walker and Hill, 2003). Note, some of these standard tests require an all out effort and cultural definitions/interpretations of maximal effort may be a factor affecting performances.

Motor skills per se (gross and fine coordination, accuracy of movement, speed, agility, among others), strength, power, and aerobic capacity are related in part to growth and maturation. Performances on a variety of movement tasks improve with age during childhood. Boys perform, on average, better than girls, but there is considerable overlap between the sexes during childhood for most tasks with the exception of overarm throwing. With the onset of adolescence, the performances of boys show acceleration, while those of girls improve to about 13–14 years of age and then level-off or improve only slightly. Performance during adolescence is influenced in part by individual differences in the timing of the adolescent growth spurt. Performances in a variety of tasks show well-defined adolescent spurts in boys. Measures of static strength (grip, arm pull), power (vertical jump, standing long jump, medicine ball throw), and functional strength and endurance (flexed arm hang) show peak gains, on average, after peak height velocity (PHV), while measures of speed and agility (shuttle run) and speed of arm movement (as in the number of times two plates, 20 cm in diameter and separated by 60 cm, are tapped in 20 s) show peak gains before PHV. Data-relating performances of girls to the adolescent spurt are not extensive. Like boys, girls show an adolescent spurt in static arm strength after PHV, but the magnitude of the growth spurt in strength is only about one-half of the maximum gain in boys. Limited data for other tasks are inconsistent compared with the adolescent trends in performance tasks observed in boys (Malina et al., 2004).

Age- and sex-associated variation in measures of submaximal and maximal aerobic power is similar to those for muscular strength and power. Sex differences are minor prior to adolescence and are magnified during the growth spurt. In contrast to strength and power, maximal aerobic power ($\dot{V}O_2$ max) has a growth spurt that occurs, on average, coincidentally with PHV in both sexes. Estimates for the growth spurt in submaximal power (PWC_{170}) are variable in timing relative to PHV (Malina et al., 2004).

It may be hypothesized that prolonged childhood characterized by relatively slow growth and later maturation provides the time needed for the development of strength, power, and coordination per se and the development and refinement of movement skills essential to the hunting and gathering lifestyle. The relative importance of skill versus strength, power and endurance in hunter-gatherer societies, however, is a topic of debate (Blurton Jones and Marlowe, 2002; Kaplan et al., 2000).

Accuracy of performance

Accuracy in projecting an object (stone, arrow, spear), the ability to hit a given point with the projected object, is an essential to many forms of hunting. In addition to permitting killing at a distance, it also reduces associated risks of being in close proximity to large animals/big game prey. Proficiency in one-handed throwing has been suggested as important in hominid evolution, specifically in the evolution of the brain (Calvin, 1982, 1983; Darlington, 1975). Precision (accuracy) in one-handed throwing in hunting requires the coordination of three elements, the thrower (who may be moving), the object thrown, and the target (a stationary or moving animal). It is also suggested that the hand of Australopithecus afarensis was adapted for forceful and precise throwing (Isaac, 1987; Marzke, 1983).

Children and adolescents tend to perform reliably on throwing accuracy tests (Malina, 1968). Throwing accuracy tends to increase, on average, with age and scores are higher in boys than in girls (Keogh, 1965; Malina and Roche, 1983; Wickstrom, 1983). Corresponding data on the projection of arrows with a bow are limited. The ability to hit a target (25-cm circumference) propped on a 4-m pole from a distance of 8.8 m with an arrow projected by a bow in youth 10–16 years of both sexes and women and from a distance of 14.3 m in men 17 years of age and older was field tested in a sample of Ache. Success in 10 attempts, i.e., arrows stuck into the target, was quite poor, 0 of 70 in male youth, 2 of 344 in all women (presumably including female youth) and 81 of 1934 in men (Walker et al., 2002). In an analysis limited to 57 males 10–65 years, age and strength were significant predictors of accuracy. Although there was considerable variation in successful hits across the age range, the percentage of successful hits increased with age to about 40 years, followed by a plateau. Field observations of hunting ability (return rate, probability of a kill) also peaked at about 40 years of age (Walker et al., 2002).

A similar experiment with 100 Hadza males 4–77 years of age considered accuracy of shooting an arrow with a bow at target at a distance of 15 and 25 m (Blurton Jones and Marlowe, 2002). The target was a 62×61 cm^2 rectangle on which three concentric circles 33, 20, and 4 cm in diameter were painted. Each individual had three attempts at each distance on 2 days for a total of 12 attempts. A measure of bow pull strength for 71 males was also recorded. Accuracy scores increased linearly with age from childhood ($\sim$10 points) to the early 20s ($\sim$24 points), and then slightly through the 30s ($\sim$27 points). Reputation as a good hunter also reached a peak in the 30s. Inter-individual variability in accuracy scores was considerable; it appeared to be greatest in the teen ages and also in adults 40–60 years of age. Of interest, the three highest scores were made by a teenager and by two adults, one in his 40s and the other in his 70s. Body size and bow pull strength were significant correlates of arrow shooting accuracy (Blurton Jones and Marlow, 2002).

Results of the two field studies suggest that accuracy in shooting an arrow with a bow is related to hunting ability (return rate) among the Ache and hunting reputation among the Hadza. Note, however, that the use of bows and arrows and spear throwers are rather recent in evolutionary terms, about 11,000–17,000 ybp, respectively, but the presence of arrow points suggests earlier use of bows, about 65,000–70,000 ybp (Marlowe, 2005). Proficiency in one-handed throwing, on the other hand, probably had a considerably longer evolutionary history.

It is likely, perhaps, that accuracy of throwing a projectile or projecting an arrow, or factors related to accuracy may have been under strong selective pressures among male hunter-gatherers, enhancing their hunting success and in turn their reproductive success. Proficiency in hunting from a distance may also enhance survival by reducing risk of injury and perhaps death. Data suggest that successful hunters among the Ache, Hadza, !Kung, Lamalera, and Meriam have greater reproductive success (higher fertility, more offspring surviving to 5–9 years) than other men in the respective groups (Smith, 2004). Among Ache males, increased fertility and offspring survival are both significantly related to hunting ability defined as daily productivity per number of hours spent hunting (Kaplan and Hill, 1985). In a field study of hunting ability (return rate, probability of a kill) among Ache males, age (experience) and skill were of primary importance, while strength and body size were not (Walker et al., 2002). The results highlight the importance of hunting-specific skills and practice; Ache youth begin hunting about 12–15 years and peak hunting ability occurs at about 40 years of age (Walker et al., 2002). Moreover, peak hunting ability occurs well after peak development of muscular strength and endurance and estimated aerobic capacity (Walker and Hill, 2003; Walker et al., 2002).

Spatial ability, the ability to create, maintain and mentally transform a visual image, is a factor related to accuracy of throwing (Jardine and Martin, 1983; Kolakowski and Malina, 1974). Males tend to have greater facility in spatial abilities than females (Linn and Petersen, 1985; Weiss et al., 2003). A study of boys 14–16 years of age required them to throw a baseball (5.0–5.25 oz, 142–149 g, Elert, 1999) as fast and as accurately as possible at a target over a distance of 9.1 m (see Malina, 1968, 1969 for details of the target and scoring). Two bouts of 10 throws were given with a brief rest between bouts; performance scores were averaged over the 20 throws. Regression analysis assessed the extent to which spatial ability scores (Primary Mental Abilities Test) were predictive of throwing accuracy. Spatial ability was related to vertical deviation and concentric circle accuracy. When vertical deviation accuracy was allowed for, the relationship of concentric circle accuracy to spatial ability disappeared; when the converse was done, vertical deviation accuracy retained its relationship with spatial ability (Kolakowski and Malina, 1974). The relationship between spatial ability and accuracy in the vertical plane is interesting in that vertical deviation on an upright target would translate into skill and judgment with respect to distance if the target laid on the ground, i.e., under or over-shooting. Although only a small percentage of the variance in ball throwing accuracy over about 9 m was accounted for by spatial ability (14%), the data suggest evidence relating spatial skills to throwing skill, an important component of the hunting enterprise which may have had a selective advantage.

