

The Energetic Paradox of Human Running and Hominid Evolution¹

by David R. Carrier

THE FEATURE THAT DIFFERENTIATES HOMINIDS from other primates is not large brain size, but the set of characters associated with erect bipedal posture and a striding gait. Long before the rapid increase in relative brain size that took place during the Pleistocene, early australopithecines possessed the postcranial morphology of an erect, striding biped (Lovejoy, Heiple, and Burstein 1973). Evidence for the bipedal gait of early hominids is provided by the morphology of the 3.5-million-year-old postcranial material from the Hadar Formation of Ethiopia (Johanson, Taieb, and Coppens 1982, Lovejoy, Johanson, and Coppens 1982), early Pleistocene material from eastern and southern Africa (Preuschoft 1971), and the Pliocene trackways (3.6 to 3.8 million years old) discovered at Laetoli in northern Tanzania (Leakey and Hay 1979, White 1980). Together these suggest that early australopithecines were relatively small-brained creatures, possessing structural adaptations for upright walking and running that in a broad sense are remarkably similar to those of modern man. The aspects of locomotion that unite the hominids as a group are also uniquely hominid in character and distinctly peculiar for mammals. Consequently, the study of human locomotion, in addition to explaining much of the biology of the one remaining hominid, may prove to be one of the more powerful inductive approaches to the study of hominid evolution.

The energetic cost of transport (oxygen consumption per unit body mass per unit distance traveled) for running humans is relatively high in comparison with that for other mammals and running birds. Early comparative studies showed that a mam-

mal the size of man should consume roughly 0.10 ml of oxygen per gram body mass per kilometer traveled (Taylor, Schmidt-Nielsen, and Raab 1970), but the measured value for man is over twice this amount (0.212 ml). A recent analysis of 64 species of running birds and mammals (Taylor, Heglund, and Maloiy 1982) confirms the initial observations that the cost of transport is relatively high for human runners.

It is somewhat surprising, therefore, that among cursorial mammals man is one of the best distance runners. While game animals are faster over short distances, they generally have less endurance than man. Aside from published accounts of endurance performance in the domestic horse and camel, which have been bred for endurance racing, very little is known about the stamina of mammals. What little information is available is usually taken from anecdotal accounts of animals performing in a variety of climatic and topographic environments (see Howell 1965), and consequently interspecific comparisons are hazardous. Comparisons between man and a number of cursorial species can be made, however, in the context of a contest between predator and prey.

Hunters of a number of different cultures are known to run down prey by dogged pursuit often lasting one or two days (Krantz 1968, Watanabe 1971). Bushmen are reported to run down duicker, steenbok, and gemsbok during the rainy season and wildebeest and zebra during the hot dry season (Schapera 1930). Tarahumara Indians chase deer through the mountains of northern Mexico until the animals collapse from exhaustion and then throttle them by hand (Bennett and Zingg 1935, Pennington 1963). Paiutes and Navajo of the American Southwest are reported to have hunted pronghorn antelope (one of the fastest of all mammals) with this same technique (Lowie 1924; Foster 1830, cited by Lopez 1981:111). Furthermore, Aborigines of northwestern Australia are known to hunt kangaroo successfully in this way (Sollas 1924, McCarthy 1957). In these examples the stamina of prey animals generally considered to be specialized for running and presumably putting forth their best effort proves to be less than that of man.

Energetically inefficient transport and endurance running would seem to be incompatible. The combination of these two attributes presents obvious morphological and physiological problems. For instance, there must be a way of dissipating the high levels of metabolic heat produced during long-term muscle action. In addition, extended periods of high energy demand require large body stores of glycogen and fatty acids and an effective means of mobilizing these stores. It is clear that during the sequence of evolutionary steps that led from pre-hominids to *Homo sapiens* these problems have been overcome. How this was accomplished and what factors might

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DAVID R. CARRIER is a doctoral candidate in zoology at the University of Michigan (c/o Division of Biological Sciences, University of Michigan, Ann Arbor, Mich. 48109, U.S.A.). Born in 1955, he was educated at the University of Utah (B.S., geology, 1980; B.S., biology, 1980; M.S., biology, 1982). He views himself as a functional and evolutionary morphologist and is particularly interested in vertebrate locomotion and the ontogeny of the musculo-skeletal system. His publications include "Postnatal Ontogeny of the Musculo-Skeletal System in the Black-tailed Jack Rabbit (*Lepus californicus*)" (*Journal of Zoology* [London] 201:27-55) and, with D. M. Bramble, "Running and Breathing in Mammals" (*Science* 219:251-56). The present paper was submitted in final form 9 1 84.

have initiated this sequence of specialization is the subject of the present analysis.

DISSIPATION OF METABOLIC HEAT

The normal core body temperature of eutherian mammals ranges from 36°C to 38°C (Morrison and Ryser 1952). The lethal core temperature of these mammals is only 6°C higher, ranging from 42°C to 44°C (Adolph 1947). Using empirical measures of the cost of transport, Taylor (1974) has calculated that the maximal exercise heat loads generated by medium-sized and large animals (greater than 10 kg body mass) are nearly an order of magnitude greater than the maximal environmental heat that they are likely to encounter in nature. If metabolic heat is produced more rapidly than it can be dissipated, body temperature rises. Thus, adequate thermal regulation is critical for animals that run for extended periods. For example, cheetahs sprint at speeds exceeding 100 km/hr, and extrapolation of measurements made at lower speeds suggests that at 100 km/hr heat production would be more than 60 times greater than at rest (Taylor and Rowntree 1973a). The cheetah stores most of this heat, and therefore as it runs its body temperature rises. Once the rectal temperature reaches 40.5°C the animal refuses to run. Taylor and Rowntree estimate that if a cheetah terminated a sprint once its body temperature reached 40.5°C, it could run for only 1 km. This approximates the actual distance that cheetahs pursue their prey in the wild. It seems that the duration of the cheetah's sprint may be determined not by fatigue but by the amount of heat it can store before it reaches a limiting body temperature.