Results of the study with adolescent boys were generally replicated in twins of both sexes 13–19 years and their parents (Jardine and Martin, 1983). The study of twins, however, showed similar relationships between spatial ability and throwing accuracy (overarm and underarm) in the vertical and horizontal planes. The throwing tasks used a tennis ball (2.0–2.06 oz, 56.7–58.5 g, Elert, 1999) in contrast to a baseball which is about 2.5 times heavier, while the underarm throw was more like a toss or lob in contrast to a forceful throw. On the other hand, a study of college age students of both sexes noted no relationship between measures of spatial ability and accuracy in throwing a 25 g dart at a target 3-m away (Watson and Kimura, 1991). Differences between throwing tasks should be noted. Dart throwing over a short distance is quite different biomechanically and in terms of forces generated from overarm ball throwing over a longer distance.

Early agriculturalists

The shift to agriculture altered patterns of physical activity, perhaps in males more so than in females. Among hunter-gatherers, activities of males were often described as continuous and largely endurance-based—walking, tracking, running, and so on (see above). Activities of females were probably more intermittent and muscular strength and endurance-based—digging, picking, cutting, chopping, carrying (infants and food stuffs), and others. With the advent of agriculture, gathering probably continued for some time. It is likely, however, that activities of men shifted to a more intermittent pattern with an emphasis on muscular strength and endurance. Activities associated with agriculture and domestication, for example, include field preparation (clearing, plowing, irrigation canals), planting (digging, tilling), weeding, harvesting (cutting, picking, carrying), conversion of crops to food (e.g., corn-shucking, removing grains, grinding), care of animals (feeding, cleaning, herding, milking, cutting and carrying feed), and a more settled home base (cutting, gathering, carrying wood, carrying water).

TABLE 2. Principal sources of food in the Tehuacan Valley, south central Mexico: Estimated percentages in the diet through time (years before present, ybp)

		Plants	
Period	Meat	Wild	Cultivated
8500–7000	54	41	4
7000–5500	34	52	14
5500–4300	30	49	21
4300–3500, Limited data			
3500–2900	27	18	55
2900–2200	25	17	58
2200–1300	18	17	65
1300–460	17	8	75

Collated from MacNeish (1967).

The change in activity patterns in the transition from hunting and gathering to agriculture is also evident in a general reduction in sexual dimorphism in skeletal characteristics. Using the ratio of anteroposterior to mediolateral bending rigidity at the femoral midshaft, sexual dimorphism ranged from 9 to 27% among recent archeological hunter-gatherers ranged compared with about 3–9% among recent archeological agriculturalists (Ruff, 2005). Of interest, estimated sexual dimorphism in anatomically modern Homo sapiens ~30,000 to 10,000 ybp (22%) is in the upper part of the range for recent archeological hunter-gatherers (Ruff, 1987, 2005). The overall trend indicates a reduction in sexual dimorphism in the transition from hunting and gathering to agriculture. The difference is related to increased anteroposterior bending of the femur in hunter-gatherer males. It is associated with increased flexion of the knee joint which is observed with increased movement (run, walk) over long distances (Ruff, 2005). The latter, of course, was/is characteristic of hunter-gatherer males (see above).

Although estimated dates vary somewhat, the transition from the hunter-gatherer lifestyle to one dependent on agriculture and domestication began in the fertile crescent of the Near East about 12,000 to 10,000 ybp and was reasonably complete by about 7,000 ybp. Recent evidence suggests at least 10 independent centers for the origin of crop cultivation in the Old and New World (Balter, 2007). It is not known what triggered the shift from hunting and gathering to agriculture. Suggested factors include climate change (warmer), population density, food resource availability, energetic returns (kcal/hr foraging versus farming) and cultural complexity (Reed, 1978).

The shift to agriculture was probably gradual and varied in different parts of the world. Changes in food acquisition and diet associated with agriculture were also grad-

TABLE 3. Estimated physical activity levels (PAL) in earlier populations and mean physical activity levels in contemporary populations

Source	Sample	PAL Males	PAL Females	Comments
Leonard and Robertson (1997)	Homo erectus	2.02	1.53	calculated from estimated TEE and RMR
Leonard and Robertson (1997)	Homo sapiens	2.02	1.54	calculated from estimated TEE and RMR
Ulijaszek (1991)	Paleolithic	2.0		presumably males
Eaton and Eaton (2003)	Paleolithic	1.75		"most closely approximates the Paleolithic standard"
Leonard (2004, 2008)	Hunter-gatherers			
	!Kung	1.68	1.56	
	Ache	2.17	1.88	
	Inuit	1.88	1.80	
Ulijaszek (1991)	Hunter-horticulturalists	1.81		mean of four samples, range 1.42-2.09
	Agriculturalists	1.89		mean of 13 samples, range 1.52-2.32
Leonard (2004, 2008)	Agriculturalists	2.07		mean of 6 samples, range 1.58-2.40
			1.89	mean of 6 samples, range 1.63-2.03
Dufour and Piperata (2008)	Agriculturalists	1.92		mean of 17 samples, range 1.56-2.40
			1.78	mean of 15 samples, range 1.47-2.35
Dufour and Piperata (2008)	Yapu		1.77	subsistence agriculturalists
Dufour and Piperata (2008)	Caxiuana		1.55	subsistence agriculturalists
Leonard et al. (1996)	Evenki, Siberia	1.80	1.61	herders
Snodgrass et al. (2006)	Yakut, Siberia	1.68	1.50	mixed subsistence (hunt, fish, herd, gather, horticulture)
Black et al. (1996)	Affluent societies 18–29 yrs	1.85	1.70	summary of doubly labeled water TEE as of 1994
	30–39 yrs	1.77	1.68	
	40–64 yrs	1.64	1.69	
	65–74 yrs	1.61	1.62	
	75+ yrs	1.54	1.48	

PAL = TEE/BMR (total energy expenditure/basal metabolic rate), see text for details.

ual. It is likely that hunting and gathering persisted for some time as cultivated crops made their way into the diet. This possibility has been labeled "low-level food production" (Smith, 2001). This trend is indicated for principal food sources in the Tehuacan Valley in south-central Mexico (Table 2). The replacement of wild plants and meat by cultivated plants was rather gradual over a span of about 5,000 years. At 8,500–7,000 ybp, meat, wild plants and cultivated plants contributed an estimated 54, 41, and 4%, respectively, of the principal sources of food. By 3,500–2,900 ybp, cultivated plants contributed an estimated 55% of the principal sources of food available, while meat and wild plants contributed 27 and 18%, respectively (MacNeish, 1967). It is also at this time that the area is described as a fully agricultural settled village. By the time of the conquest, cultivated plants contributed about 75% of the principal sources of food. Of interest, the diet of most rural Mesoamerican rural communities in the 1970s was ~95% of plant origin (Newman, 1975). Estimated diets of several contemporary hunter-gatherers do not indicate such overwhelming reliance on foods of plant origin. Variation, however, is considerable, e.g., 67% of plant origin among the !Kung, 44% among the Ache, 32% among the Hiwi, and only 4% among the Inuit (Leonard, 2004; see also Jenike, 2001). An estimate of 65% food of plant origin has been suggested for Paleolithic humans (Eaton et al., 1997).