Mammals dissipate heat by evaporative or nonevaporative means. The African hunting dog is exceptional in that it appears to dissipate large exercise heat loads, for extended periods, through nonevaporative means (Taylor et al. 1971). Most medium-sized to large mammals rely on evaporative cooling to maintain body temperature while running (see Richards 1970; Taylor 1974, 1977). Evaporative cooling is accomplished by two separate mechanisms: (1) respiratory evaporation occurring at the nasal mucosa, buccal, and tongue surfaces (panting) and (2) evaporation of sweat from the general body surface. Panting is almost universally employed by medium-sized to large mammals. The only groups that do not rely heavily upon panting are the Old World Anthrozoidea (including man) (Robertshaw, Taylor, and Mazzia 1973, Hanna and Brown 1983), horses, and camels (Robertshaw 1975). These three groups maintain body temperature during extended exercise by sweating. In addition to these animals, some bovids (Taylor and Lyman 1972) and kangaroos (Dawson, Robertshaw, and Taylor 1974) also use sweat glands for thermoregulation. In contrast, suids (Robertshaw 1975) and some carnivores (Taylor et al. 1971) have sweat glands on the general body surface, but these do not appear to be associated with thermoregulation. Sweat glands on the general body surface are lacking in Rodentia, Proboscidea (Robertshaw 1975), and Lagomorpha (Jenkinson 1970).

SWEATING VS. PANTING

A number of physiologists have considered the advantages and disadvantages of sweating and panting to achieve evaporative cooling (Schmidt-Nielsen 1964, Hales 1974, Taylor 1977). The present discussion will be confined to those aspects which influence thermoregulation during exercise.

Evaporative cooling from the respiratory surfaces offers the following advantages over evaporative cooling from the skin:

1. The skin of sweating animals is cooler (as a result of the evaporation) than the skin of panting animals. When air temperature exceeds skin temperature, animals gain heat from the environment. Accordingly, panting animals have a slower in-

ward flow of heat from the hot environment than sweating animals. Taylor and Rowntree (1974) have shown that in a hot environment (47°C) heat flows into sweating animals at about twice the rate that it flows into panting animals. For the same reason, when environmental temperature is low the cooler skin temperature in sweating animals results in a smaller gradient for nonevaporative heat loss (heat loss by radiation when skin temperature exceeds ambient temperature). Thus, sweating animals gain more heat from a hot environment and are capable of losing less heat by nonevaporative means than panting ones.

2. Because panting restricts evaporation to the nasal, buccal, and pharyngeal cavities, panting animals lose little salt. Sweating animals, on the other hand, must deal with large salt losses (Schmidt-Nielsen 1980).

3. Panting provides forced convection across the evaporative surfaces, whereas sweating requires animals to rely on free convection or wind. (This should not be a problem for a running animal, particularly if it lacks hair.)

Evaporative cooling from the skin offers the following advantages:

1. Sweating provides an additional evaporative surface. Taylor and Rowntree (1974) measured the maximum rates of evaporative heat loss from a group of panting and a group of sweating animals in response to exercise. They found that the rates of evaporation from the respiratory surfaces were similar, but the sweating animals had much higher maximal rates of evaporation because of the evaporation that occurred at the skin surface.

2. Sweating is independent of the respiratory cycle. As a running animal increases speed, its oxygen consumption increases in a linear fashion (Taylor, Schmidt-Nielsen, and Raab 1970). However, as running speed changes it is unlikely that the respiratory air flow required for metabolism will match the flow needed for heat loss, since the rate at which heat can be dissipated will vary with ambient temperature and humidity. Furthermore, the breathing cycle of quadrupeds is strictly controlled by the body motions of the running animal (Bramble and Carrier 1983). This coupling of locomotor and respiratory cycles will make it impossible for a running animal to vary the air flow over the respiratory evaporative surfaces to the same degree that is possible in typical stationary panting. Consequently, the flexibility and possibly the total effectiveness of panting as a means of evaporative cooling may be limited in a running mammal. Indeed, the amount of heat that can be lost through evaporation from the respiratory surfaces severely limits the maximum rate of heat dissipation during running in animals that rely solely on panting (Taylor and Rowntree 1974).

In this context, the mechanisms of heat dissipation in the red kangaroo are of interest. This marsupial uses three evaporative cooling mechanisms: panting, sweating, and saliva spreading (Dawson, Robertshaw, and Taylor 1974). However, it sweats only during exercise. Under conditions of severe thermal stress, the resting kangaroo pants and spreads saliva. For the red kangaroo and other mammals, sweating provides an additional avenue of heat dissipation that may offer more flexibility and be more compatible with running as a mechanism of thermoregulation.

RUNNING HUMANS

The sweat glands of man are distinctive for the high secretory level at which they operate. No other species is known to sweat as much per unit surface area as man (Eichna et al. 1950, Schmidt-Nielsen 1964, Newman 1970). Human sweat glands may also be subject to a higher level of neuronal control than the sweat glands of other species. At present, it appears that only camels, horses, and Old World Anthrozoidea possess directly innervated sweat glands. The sweat glands of other

groups either lack a nerve supply (e.g., canids) or possess one that does not make direct contact with the gland (e.g., bovids) (Robertshaw 1975). Furthermore, the neurons supplying the glands of anthropoid primates are cholinergic, whereas the glands of horses and camels are adrenergically innervated. Robertshaw (1975) has suggested that the rapid hydrolysis of acetylcholine by acetylcholinesterase may provide the cholinergic glands of anthropoid primates with finer neuronal control than is possible with adrenergic modes of transmission.