In addition to changes in the environment and diet associated with agriculture and domestication, several new stresses emerged. These included threat of periodic crop failures and dietary deficiencies (nutritional stress), dependency on others for food production, problems associated with the removal of human and animal wastes (especially animal-borne diseases via the bowel-to-mouth route), population movement after crop failure or when productivity of soil declined, and perhaps others. It was probably at this time that population size approached numbers sufficiently large to maintain infectious diseases at endemic levels (Armelagos and Dewey, 1970). Skeletal and dental evidence from several regions of the world generally suggest a temporal decline in health status associated with the transition to agriculture (Cohen and Armelagos, 1984; Larsen, 1995).

Wild game that comprised the diets of earlier populations most likely had less fat. With domestication, the diets of animals changed as did those of humans. Selective breeding for meat content and fattening of animals in feed pens on a large scale, however, has occurred relatively recently, in the 19th century (Eaton and Shostak, 1986). The significance of such changes is obvious given current concern for dietary fat of animal origin. Tissue and lipid profiles of humans reflect in part the lipids in the diet. Meat from domesticated bovids, for example, not only has a higher lipid concentration, but also has a different lipid composition from that of wild bovids (Crawford, 1968). The latter has a higher proportion of polyunsaturated to nonessential amino acids, which probably reflects oil-rich vegetation (nuts, seeds, leaves) that they feed upon in the wild (Crawford, 1968).

Physical activity of hunter-gatherers and agriculturalists

Observations on contemporary hunter-gatherers and agriculturalists provide insights into patterns of habitual physical activity. Physical activity level (PAL), the ratio of total energy expenditure (TEE) to basal metabolic rate (BMR) or resting energy expenditure (REE), is a commonly used indicator which provides an approximation of the contribution of activity-related energy expenditure over 24 h. PAL, however, is not equivalent to activity energy expenditure as it includes an adjustment for body size while estimates of activity energy expenditure do not (Black et al., 1996).

In contemporary societies of developed countries, a PAL of 1.6–1.7 is characteristic of a sedentary lifestyle with little or no strenuous leisure activity, while a PAL between 2.0 and 2.4 is indicative of strenuous work or highly active leisure (Black et al., 1996). A PAL of 3.0+ suggests an extremely active lifestyle as with some forms of systematic training for sport.

Estimated PALs for earlier and contemporary populations are summarized in Table 3. It should be noted that some of the same samples are included in the compilations cited. Estimated PALs for contemporary hunter-gatherers and agriculturalists indicate considerable variation among groups. Ranges of PALs in hunter-gatherers are 1.68–2.17 in males and 1.56–1.88 in females; corresponding ranges among agriculturalists are 1.58–2.40 in males and 1.63–2.03 in females (Leonard, 2004, 2008). In a summary limited to adult males, PALs range from 1.42 to 2.09 in four hunter-gatherer and hunter-horticulturalist groups and from 1.52 to 2.32 in 13 cultivators (Ulijaszek, 1991). A recent summary of PALs for males from 17 farming communities in developing countries indicates a generally similar range of estimated PALs, 1.56 to 2.40; among females in 15 farming communities, estimated PALs overlap those of males and range from 1.47 to 2.35 (Dufour and Piperata, 2008). Estimates of maximal aerobic power ($\dot{V}O_2$ max, ml/kg/min) in male hunter-gatherers, pastoralists, simple agriculturalists, and rudimentary horticulturalists also overlap considerably and are, on average, higher than those of adults in developed countries (Eaton et al., 1988).

Sex differences within groups are also variable. Among three hunter-gatherer groups—!Kung, Ache and Inuit, and Evenki herders, and Yakut mixed-subsistence groups, males have, on average, higher estimated PALs than females. The sex difference varies from 0.08 in the !Kung to 0.29 in the Ache (Table 3). Among males and females in the same agricultural communities, sex differences in estimated PALs are inconsistent. In the six samples reviewed by Leonard (2004, 2008), males have a higher estimated PAL in three with differences ranging from 0.03 to 0.42; females have a higher estimated PAL in three samples but the differences are small, 0.03 to 0.05. In the eight agricultural samples summarized by (Dufour and Piperata, 2008), males have a higher estimated PAL than females in only two samples, while in the remaining six samples, the sex difference in estimated PALs is negligible (Dufour and Piperata, 2008). Age variation within samples of hunter-gatherers and agriculturalists is not ordinarily considered. Among affluent populations, males 18–39 years have higher PALs than females of the same age, but at older ages, sex differences in PALs are inconsistent (Black et al., 1996).

Allowing for the limitations of the available data, the evidence does not suggest a major difference in the PAL and also aerobic fitness between contemporary hunter-gatherer and agricultural populations and by inference in the transition from hunting-gathering to agriculture. The reported PALs also overlap estimates for Homo erectus and Homo sapiens, which do not differ, 2.0 in males and 1.5 in females (Table 3).

Hunting-gathering and agricultural lifestyles are in stark contrast to more contemporary lifestyles, specifically in developed, industrialized countries, which are characteristically sedentary. Although there is overlap among contemporary hunter-gatherers, agriculturalists and affluent populations, estimated PALs tend to be higher in hunter-gatherers and agriculturalists than in affluent industrialized populations. The difference is more apparent when body mass is taken into account. Per unit body mass, subsistence hunter-gatherers and agriculturalists have a higher estimated daily energy expenditure than affluent industrial populations; estimated daily energy expenditure is about 600–1,000 kcal greater at the same body mass in the former (Leonard, 2004, 2008).

PALs decline with age, on average, and age is not ordinarily controlled in the data for hunter-gatherers and agriculturalists. It is also likely that life expectancies of both hunter-gatherers and agriculturalists were lower. Evidence from the Ache and Hadza indicate peak hunting ability in the fifth decade and slow decline with age (Walker et al., 2002). This may suggest a reasonably stable level of physical activity into the fifth and sixth decades in males, while PALs decline at these ages in affluent societies (Table 3).

Data for PALs of youth in hunter-gatherer communities are lacking. Youth from rural areas of developing countries have higher estimated PALs than youth from cities of developing countries and also than youth from industrialized countries, and the differences increase with age from childhood into adolescence (Torun et al., 1996). Sex differences in PAL among youth from rural areas of developing countries are negligible during childhood and the transition into adolescence (10–14 years), but indicate a higher PAL in adolescent males than females 15–19 years (Torun et al., 1996).

Twin concerns of the present: physical inactivity and obesity

Reduced levels of physical activity are commonly viewed as a major contributor to the increased prevalence of degenerative diseases in the past 50 years or so and the obesity epidemic in the past 25 years. As noted, both physical inactivity and obesity are major risk factors for morbidity and mortality among adults in developing and developed countries and are increasingly being implicated as major risk factors for morbidity in children and adolescents.

Secular decline in physical activity

A decline in levels of habitual physical activity and energy expenditure in recent populations from developed countries and segments of developing countries is accepted. Unfortunately, data do not permit an estimate of when the trend started because the transition was probably parallel to the change in subsistence patterns from hunting and gathering to agriculture to urbanization to industrialization. The transition was probably a continuum distributed across centuries and millennia. In contrast, relatively recent trends are suggested in available data.