The rate at which heat is lost from running humans is greatly increased by their relative lack of hair. The fur coat of most mammals not only insulates the animal from the environmental heat, but also insulates the environment from heat produced by the animal. Accordingly, mammals with thick insulatory coats will have difficulty dissipating heat generated through exercise. The paucity of hair on the human body results in greater thermal conductance than would be possible with a full coat of hair. The thermal conductance of a hairless mammal should be further increased by the increased convection during running, as the animal moves through the air. Mammals with thick coats will not experience this increase in convection when running. Cena and Monteith (1975) have shown that the thermal conductivity of sheep fleece (4 cm thick) is not affected by air flow of up to 18 km/hr. In rabbits, wind speeds below 11 km/hr do not affect the conductivity of the fur (1.8 cm thick), but an increase of wind speed to 18 km/hr doubles its conductivity. It appears that air moving parallel to the surface of fur coats at speeds equivalent to endurance running speeds of humans (i.e., 10–20 km/hr) fails to penetrate or even disturb the stagnant air trapped between the hairs of other mammals. This stagnant air provides nearly all the thermal resistance of the system. The adaptive value of man's largely glabrous condition may, more than anything else, be the facilitation of heat dissipation while running.

In summary, the combination of well-developed sweat glands and the relative absence of body hair in man makes it probable that running humans display very high thermal conductance, with maximal values well above those of most cursorial mammals. The human mechanisms of thermoregulation (sweating, as opposed to panting, and hairlessness) are probably more effective at dissipating metabolic heat produced in running than are the regulatory mechanisms used by other mammalian cursors. Supporting this is the observation that certain sweating primates (i.e., spider monkeys, stump-tail macaques, baboons, and chimpanzees) are capable of greater maximum rates of heat dissipation during running than are mammals dependent upon panting (Taylor and Rowntree 1974). Unfortunately, measurements of maximal rates of heat dissipation from large animals during exercise are almost nonexistent, and so direct comparisons with man cannot yet be made.

COST OF TRANSPORT

Running humans expend approximately twice as much energy per unit mass as typical mammalian quadrupeds of the same size but are nevertheless adept at endurance running. Man's capacity for endurance locomotion, both running and walking, may result from the way in which the cost of transport varies with the speed of travel (fig. 1). First, humans walking at optimal speed consume only half the energy (used in transport) required to cover the same distance while running (Cavagna and Kaneko 1977, Rodman and McHenry 1980). This is clearly not the case for horses (Hoyt and Taylor 1981) or for other large cursors (see Taylor, Heglund, and Maloiy 1982). Second, while quadrupedal cursors have specific speeds at which energy expenditure is minimized for each of their various gaits (Hoyt and Taylor 1981), the cost of transport for a running human does not depend on speed (Boje 1944, Mar-

garia et al. 1963, Cavagna and Kaneko 1977). Consequently, a man running a marathon will consume the same amount of energy for transport whether he runs at a slow jog or at a world-class pace.

WALKING

Unlike human running, human walking is at least as economical as the walking of typical mammalian quadrupeds (Rodman and McHenry 1980; also see Tucker 1975). The efficiency in walking is related, in part, to a finely tuned system of storage and recovery of the energy used for motion within each stride. Walking birds and mammals benefit from an exchange between the kinetic energy and the gravitational potential energy of the center of mass within each stride (Cavagna, Heglund, and Taylor 1977). Gravitational potential energy is stored as the center of mass rises during a step. This energy is then recovered as the body falls forward and is subsequently converted back into potential energy as the center of mass again rises over the other leg. For this reason, walking has been likened to an inverted swinging pendulum or an egg rolling end over end (Cavagna, Saibene, and Margaria 1963). The bipedal posture of man is ideally suited for this pendular motion. Throughout most of the support phase, the limb pivots on a plantigrade foot. In contrast to the situation of most quadrupedal cursors, no muscular effort is required to maintain ankle extension. Most importantly, the center of mass rolls in an arc over the point of support (foot) on a relatively straight leg, so that the potential energy gained in the rise roughly equals the kinetic energy lost in the descent (Alexander 1976).

Energy savings due to this transfer between potential and kinetic energy are substantial. In humans walking at a speed of approximately 4 km/hr, the recovery of mechanical energy attains a maximum of 65–70% (Cavagna, Thys, and Zamboni 1976). Equivalent savings have been measured in bipedal birds (turkey and rhea) walking at similar speeds (Cavagna, Heglund, and Taylor 1977). In contrast, the percentage recovery

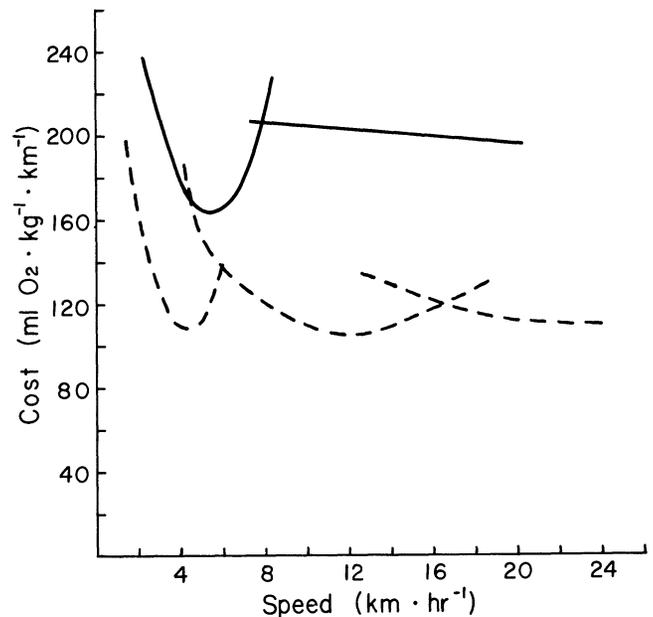


FIG. 1. The energetic costs of walking and running in the horse and in man. The oxygen consumed in moving a unit distance is minimized at a narrow range of speed in all three gaits—walk, trot, and canter—of the horse (dashed curves) and in the walk of man (solid curve). In contrast, the cost of transport is independent of running speed in man (solid line). (Modified from Hoyt and Taylor 1981 and Margaria et al. 1963.)

appears to be lower in quadrupedal mammals. Rams walking at intermediate speeds (3–4 km/hr) recover a maximum of only 35%. Dogs and monkeys recover no more than 50% of the mechanical energy used while walking (Cavagna et al. 1977).

The efficiency of walking changes with speed (Cavagna and Kaneko 1977, Hoyt and Taylor 1981). This is true for both men and horses (fig. 1). There is an intermediate speed at which the energetic cost to walk a unit distance is minimized. As velocity is increased or decreased away from this optimal speed, the cost of transport rises rapidly. The cost of transport for a walking human is minimized at speeds ranging from 5 to 6 km/hr. The optimal walking speed of the larger horse is slower (4 to 5 km/hr).

Optimal walking speeds are related, in part, to the energetic properties of the contractile component of skeletal muscle. There is a speed of muscle shortening at which efficiency is maximized (for a review, see Goldspink 1977). This demands that, in terms of energy expenditure, there be an optimal stride frequency. Also, the ability of muscle to generate force diminishes as the muscle is stretched beyond or shortened below its so-called optimal length (Gordon, Huxley, and Julian 1966). Consequently, there must also be an optimal stride length with regard to muscle function. Because speed is the product of stride length and stride frequency, the contractile properties of muscle can be expected to limit animals to energetically optimal speeds in all gaits. However, for running humans this appears not to be the case.

RUNNING

As is the case for walking, the energetic cost of transport for running quadrupeds appears to change with speed, being minimal at intermediate speeds within each gait. By training horses to extend their gaits beyond normal speeds, Hoyt and Taylor (1981) have shown that for each gait there is a specific speed at which the amount of oxygen used to move a given distance is minimal (fig. 1). When the horses were allowed to select their own speeds, they chose speeds that coincided with the energetic optimum within each gait. The optimal speed for each gait is also the preferred speed. As a result, there are ranges of speed that the animals never use for any sustained period. Evidence that other cursorial mammals have optimal running speeds comes from the observation of Pennycuik (1975) that migrating wildebeest and gazelle use only a restricted range of speeds within each gait.

Given these observations on what might be expected to be a general pattern for vertebrates, it is somewhat surprising to find that *Homo sapiens* does not have a single energetically optimal running speed. Over the range of speeds (8–20 km/hr) used by humans when running long distances, the cost per unit distance does not vary significantly with speed (Margaria et al. 1963, Cavagna and Kaneko 1977, Hagan et al. 1980). The recognition of this apparent difference between humans and quadrupeds raises two immediate questions. First, what is it about humans that detaches the cost of running from speed? Second, what advantages or disadvantages does this unusual situation create for the running human? Although the answers to these two questions await further experimentation, several points can be made.

There is no evidence to suggest that there is anything particularly unusual about human skeletal muscle. It seems to be subject to the energetic and mechanical constraints typical of other vertebrate skeletal muscle (see Thorstenson 1976). Furthermore, the marked ability of humans to make use of energy stored elastically in the tendons and muscles while running (Cavagna and Kaneko 1977) is not unusual for mammalian cursors (Cavagna, Heglund, and Taylor 1977). Given the ordinary nature of human skeletal muscle, man would be expected to exhibit an optimal running speed.

Man does differ from quadrupeds, however, in the way in

which the lungs are ventilated during running. When a quadruped trots or gallops, the muscles and bones of the thorax must absorb the shock of impacting on the front limbs. In addition, during a gallop all mammals exhibit some degree of axial bending in the dorso-ventral direction. This motion compresses and then expands the thoracic space with each stride. These aspects of gait restrict the ventilation of quadrupeds to one breath per locomotor cycle (Bramble and Carrier 1983, Hornicke, Meixner, and Pollmann n.d.). In contrast, the upright bipedal gait of humans makes possible a large number of breathing patterns (e.g., two strides per breath, three strides per breath, etc.). Therefore, while the breathing frequency of a running quadruped equals its stride frequency, man can vary breath frequency relative to stride frequency (Bramble and Carrier 1983).

The objective of lung ventilation is to meet the metabolic demand for oxygen. However, in running mammals this is more complex than is generally recognized. As running speed increases, the need for oxygen increases rapidly in a linear manner (Taylor, Schmidt-Nielsen, and Raab 1970). For any given level of aerobic exertion, the tissues' need for oxygen will be met by a specific lung minute volume, which is the product of the breathing frequency and the tidal (lung) volume. However, as a consequence of the elastic resistance of the thorax, airway resistance, and dead-space volume, there is a specific rate and depth of breathing, for any minute volume, that maximizes ventilatory efficiency (Otis, Fenn, and Rahn 1950, Crosfill and Widdicombe 1961, Yamashiro and Grodins 1973). A further limitation results from the way in which speed is varied while running. There appears to be a specific combination of stride length and stride frequency that minimizes energy consumption for any running speed (Knuttgén 1961, Cavanagh and Williams 1982). For sustained economical transport a running mammal must therefore (1) employ an energetically appropriate blend of stride length and stride frequency, (2) match the metabolic demand for oxygen via lung ventilation, (3) ventilate the lungs with an energetically suitable combination of breath frequency and volume, and (4) breathe in synchrony with the locomotor motions of the body.

The tight 1:1 coupling between breath and stride frequency of quadrupeds may therefore result in a running speed, within each gait, that is energetically optimal for breathing. As running speed diverges from a theoretically optimal speed, the motions of the body necessary for breathing may begin to interfere with the motions required for running, decreasing the efficiency of the entire system. This would have the effect of making the cost of transport dependent on running speed (within a single gait), as it has been shown to be in the horse. In contrast, the capacity of humans to alter the breathing pattern while running would eliminate this problem. The striding bipedal gait of humans, by relaxing constraints imposed on lung ventilation, may broaden the range of speeds which are energetically viable.

The lack of an optimal running speed could be viewed as a disadvantage, because every speed within the aerobic scope of man is as costly as any other. This is particularly significant in that man is a relatively inefficient runner compared with other mammalian cursors. On the other hand, given the physiology necessary to cope with high levels of energy consumption and metabolic heat production, a constant cost of transport could provide humans with the option of running at a wide variety of speeds. Quadrupeds, such as the horse, that appear to be specialized for a narrow range of speeds within each gait may in a practical sense be limited to these optimal speeds.