Physical activity levels. Estimates of physical activity levels (PALs) based on the doubly labeled water (DLW) method in children and adolescents are summarized in Table 4. The DLW method for measuring TEE has been available since the 1980s and is generally considered the "gold standard." Two summaries of PALs in children and adolescents based on DLW data from the 1980s through the early or mid-1990s provide a recent baseline (Black et al., 1996; Torun et al., 1996). PALs based on the DLW method for children and adolescents in studies done since the mid-1990s were collated and are also summarized in Table 4 (references to specific studies are indicated in the Appendix). Mean PALs (weighted for sample sizes in individual studies) have declined in recent samples of boys

TABLE 4. Estimated physical activity levels (PAL) in children and adolescents: Comparisons of estimates in samples from 1980s–1994 and from 1996–2005

	Age	Boys				Girls			
	Range	*N*	Mean	SD	Range	*N*	Mean	SD	Range
Children									
Summaries of DLW data 1980s–1994									
Black et al. (1996)	7–12	32	1.74	0.22		24	1.68	0.116	
Torun et al. (1996)	6–13	53	1.79[a]		1.71–1.86	75	1.80[a]		1.69–1.96
Summary of DLW studies 1996–2005[b]	6–13	316	1.62		1.36–1.77	697	1.59		1.24–1.74
Adolescents									
Summaries of DLW data 1980s–1994									
Black et al. (1996)	13–17	31	1.75	0.19		26	1.73	0.24	
Torun et al. (1996)[a]	14+	37	1.84[a]		1.79–1.88	34	1.69[a]		1.66–1.72
HR monitoring data 1980s–1994									
Torun et al. (1996)[c]	14+	77	1.91[a]		1.71–1.94	44	1.63[a]		1.61–1.88
Summary of DLW studies 1997–2005[b]	13+	54	1.81[a]		1.57–1.91	81	1.74[a]		1.65–1.79
HR, indirect calorimetry studies 1999–2003[b]	13+	117	1.73[a]		1.60–1.79	119	1.70[a]		1.58–1.78
DLW + HR studies 1997–2005	13+	171	1.75[a]		1.57–1.91	200	1.72[a]		1.58–1.79

[a]Weighted means.
[b]References for specific studies are in the appendix; for several samples, BMR was predicted from body weight.
[c]Weighted means are based on samples of youth with adequate heights and weights and youth who were stunted or underweight; there were no significant differences in estimated TEE and PAL between the groups within sex.

and girls 6–13 years of age, but mean PALs for adolescents 14–18 years have not changed appreciably, though data for adolescents are less extensive than for children. Data for adolescents based on heart rate monitoring and indirect calorimetry are more available. Allowing for differences in methods, the data for adolescents overlap between samples from the 1970s through the early 1990s and more recent estimates. Although not shown in the table, weighted means for children and adolescents with adequate heights and weights and youth who were stunted or underweight also did not differ significantly within sex (Torun et al., 1996). This has since been verified with the DLW method in stunted and non-stunted Brazilian youth (Hoffman et al., 2000).

Energy expenditure. Estimates of absolute and relative total energy expenditure (TEE, kcal/day and kcal/kg/day) for studies of children since the 1970s and adolescents since the mid-1960s were also collated. Data are based on heart rate monitoring, indirect calorimetry and activity diaries, singly and in combination, and the DLW method. In addition to intra- and interindividual variation in TEE among free-living youth, potential variation associated with the different methods should be noted. Results from DLW, heart rate monitoring, and diary and time and motion studies agree reasonably well, but the diary method tends to underestimate TEE of older adolescents (Torun et al., 1996). Samples were grouped by age to approximate the ranges used in the summaries of PAL (Black et al., 1996; Torun et al., 1996). All samples are from Western Europe and the United States with the exception of one each from Japan and Taiwan (references to specific studies are given in the Appendix). Sample sizes are relatively small and probably do not include obese youth. Absolute TEE is greater in obese youth given the energy cost of moving a larger body size, but per unit body weight, TEE is less in obese youth (Bandini et al., 1990; Lazzer et al., 2003; Treuth et al., 1998). The health- and performance-related physical fitness of obese children and adolescents is also compromised, specifically in test items that require movement, projection or lifting of the body through space (Malina, 2001).

Data for absolute (kcal/day) and relative (kcal/kg/day) TEE are plotted in Figures 1 and 2 for children and adolescents 7–13 years and 14–18 years, respectively. Absolute TEE shows no trend over time in children 7–13 years, but tends to increase over time among adolescents 14–18 years which likely reflects the secular increase in body mass. Relative TEE, on the other hand, tends to decline over time in children 7–13 years of age but to increase slightly over time in adolescents 14–18 years of age. This is consistent with the PAL data summarized in Table 4.

It is generally assumed that levels of habitual physical activity of children and adolescents earlier in this century were greater compared with the contemporary youth. Documenting levels of energy expenditure and physical activity in earlier samples is difficult, in part because it apparently was not a priority. Results of a comprehensive study of the estimated daily energy expenditure of children and adolescents at a boarding school in Hampshire, England, provide some insights (Bedale, 1922–1923). The sample included 45 boys and 55 girls, 8–18 years of age. The Douglas bag technique was used. BMR was measured with subjects in bed prior to the awakening bell in the morning. Energy costs of sitting in class, class activities, and other activities, including walking, running, football, lacrosse, cricket, gymnastics, outdoor work, gardening, haymaking, dancing, among others, were estimated. Data were reported for "typical school days" for boys and girls in several age groups. Estimated TEE and TEE per unit body mass are summarized in Table 5. For comparison, corresponding estimates for children and adolescents studied from the mid-1960s are included. As in studies of the PAL, the estimates for TEE are grouped into two broad age groups, 7–13 years and 14–18 years, and into two time intervals, before 1994 and 1995 to the present.

Compared with the sample of school youth in the United Kingdom in 1919–1921, more recent youth expend less absolute energy daily and less energy per unit body mass. Among youth 7–13 years of both sexes, absolute and rela-