STORAGE AND UTILIZATION OF ENERGY

Depletion of muscle glycogen stores is one factor that has been implicated in the development of muscle fatigue during pro-

longed exercise, forcing animals to stop or slow their pace (Ahlborg et al. 1967, Bergstrom et al. 1967). The rate at which muscle glycogen is depleted depends on the level of blood glucose (supplied by liver glycogen) and the rate of fat oxidation (Holloszy and Booth 1976). Consequently, the high metabolic rate of running humans combined with their great stamina leads to the prediction that conditioned persons will have unusually large reservoirs of (1) muscle glycogen and triglycerides (which can be hydrolyzed to free fatty acids), (2) triglycerides stored as adipose tissue, and (3) liver glycogen. At present the literature does not contain the information necessary to address this issue. The body's reservoir of glycogen and free fatty acids varies dramatically depending on the diet and physical condition of the animal (Bergstrom et al. 1967, Paul and Issekutz 1967). This combined with a relative lack of information from species other than man makes interspecific comparisons impossible at this time.

A diet enriched in carbohydrates, maintained for several days, doubles muscle glycogen and enhances endurance in humans (Bergstrom et al. 1967, Karlsson and Saltin 1971). Conversely, a diet rich in protein and fat decreases muscle glycogen and prematurely depletes glycogen during exercise (Gollnick et al. 1972). Humans can adjust the concentration of glycogen in the muscles, and thus their physical performance, by short-term changes in diet. It is unknown whether this allows humans to concentrate glycogen at higher levels than those reached by other mammals. Presumably the option of "carbo-loading" is not available to those predators that are strict carnivores (e.g., canids and felids).

During exercise the mobilization and rate of utilization of carbohydrates and fatty acids by muscles is controlled largely by the circulating concentrations of five hormones: epinephrine, norepinephrine, adrenocorticotrophic hormone (ACTH), glucagon, and thyroxine (Stryer 1975). Because only low levels of these hormones are stored in the body, a fresh supply must be synthesized as the need arises. With the exception of glucagon and ACTH, all are produced by the thyroid and adrenal glands. As has been noted by Spuhler (1979), these glands are relatively large in humans. Spuhler suggests that relatively large gland size may result in higher levels of hormone production and, in turn, could be associated with the high energetic demands of human endurance running.

ENDURANCE RUNNING AND PREDATION

There are important differences in locomotion between man and typical quadrupeds (fig. 2). In most quadrupeds, heat dissipation is coupled to the respiratory cycle. This in itself is likely to decrease the capacity to dissipate heat while running. Added to it is the limitation that energy-efficient lung ventilation requires a specific combination of breath frequency and volume for any minute volume. The breathing cycle is in turn largely controlled by the locomotor cycle, which is energetically limited to a specific combination of stride frequency and length for any given running speed. These suggested constraints may combine to force a mammal to run at a narrow range of speeds in each gait and limit its maximum rate of heat dissipation. In contrast, in man heat dissipation is not tied to respiration, and lung ventilation is largely independent of locomotion. Therefore, running humans should display greater plasticity in the critical functions of respiration and heat dissipation than running quadrupeds.

Compared to that of other mammals, man's energetic cost of transport is relatively high. Nevertheless, humans possess exceptional locomotor stamina. Several of the characters believed to contribute to man's endurance capacity may be primitive characters for Old World Anthropoidea:

1. The combination of cholinergic sweat glands and general absence of body hair provides man with an effective means for

dissipating large exercise heat loads. Sweat glands that are controlled by synapsing, cholinergic neurons occur in Old World anthropoids and appear to be confined to this group (Robertshaw 1975). These primates are capable of greater maximal rates of evaporative cooling during exercise than are certain cursorial mammals that depend on panting for thermoregulation (Taylor and Rowntree 1974). Many of the great apes (Pongidae) have large bald areas (lack hair) on the face, chest, and rump.

2. The arboreal modes of locomotion of many anthropoids necessitate modifications of the limbs and trunk that are transitional to upright bipedal posture and allow limited bipedal locomotion in some modern forms (Tuttle 1975). This trend towards bipedality presents the possibility of enhanced transfer between gravitational potential and kinetic energy while walking. Bipedality also releases the mechanical constraints imposed on the breathing cycle by locomotion, thereby making possible a variety of breathing patterns.

3. The adrenal and thyroid glands of primates are hyperplastic compared with those of other mammals (see Spuhler 1979). This hyperplasticity may increase the levels of those hormones critical to the mobilization and utilization of fatty acids and glucose by muscles.

4. The omnivorous diet of most anthropoids opens up the possibility of increased glycogen storage in the muscles through carbo-loading.

Hence, in these respects hominids may have been pre-adapted to endurance running. However, in order to become an endurance runner man has had to overcome the handicap imposed by a relatively high energetic cost of transport. Given this constraint, the fact that humans have exceptional stamina suggests that at some point in the evolution of hominids there was strong selective pressure for endurance running.

Mammals run for a limited number of purposes. Running is often a form of play, especially among young cursorial mammals. This is likely to be of value mainly for the conditioning and training it provides for running under other circumstances. In some instances running is used for migration. However, most species migrate at a walk, and running is reported to be rare in this context (Pennycuik 1975). Prey animals depend heavily upon running speed and endurance to avoid predators. Because of the great speed of the large predators, running is unlikely to have been of much value to man's early ancestors as a means of escape. Running is also used by predators to capture prey. Predation is a behavior in which running ability, particularly endurance running, might have been useful to early hominids. Although most mammalian predators rely on speed and acceleration to overtake prey animals, a few groups (e.g., *Lycan*) make use of exceptional endurance. The physiology and morphology of modern man, combined with what is known from hominid fossils, suggest that long before the development of complex culture and hunting weapons, early hominids may have been endurance predators equipped with biological weapons for hunting very different from those of other mammalian predators.