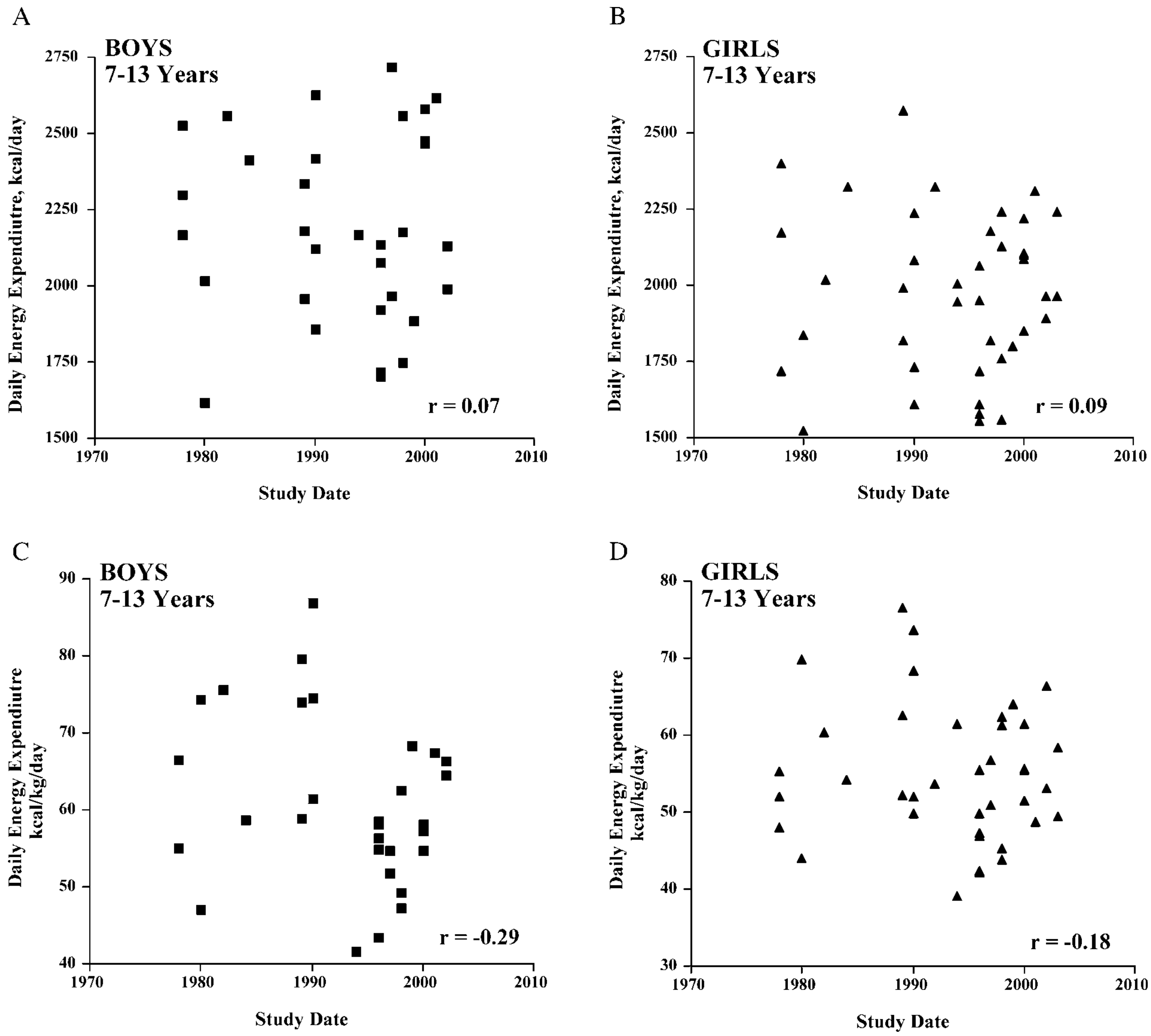

Fig. 1. Estimated total energy expenditure (TEE) in children 7–13 years from the late 1970s through the present: **A** - boys, kcal/day; **B** - girls, kcal/day; **C** - boys, kcal/kg/day; **D** - girls, kcal/kg/day. Correlations indicated in each figure are partial correlations between TEE and year of study controlling for mean age of the subjects. Sources of data are indicated in the Appendix.

tive TEE of the more recent samples are less than those of school students in 1919–1921, and those for children surveyed more recently (after the mid-1990s) are lower than those surveyed before 1994 (see also Table 4 and Fig. 1). Compared with the small samples of children studied in 1919–1921, children 7–13 years surveyed after the mid-1990s have a lower absolute TEE by about 11% in boys and 22% in girls and a lower relative TEE by about 38% in boys and 22% in girls, which of course highlights the increase in body mass in more recent children.

Among adolescents 14–18 years of both sexes, on the other hand, absolute and relative TEE are lower in samples surveyed before 1994 by about 20% in both sexes compared with the school sample of 1919–1921. More recent adolescents also have a lower absolute TEE than the 1919–1921 adolescents by about 5% in males and 13% in females, but a lower relative TEE by about 17% in both sexes. The observations for more recent adolescents highlight their greater body mass compared with the youth of 3–4 generations ago. The data for adolescents studied between ~1965 and the present suggest a slight increase in absolute and relative TEE over time (see also Fig. 2).

Corresponding estimates of physical activity in adults are not available. Recalled physical activity at 15, 30, and 50 years in a large sample of Swedish men (n = 33,466) provides some insights. Trends are summarized in Figure 3. Estimated total daily physical activity (MET hours per day; kcal/kg/hr/day) declined from the 1930s to the 1990s. The decline in activity was especially marked at 15 years of age from the 1940s through the 1960s which was due to a reduction in work or occupational activity. At the three ages, the decrease in physical activity over time was due in large part to a reduction in occupational and leisure time activities (Norman et al., 2003).

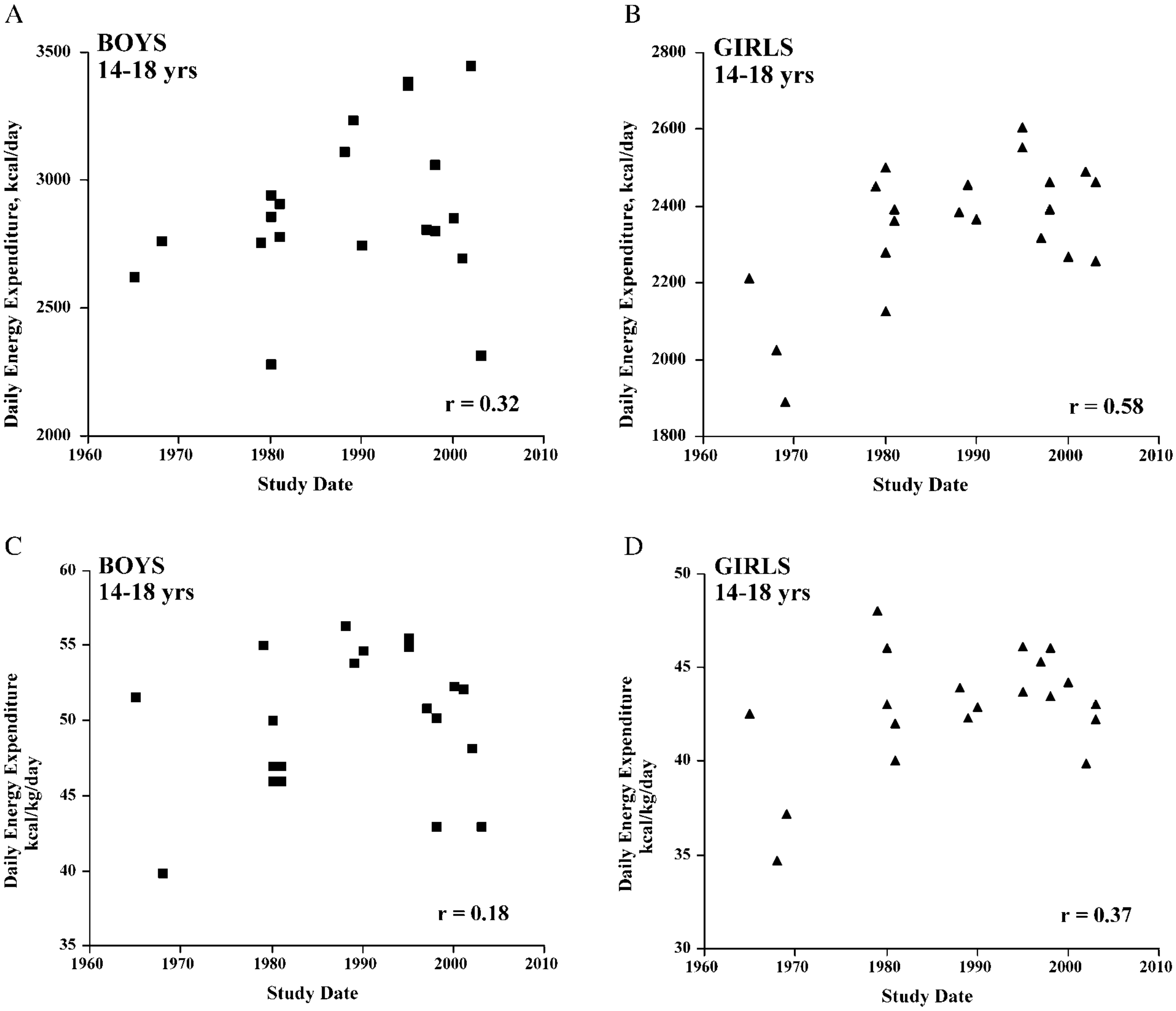

Fig. 2. Estimated total energy expenditure (TEE) in adolescents 14–18 years from the mid-1960s through the present: **A** - boys, kcal/day; **B** - girls, kcal/day; **C** - boys, kcal/kg/day; **D** - girls, kcal/kg/day. Correlations indicated in each figure are partial correlations between TEE and year of study controlling for mean age of the subjects. Sources of data are indicated in the Appendix.