If, as is the case for running humans, the cost of transport of early bipedal hominids did not change with running speed, then they would have been free to pursue prey at any speed within their aerobic range. They could therefore have picked the speed least economical for a particular prey type. This would have forced the prey to run inefficiently, expediting its eventual fatigue. For example, a man in running pursuit of a horse would do best to proceed at roughly 16–17 km/hr. This is the speed midway between the optimal speed of the trot and the optimal speed of the gallop (fig. 1) and is a speed at which the animal prefers not to run (Hoyt and Taylor 1981).

An animal pursued at its least economical running speed would be faced with two options. It could maintain distance

CONSTRAINTS ON SUSTAINED RUNNING

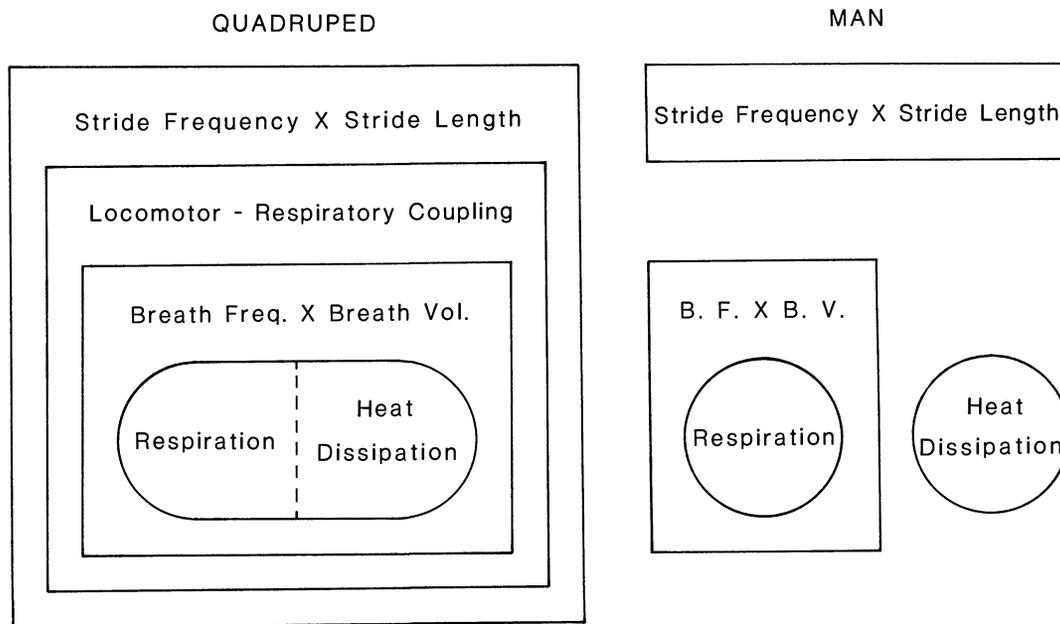


FIG. 2. Constraints on sustained running in typical quadrupedal mammals and in man. Boxes represent possible constraints on the circled functions of respiration and heat dissipation.

from the predator by running at the nonoptimal speed, or, more likely, it could race ahead at a faster and more efficient speed. The latter of these two escape strategies would lead to intermittent running and resting. The prey animal would outdistance the predator and, upon stopping to catch its breath, would find that the predator was still in pursuit, forcing it to charge off once again. It would be forced into an intermittent running pattern by the contrasting needs to avoid the pursuing predator and to avoid unnecessary fatigue and heat stress if the predator has given up the chase. This seems, from my own observation, to be what happens when pronghorn antelope (*Antilocapra*) are pursued by a running human.

Although intermittent running provides brief rest periods, it is probably less economical than continuous running. Tests on humans show that the work efficiency of intermittent exercise on cycle ergometers can be as much as 26% lower than that of continuous exercise at the same average power output (Edwards et al. 1973). Compared with continuous exercise, intermittent exercise has also been shown to elevate core body temperature and decrease evaporative heat loss as a result of reduced sweating (Ekblom et al. 1971). Therefore, whether the prey ran at the pace set by the theoretical predator or chose to run intermittently, the end result would be inefficient transport. In a contest of endurance, a predator whose cost of transport did not vary with running speed would likely have a substantial advantage over a prey animal that possessed restricted, energetically optimal speeds in each gait.

In the example of a man attempting to run down a horse, the much greater efficiency of the horse would likely outweigh any benefit that the constant cost of transport provided the man. In all probability the man would become exhausted long before the horse. However, part of the reason that horses are much more efficient than humans is the difference in body size between the two species. The cost of transport scales to the -0.40 power of body mass (Taylor, Schmidt-Nielsen, and Raab 1970). In general, large mammals consume less energy in locomotion than do small mammals. Where predator and prey are equal in body size or the prey is smaller, a constant cost of

transport could give a predator a distinct energetic advantage if the prey had specific optimal running speeds.

Another aspect of human biology that would be useful for an endurance predator is man's exceptional ability to dissipate heat while running. It is true that the greater energy consumption of running humans generates a relatively large exercise heat load. However, the well-developed sweat glands of man make the whole body surface available for evaporative cooling. Since evaporative cooling in humans is not limited, as it is in panting mammals, by the rate and volume of lung ventilation, it represents a means of thermoregulation that is compatible with running. In addition, one fortunate consequence of the lack of body hair in humans is an increase in thermal conductance with increasing running speed (apparent wind speed). Higher rates of convection with increasing running speed will be much less prevalent in mammals equipped with a more typical complement of body hair because of the stagnate layer of air maintained by the fur. These thermoregulatory characteristics of man would certainly benefit an endurance predator.