Physical Fitness. Measures of physical fitness are often treated as proxies for physical activity. As noted earlier, physical activity is only moderately related to physical fitness in youth, but the relationship is stronger in adults. Measures of fitness in youth are related in part to body size and maturity status, and are also influenced by changes in lifestyle, specifically reduced physical activity, which may interact with changes in body size (Malina et al., 2004).

Data for grip strength date to more than 150 years ago. Secular changes in static strength, of course, must be tempered because it is likely instruments have changed over time. Motivation is an additional factor in obtaining maximal efforts. Allowing for these caveats, secular gains are apparent in height, weight, and grip strength in Belgian (1830s–1971), American (1899–1964; mid-1930s to late 1950s), and Japanese (1923–1969) children and adolescents, and the gains in strength were largely proportional to changes in body size (Malina, 1978). Relative to secular gains in height, back strength of Japanese children and adolescents in 1969 was proportionally less than in 1929. Back strength is a more difficult measure to obtain than grip strength and may be influenced by minor variations in technique (Malina, 1978).

More recent data for European youth suggest declines in muscular strength. Russian youth 11–17 years in the mid-late 1980s were not as strong (grip) as peers in the 1960s. Data for height and weight over this interval were not reported, but mean ages at menarche were stable from the early 1960s to the early 1980s (Godina, 1998). Data for eight measures of strength for Danish youth of the same height (150 cm) in 1956 and 1981 indicated a decline in strength in both sexes over the interval of 25 years (Heebøll-Nielsen, 1982).

Beginning in the 1960s, physical fitness test batteries were commonly administered to school children in many countries. The batteries included a variety of performance-related items, e.g., dashes, jumps, shuttle runs, ball throws for distance, sit-ups, distance runs, etc. Comparisons of four national surveys in the United States between

TABLE 5. Estimated average absolute (kcal/day) and relative (kcal/kg/day) TEE in children and adolescents across time. All means are weighted for sample size

	7–13 Years				14–18 Years			
	n	Years	kcal/day	kcal/kg/day	*n*	Years	kcal/day	kcal/kg/day
Males								
1919–1921[a]	12	9.6	2,401	84.5	25	15.5	3,270	62.6
Prior to 1994[b]	949	10.7	2,234	65.0	724	15.2	2,722	48.6
1995 to 2005[b]	576	11.1	2,137	52.2	357	15.3	3,116	52.1
Females								
1919–1921[a]	27	11.5	2,500	67.3	27	15.8	2,866	53.8
Prior to 1994[b]	870	10.9	2,038	57.6	817	15.4	2,296	42.8
1995–2005[b]	990	10.6	1,944	52.7	403	15.2	2,493	44.7

[a]The study was carried out from June 1919 to June 1921. Calculated from data reported in Bedale (1922–1923).
[b]Based on data summarized in Figures 1 and 2; see Appendix for specific studies. Studies for children 7–13 years date to about 1978 while those for adolescents 14–18 years date to about 1965. If specific dates of a study were not reported, two years were subtracted from the date of publication to estimate the year the study was conducted.

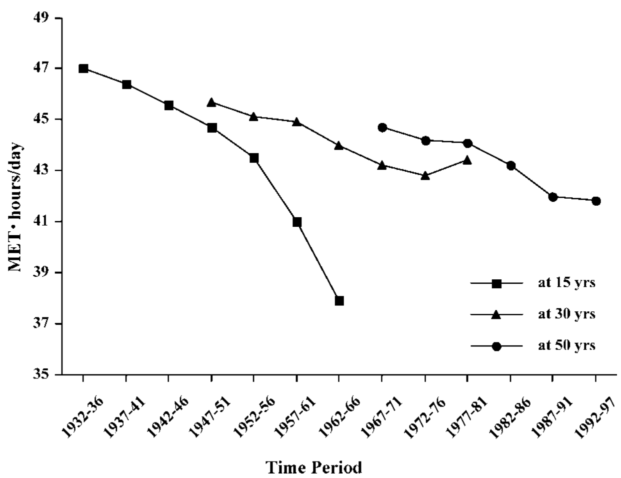

Fig. 3. Estimated temporal trends in recalled total daily physical activity of men at 15, 30, and 50 years from the 1930s through the 1990s. Drawn from estimates reported by Norman et al. (2003). Estimates were based on linear regression, adjusted for BMI, smoking at the respective age, and education.

1958 and 1985 indicated major improvements in the fitness of 10- to 17-year-old youth of both sexes between 1958 and 1965, but there was little change in fitness from 1965 to 1985 (Malina, 2007). The improvement in fitness from 1958 to 1965 reflected in part national emphasis on physical fitness testing in schools in the 1960s. More recent national fitness data are not available for American youth.

Among youth from southwestern Poland, performances in strength and endurance tasks declined in each 10-year survey from 1965 to 1995 (Raczek, 2002). Declines in strength and endurance were most marked after 12–14 years in both sexes across surveys. On the other hand, running speed did not change between 1965 and 1985, but was especially poorer in 1995, while agility did not change appreciably among the four surveys. Of interest, height increased systematically across the four surveys 1965 to 1995 so that the fitness of children actually deteriorated relative to body size. More recently, comparisons of Polish youth 7–19 years in 1979, 1989, and 1999 on the EUROFIT test indicated improvements between 1979 and 1989, but deterioration between 1989 and 1999 in both sexes (Przewęda and Dobosz, 2003). The regression in fitness was especially apparent in power of the upper and lower extremities, running speed (sprints), and endurance distance run.

Five tests of fitness were administered to 16-year-old Swedish secondary school children in 1974 and 1995 (Westerstahl et al., 2003). Performances on the bench press, sit-ups, and 9-min endurance run were poorer in 1995 compared with 1974 in both sexes. The vertical jump improved over time in boys but not in girls, while both boys and girls improved in the two-hand lift. The increase in the BMI over time explained variable portions of the variance in the fitness tests, leading the authors to suggest a significant role for decreased physical activity. Comparisons of South Australian youth 10–11 years in 1985 and 1997 indicated, on average, a decline in aerobic fitness (1.6 km run/walk time) and running speed (50-m dash), but no differences in the standing long jump (Dollman, 2003).

The pattern of secular change in the physical fitness and motor ability of Japanese school youth 12–17 years between 1964 and 1997 shows a somewhat variable pattern (Nishijima et al., 2003a, 2003b). Composite fitness and motor ability (performance) scores increased from 1964 to 1974, increased slightly (fitness) or remained stable (motor) between 1975 and 1985, and then declined from 1986 through 1997. The early improvements in fitness and motor ability may be related in part to secular gains in height from 1964 to 1984, about 5 cm in boys and 3 cm in girls at 17 years of age (Nishijima et al., 2003a), whereas the subsequent declines in fitness may be related to changing patterns of physical activity (Nishijima et al., 2003b). A different analysis of essentially the same data attributed improvements (1964–1974) to national emphasis on practice and fitness in the schools, the levelling-off of fitness (1975–1985) to increased television viewing in Japanese homes, and subsequent declines in fitness to greater emphasis on scholarship and activity for pleasure in schools and increased use of video games (Shingo and Takeo, 2002).

Performances of Australian youth 12–15 years (Tomkinson et al., 2003a) and youth 6–19 years from 11 countries (Tomkinson et al., 2003b) on the 20-m multistage shuttle run test, a measure of cardiorespiratory endurance, suggest a systematic decline in aerobic fitness between 1981 and 2000. The overall mean decline

TABLE 6. Secular change in the estimated prevalence (%) of obesity in the United States population 1960–2004 by sex and age[a]

	Age groups							
	6–11 years[b]		12–19 Years[b]		20–34 Years[c]		20–74 Years[c,d]	
Year of survey	Males	Females	Males	Females	Males	Females	Males	Females
1960–1962	–	–	–	–	9.2	7.2	10.7	15.7
1963–1965	4.0	4.5	–	–				
1966–1970	–	–	4.5	4.7				
1971–1974	4.3	3.6	6.1	6.2	9.7	9.7	12.2	16.8
1976–1980	6.6	6.4	4.8	5.3	8.9	11.0	12.8	17.1
1988–1994	11.6	11.0	11.3	9.7	14.1	18.5	20.6	26.0
2001–2004	18.7	16.3	17.9	16.0	23.2	28.6	30.2	34.0

[a]Adapted from National Center for Health Satistics (2006). Data are for the United States civilian noninstitutionalized population.
[b]Criteria for obesity are based on age- and sex-specific percentiles for the BMI. Obesity was defined as BMI $\geq$ 95th percentiles for age and sex. The sample of youth in the 1996–1970 national survey was 12–17 years.
[c]Obesity is a BMI $\geq$30 kg/m^2.
[d]Age-adjusted to the 2000 standard population.

weighted for sample size in the international comparison was -0.43% per year.

Data for maximal aerobic power ($\dot{V}O_2$ max, peak $\dot{V}O_2$) for American youth date to the late 1930s in boys and the l960s in girls; hence, insights into secular changes, although several limitations should be noted. The data were based on relatively small samples combined across several ages and included both treadmill and cycle protocols; peak $\dot{V}O_2$ for the cycle was multiplied by 1.075 (Eisenmann and Malina, 2002). Since the protocol required willingness to exercise to exhaustion, sample selectivity should be noted; it is likely that overweight and obese youngsters are excluded.

The regression line for absolute aerobic power (L/m) was flat from the late 1930s to 2000 in boys 6–12 years, but that for boys 13–18 years suggested an increase over time. The corresponding regression line was stable from the 1970s in girls 6–11 years and from the 1960s in girls 12–14 years of age, but among older girls 15–18 years, it was curvilinear, suggesting an increase from the early 1960s to the late 1970s and a decline into the late 1990s. When expressed per unit body weight (ml/kg/min), accommodating to some extent secular change in body mass, the regression lines for peak $\dot{V}O_2$ indicated fairly stable levels between the 1930s and the present in boys. The trends for relative maximal aerobic power in girls, however, were similar to those for absolute values (Eisenmann and Malina, 2002).

Trend lines, of course, need to be interpreted with care, especially since the early data points are few and may influence the regressions, especially in boys. Examination of the individual data points for absolute peak $\dot{V}O_2$ in boys suggests that the highest values occur in the late 1960s through the 1970s, whereas subsequent values are somewhat lower. From this perspective, the general trend may be consistent with the decline since the 1980s in aerobic capacity assessed with the 20-m shuttle run (Tomkinson et al., 2003b).

Secular data on the aerobic fitness of adults are confounded in part by age-associated decline in fitness. Some evidence suggests that regular endurance training reduces the rate of decline in $\dot{V}O_2$ max in men and women 40–60 years (Bovens et al., 1993) and men 60–70 years of age (Rogers et al., 1990). Corresponding data for active and inactive adults suggest a similar trend, though results are variable. It has been hypothesized that the pattern of change $\dot{V}O_2$ max with age differs between active and inactive individuals. Accordingly, $\dot{V}O_2$ max declines rapidly in inactive individuals during the 20s and 30s, and then declines more slowly with aging, but declines at a much slower rate in active individuals who maintain a regular program of activity (Buskirk and Hodgson, 1987). More recently, it has been noted that about 50% of the age-related decline in $\dot{V}O_2$ max in cross-sectional samples of men and women was accounted for by percentage fat and level of physical activity (Jackson et al., 1995, 1996). A related factor in the decline in $\dot{V}O_2$ max with age is loss of muscle mass (Fleg and Lakatta, 1988), although regular endurance activity in older individuals can maintain skeletal muscle adaptations (Proctor and Joyner, 1997).

Secular increase in obesity

The prevalence of obesity among children, adolescents, and adults has increased dramatically since the mid-1980s in many countries throughout the world (Lobstein et al., 2004; Janssen et al., 2005). Trends in obesity for the United States are summarized in Table 6 as an example. The data are derived from a series of national surveys dating to 1960–1962. The prevalence of obesity was about 5% in children and adolescents and about 10% in young adults from 1960 through 1980 with negligible sex differences. The same trend is apparent in age-adjusted estimates for adults 20–74 years, though the prevalence of obesity is greater in females than males in the three surveys.

The prevalence of obesity doubled in children and adolescents between 1976–1980 and 1988–1994 and increased by more than one-third in young adults during this interval. Moreover, within each age group, there appears to have been a greater increase in the upper percentiles of the BMI, producing an effect of increasing skewness in the distribution over time (Flegal and Troiano, 2000). Since 1988–1994, the prevalence of obesity has continued to increase in the United States population through 2001–2004 (Table 6). The sex difference in prevalence of obesity is relatively small among children and adolescents but has increased in adults among whom proportionally more females are obese than are males. Similar trends are apparent in the Canadian population since about 1980, though the prevalence of obesity is not as high as in the United States population (Tjepkema, 2006; Tremblay et al., 2002).

TABLE 7. Estimated food energy available per capita for the United States population from 1909–1919 through 2000[a] and mean daily energy intake in the United States population from 1971 to 2000[b]

Food energy available			Mean daily energy intake (kcal/day) by age group (years) and sex								
			6–11	12–15		16–19		20–39		20–74[c]	
Years	kcal/day	Year of survey	Both Sexes	Males	Females	Males	Females	Males	Females	Males	Females
1909–19	3,400										
1920–29	3,400										
1930–39	3,300										
1940–49	3,300										
1950–59	3,100										
1960–69	3,100										
1970–79	3,200/2,220[d]	1971–1974	2,045	2,625	1,910	3,010	1,735	2,784	1,652	2,450	1,542
		1976–1980	1,960	2,490	1,821	3,048	1,687	2,753	1,643	2,439	1,522
1980–89	3,400										
1990–99	3,700/2,680[d]	1988–1994	1,892	2,578	1,838	3,097	1,958	2,965	1,958	2,666	1,798
2000	3,900	1999–2000	2,025	2,460	1,990	2,932	1,996	2,828	2,028	2,618	1,877

[a]Adapted from Gerrior et al. (2004).
[b]Adapted from Briefel and Johnson (2004).
[c]Age-adjusted to 2000 population.
[d]Adjusted for spoilage and wastage in 1970 and 1997.

Excess energy intake and reduced physical activity are generally viewed as the primary contributing factors to, what is often labeled, the worldwide epidemic of obesity. Unfortunately, data specifically addressing energy intake and physical inactivity in the context of the secular increase in obesity are not available. Food energy available per capita (kcal/capita/day) in the United States population from 1909 to 2000 is summarized in Table 7. The data do not refer to actual food intake. Food energy available per capita declined from 1920–1929 to 1960–1969, increased to a small extent in 1970–1979 and then increased to a larger extent in 1980–1989 and subsequent years. After correcting the estimates for spoilage and wastage, food energy available per capita increased by 460 kcal/capita/day from 1970 to 1997 (Table 7).

Estimated energy intakes of adolescents in the United Kingdom have declined, on average, from the 1930s to the 1980s, 2,640 to 1,880 kcal/day in girls (−29%) and 3,065 to 2,490 kcal/day in boys (−19%) 14–15 years of age (Durnin, 1992). Corresponding data for the United States over this interval are not available, but mean daily energy intakes in four national surveys between 1971 and 2000 are summarized in Table 7. With the exception of adolescent females 16–19 years, mean daily energy intakes of children and adolescents did not change appreciably among surveys, including the interval in which the prevalence of obesity doubled (1976–80 to 1988–94, Table 6). Among United States adults, on the other hand, mean energy intake increased from 1976–80 through 1988–94, but did not change appreciably from the early 1990s to 1999–2000 (Table 7).