There is some anecdotal evidence which suggests that the way in which humans dissipate heat while running does play a significant role in human hunting. Dawson, Robertshaw, and Taylor (1974) found that in spite of sweating and increased respiratory cooling, red kangaroos are unable to dissipate all of the heat produced while running at speeds between 4 and 22 km/hr. They calculated that, hopping at speeds in this range, a kangaroo would reach a lethal temperature in one to two hours. Consequently, it comes as no surprise that Aborigines of the warm desert of northwestern Australia are reported to run down kangaroos (Sollas 1924, McCarthy 1957). On very hot summer days it is a relatively simple matter for a man to chase down the hare, *Lepus californicus* (Schmidt-Nielsen 1964), though in the cool of early morning or during the winter this is a seemingly impossible task. Hottentots are reported to run swift prey animals to exhaustion in the heat of the sun (Schaper 1930). Furthermore, Bushmen are known to run down wildebeest and zebra during the hot dry season but use alterna-

tive methods when hunting these animals during other seasons (Schapera 1930).

This analysis of the morphology and physiology of human locomotion, although incomplete and largely speculative, suggests that man is a primate that has become specialized for (among other things) endurance running. This points to a scenario concerning the origin of hominids that has been proposed in one form or another by several authors (Dart and Craig 1959, Ardrey 1961, Morris 1967, Krantz 1968). Exercising anthropoid primates can dissipate heat more rapidly than certain cursorial mammals. This suggests that the earliest hominids may have been more effective at heat loss than many other contemporary mammals. Furthermore, early australopithecines were fully bipedal. As a result, they were probably not constrained to the typical 1:1 breathing pattern of running quadrupeds. Consequently, it is possible that one of the important factors which differentiated hominids from other anthropoids, and ultimately led to the evolution of *H. sapiens*, was the occupation of a new predatory niche. This hypothetical niche was that of a diurnal predator which depended upon exceptional endurance in hot (midday) temperatures to disable swifter prey animals.

These hypothetical early hominids were endowed with a physiology and morphology that (1) allowed running speeds which forced prey to escape in an inefficient manner and (2) provided rates of maximum heat dissipation that were far above rates obtainable by the prey. Exploiting this broad range of running speeds and superior ability to thermoregulate, the early hominids were able to capture swift prey animals by pursuing them under conditions of high environmental temperature and at speeds different from those for which the animals were physiologically specialized. Initially the prey animals would have been not the large ungulates but the less cursorial hares and small artiodactyls (such as *Serengetilagus* and *Raphicerus*, which occur in the Laetoli Beds [Leakey and Hay 1979]) and the relatively helpless infants of the larger herd animals.

Alternatively, it has been argued on the basis of limb morphology that early australopithecines may not have been particularly skilled runners (Jungers 1982, Stern and Susman 1983). Also, analysis of the tools and animal bones from excavated Oldowan campsites (Leakey 1971), along with what is known of dental morphology, suggests that hunting may not have been an important hominid activity until the early Pleistocene (Wolpoff 1980). In this case, this scenario would better apply to the evolution of locomotion in *Homo* and might serve to distinguish *Homo* from the australopithecines. Whether the Hominoidea arose as a consequence of a shift to a predatory life-style or a diverging subgroup became hunters at a much later point, the predatory niche is the most obvious explanation for many of the unique characters of the primate known as man.

The model of early hominids as diurnal endurance predators leads to several testable predictions. It would be worthwhile to evaluate the endurance performances of man and modern prey animals under a variety of temperature regimens. If this scenario has any validity, the endurance performance of man relative to that of prey animals should increase with ambient temperature. In addition, the speeds at which modern primitive hunters run down prey should vary from species to species and should correspond to the prey animal's nonoptimal speed. The question of whether the constant cost of transport of human runners results from the wide variety of breathing ratios used by running humans is also relevant to this scenario. This could be tested by measuring oxygen consumption in human runners who have been trained to extend the range of speed at which the different breathing ratios are normally used. The scenario also predicts that early hominids were scantily haired. Unfortunately, the fossil record is unlikely to yield evidence on this point.

Comments

by A. K. KAPOOR

Department of Anthropology, University of Delhi, Delhi 110 007, India. 12 IV 84

This enlightening article on various aspects of bipedal and quadrupedal locomotion does not call for much comment except to link mode of locomotion with brain size and human evolution. Man can exhaust a prey animal during the heat of the day, not in the cool of the morning. This phenomenon requires a sense of timing, i.e., of when to hunt, which means thinking and hence the brain. When did the brain grow large—at the beginning of bipedal locomotion or hunting by early hominids? This question and the consequences should have been discussed here.

by TASUKU KIMURA

Primate Research Institute, Kyoto University, Inuyama, Aichi 484, Japan. 13 IV 84

Carrier proposes the new hypothesis that ancestral man could pursue a prey of a large body size at the speed energetically least economical for the animal. The hypothesis is very attractive, but he does not demonstrate it. An energetically optimum speed in quadrupedal terrestrial mammals has been experimentally proven to exist only in horses (Hoyt and Taylor 1981). Horses change gait pattern (walk, trot, or gallop) and select speeds in a manner that minimizes energy consumption. Whether this finding applies generally to terrestrial mammals as Hoyt and Taylor assume has not yet been determined. Precise experimental analyses on many kinds of animals are called for. On the other hand, this finding does contradict the linear relationship between energy cost of transport and body mass for different mammals shown by Taylor, Schmidt-Nielsen, and Raab (1970). That relationship was simply obtained from the energy cost of moving one unit of body mass over one unit of distance at infinite speed. Since the cost of moving one unit of body mass over one unit of distance depends on the speed of the animal, it is not calculated from the slope of the regression line between the energy cost per unit body mass and per unit time and speed as Schmidt-Nielsen (1975:248) proposed.

Man's lack of an energetically optimal running speed is explained by Carrier in connection with the capacity of humans to alter their breathing patterns relative to stride frequency. He and his coworker (Bramble and Carrier 1983) found that quadrupedal mammals (hares, dogs, and horses) normally synchronize their locomotor and respiratory cycles at a constant ratio of stride per breadth. Their original data showed that a 2:1 ratio appeared to be favoured in human running, though several breathing patterns were available. It is difficult to explain the continuously regular energy cost of human running relative to speed in connection with a ratio that is discontinuous in character.