Changes in estimated energy intakes relative to changes in body mass are of relevance to the secular trend in obesity. Among adolescents in the United Kingdom, body weights were, on average, similar in boys and girls from the 1930s to the 1980s (Durnin, 1992). Similarly, in the United States, mean body weights and heights showed little variation among three national surveys between the 1960s and 1976–1980 (Malina et al., 2004). Over these intervals in the United Kingdom and the United States, mean energy intakes of children and adolescents declined; by inference, the reduced energy intake likely reflects reduced energy expenditure (decreased physical activity). However, in the 1988–1994 national survey of the United States population, mean weights of children and adolescents increased compared with earlier surveys while mean heights did not appreciably change (Malina et al., 2004). With the exception of older adolescent girls, mean energy intakes did not change appreciably in youth (Table 7) which suggests that reduced energy expenditure (physical activity) contributed to the weight gain.

Trends are similar in the weights and heights of United States adults across surveys from 1960–1962 to 1999–2002. Between national surveys in 1976–1980 and 1999–2002, the time interval which corresponded to the major increase in the prevalence of obesity in the United States (Table 6), mean heights increased by 0.8 and 0.7 cm in men and women, respectively, while mean weights increased by 7.1 (9%) and 8.6 (13%) kg in men and women, respectively (Ogden et al., 2004). In contrast to youth, energy intakes of adults showed modest increases between 1976–80 and 1999–2000, suggesting that the cumulative effects of increased daily energy intake and reduced energy expenditure contributed to the weight gain and dramatic increase in the prevalence of obesity since the 1976–1980 survey.

Between the national surveys in the 1970s and 1990s, the proportion of energy intake from macronutrients changed in United States adults 20–74 years. Over this interval, the percentage of daily energy intake from fat declined, 36–33%, and that from carbohydrates increased, 44–50%, while the percentage of energy intake from protein was stable, 14–15% (Briefel and Johnson, 2004). The shift in macronutrient composition of the diet reflects the marked increase in consumption of simple carbohydrates, including high fructose corn syrup (HFCS). This is also apparent in the increase in food energy available to the American population from the 1970s on (Table 7), (which coincided with an increased per capita consumption of HFCS) products in the United States. Calories from HFCS consumed per day in the United States were negligible in 1970 and increased slightly through the 1970s. However, estimated HFCS calories consumed per day increased markedly from about 30 calories per day in 1978 to about 150 calories per day in 1985; HFCS calories consumed per day has since increased more gradually through the late 1980s and 1990s, reaching more than 200 calories per day in 2000 (Schoonover and Muller, 2006). The increased consumption of calories from HFCS also coincided with the increased prevalence of obesity in the United States in 1988–1994 national health survey which continued through 2003–2004 (Table 6; see also Bray et al., 2004).

It is possible that human metabolism is not adapted to handle HFCS, which is a synthetically produced sugar using a synthetic enzyme. Fructose is metabolized in the liver, whereas glucose is metabolized in all cells, and the digestive and absorptive processes for the two sugars are different (Bray et al., 2004). Humans may not be able to completely metabolize this specific sugar species. The enzymatic handicap, in turn, may lead to an accumulation of glycemic excesses that ultimately results in storage of high levels of fat in many people with a prevalent variant combination of a complex of polymorphic genes.

The present in the context of the past

An approximate chronology of several major transitions and cultural developments in the evolution of hominids/humans was summarized earlier (Table 1). Biological and cultural evolution proceeded in concert until relatively recently when the pace of cultural development has accelerated sharply. Further, the pace of cultural change has accelerated more recently. The industrial revolution began only about 200 years ago while the revolution in computer and biotechnology has occurred over the past 25 years or so.

During the past 150 to 200 years, there have been dramatic improvements in indicators of general health and well-being—life expectancy at birth, infant and childhood mortality, and secular improvements in growth and maturity status. The positive changes in health and growth status and adult height were primarily related to changes in the cultural environment associated with public health and nutrition (Malina, 1979). For some time, these improvements were largely limited to industrialized or developed countries, but similar gains are increasingly evident in developing countries (Malina et al., 2004).

In the past two generations, the pace of cultural development has accelerated and has exacerbated the mismatch between biology and culture which has contributed to an increasingly sedentary lifestyle in the presence of a readily and easily available food (energy) supply. These conditions contradict our evolutionary past, i.e., a physically active lifestyle of moderate and at times vigorous activity on a regular basis. In other words, we are biologically equipped for a more physically active lifestyle, while cultural circumstances permit and reinforce a sedentary alternative (Malina, 1988).

The mismatch between biology and culture is evident in a number of "maladaptations" to our recent sedentary lifestyle: decreased cardiovascular and metabolic health; increased prevalence of osteoporosis; decreased cardiorespiratory fitness and muscular strength and endurance; increased overweight and obesity; increased disease risk, morbidity, and mortality; and potential reduction in quality of life for a significant percentage of the population. It is also suggested that the increasing prevalence of obesity might contribute to a cessation, or perhaps reversal, of the steady increase in life expectancy in the United States since the mid-19th century (Olshansky et al., 2005).

Mortality rates from coronary heart disease increased dramatically after World War II, although the trend was already apparent early in the 20th century (Smil, 1989; Stern, 1979). Mortality rates peaked in the 1960s in what was labeled the epidemic of coronary heart disease, and have declined since (Stern, 1979; Tyroler, 1988). The link between heart disease and physical inactivity was hypothesized in 1953 and physical inactivity as a risk factor for heart disease was established in 1992 (Paffenbarger et al., 2001).

The prevalence of osteoporosis and osteopenia of the hip is high in adults, females more so than males and projections for the future indicate a major increase (Department of Health and Human Services, 2004). In the past 25 years, the link among obesity, adiposity, physical inactivity, metabolic complications, and some cancers in adults is being elaborated (Institute of Medicine, 2007). It is unlikely that these conditions affect Darwinian fitness, but they do impact functional capacities and quality of life.

The "maladaptations" were initially documented in adults but evidence of corresponding complications is increasingly evident in youth. The latter is probably related to the obesity epidemic of the 1980s. Obesity is a major factor in the metabolic syndrome, a clustering of risk factors associated with chronic disease. A significant percentage of children and adolescents have features of the metabolic syndrome and the risk of metabolic complications is greater in the overweight and obese (Cook et al., 2003; de Ferranti et al., 2004). Features of the metabolic syndrome cluster also with physical inactivity and reduced cardiorespiratory fitness in children and adolescents (Brage et al., 2004; Katzmarzyk et al., 1999).

The current scenario begs several questions which are relevant to contemporary human biology. How long can we sustain the pace of cultural change on a biological base that is increasingly being compromised by physical inactivity, overweight and obesity? How does the sedentary lifestyle affect out capacity to adapt to increased levels of physical activity during childhood and adolescence, young adulthood, middle age, and old age? Does regular physical activity promote longevity or are those fit for longevity more active? And, what is the role of genetic polymorphisms in adaptations to physical activity and physical inactivity?

Note

Technically, Herbert Spencer (1864) first coined the phrase "survival of the fittest," not Charles Darwin, and it was popularized by Thomas Huxley (1893–1894). According to Spencer (1864, p 144), "This survival of the fittest, which I have here sought to express in mechanical terms, is that which Mr. Darwin has called 'natural selection,' or the preservation of favored races in the struggle for life." Darwin never actually used the term "survival of the fittest" in the Origin of the Species (1859).

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