It is reasonable that the human mechanisms of thermoregulation, sweating and hairlessness, in running are more advantageous than the panting used by many mammals, though this is not a new viewpoint. Readers should be aware that cutaneous evaporation is important for thermoregulation not only in the three groups mentioned by Carrier but also in many ungulates, such as donkeys, llamas, and cattle (Whittow 1971). This does not, however, influence the fact that human sweat glands may be the most effective.

Sakura (1983) has proposed the hypothesis that ancestral man occupied a new niche of diurnal predator. Most carnivores in the tropics are active during times of low temperature and not at midday. Early humans, as newcomers, may have

adopted the hot daytime for their hunting activity. This hypothesis explains man's highly developed mechanisms of thermoregulation, though it is insusceptible to direct proof.

The bipedal walking of living nonhuman primates is not energetically economical compared with that of humans (Yamazaki et al. 1979). In human erect walking, the center of gravity of the body rises in the stance phase (Cavagna, Heglund, and Taylor 1977). In nonhuman primates, on the contrary, the center of gravity of the body drops in the stance phase of walking because the knee joint continues to flex (Yamazaki et al. 1979; Kimura et al. 1983). Nonhuman primates do not "run" bipedally in the sense of constantly having a phase of free transit (Kimura et al. 1983). The locomotion of man's ancestors could not have differed entirely from that of living nonhuman primates. On the other hand, when man regularly hunted relatively large animals on the ground he must already have practised erect bipedal walking and running. Man's acquisition of bipedal walking and running cannot be explained in terms of energy cost alone.

by MARTIN K. NICKELS

Department of Anthropology, Illinois State University, Normal, Ill. 61761, U.S.A. 29 III 84

That persistence hunting based on endurance running is employed by some hunters today is not necessarily germane to the issue of whether it was an aspect of the initial exploitation of the hominids' diurnal hunting niche. How prevalent is such endurance running in these modern hunting groups? Is it the primary tactic employed? Just how energy-efficient is it in terms of optimal foraging theory (Hill 1982)? Is there evidence that endurance hunters engage in "carbo-loading," or is this merely a training practice employed by competitive long-distance runners for sporting events?

Despite these questions, I am in basic agreement with Carrier's (and others') conclusion that occupation of a diurnal hunting (and I would add scavenging) niche is a major feature of the hominid evolutionary pattern. The question is whether endurance running is necessary to explain what we know about early hominid subsistence patterns; I think not. The archaeological evidence of deliberate butchering of animal carcasses at australopithecine-grade (including *Homo habilis*) sites in East Africa beginning at about two million years ago does not indicate how these animals died (Isaac 1983). As Carrier himself admits, the evidence could equally support either deliberate hunting or scavenging. Wolpoff (1980:151) points out that the nature of the skeletal remains from the larger animals is consistent with their having been scavenged from carnivore kills. Additional support of scavenging is the report of Shipman (1984) that some cut marks directly overlie carnivore tooth marks on some early Olduvai Gorge faunal remains. Furthermore, that chimpanzees and baboons are capable of occasional small-game cooperative hunting based on such techniques as seizing, brief chasing, stalking (Teleki 1973:168), or even synchronous persistence hunting (Harding and Strum 1976) without endurance running suggests to me that australopithecines and early *Homo* were capable of engaging in such behavior. Combined with organized regular scavenging of larger game animals and enhanced technological and communicative skills, cooperative short-range persistence hunting seems sufficient to explain the archaeological and paleontological evidence from as early as two million years ago. I see no need to introduce endurance running as a necessary ingredient in this early adaptive pattern. Persistence in pursuit does not require the continuous physical exertion involved in running; it may involve perseverance in stalking or scavenging, patience while lying in ambush, or completion of a preplanned coordinated encirclement of prey. Such strategies would be based principally on neurological changes in the brains of early hominids rather than in their aerobic physiology.

While Carrier's model does account for the enhanced human physiological ability to dissipate heat by sweating, it is not necessary to postulate endurance running as the cause of the increased heat load in early hominids. Activities related to short-range hunting and scavenging in the open during the hottest part of the day seem to me sufficient. Consequently, in my judgment, Carrier's hypothesis, while interesting, is simply unnecessary; the short-range hunting and scavenging explanation is simpler and more compatible with the available evidence.

One final question: What "biological weapons for hunting very different from those of other mammalian predators" did early hominids possess? Since such predators presumably possess weapons of speed, power, and strength, what is left for early hominids if not intelligence, cunning, and employment of technology? But employment of just such "weapons" seems more than sufficient to explain the archaeological evidence without any need for an explanation based on the enhancement of aerobic physiology.

by SATWANTI

Department of Anthropology, University of Delhi, Delhi 110 007, India. 12 IV 84

In discussing locomotor stamina, the author has described the mode of locomotion, respiratory efficiency, and capacity to dissipate heat, but the system which plays an important role in endurance running, i.e., the heart and circulatory system, has not been mentioned.

by EUGENIE C. SCOTT

Medical Anthropology, University of California at San Francisco, San Francisco, Calif. 94143, U.S.A. 11 IV 84

The relationship between human energetics, locomotion, and evolution is well summarized here. I like the idea of the capacity of humans to vary their speed of pursuit according to the least efficient speed of the prey animal. This may well be a pursuit strategy specific to persistence hunters and could perhaps be tested by looking at the speeds at which human hunters pursue prey with different optimal speeds (or by looking at nonhuman persistence hunters?).

No one has fully addressed the question of the primate origin of the human cooling system. Newman (1970), cited by Carrier, has pointed out that human thermoregulation requires considerable water for evaporative cooling. Man can "sweat like a horse" but not drink like one; we are not capable of "tanking up" large amounts of water at one time as are equids and camelids. As a result, in hot, dry environments we must drink more frequently than other savannah dwellers. As Newman has pointed out, this human cooling system was *moved* to the savannah; it did not evolve there. The human inability to consume large amounts of water at one time is a definite handicap to a savannah hunter and likely required cultural compensation before the species was able to engage in lengthy persistence hunting.

Carrier states that the efficient cooling system of humans is paralleled in Old World anthropoids, which are assumed to have originated in moist, forest habitats. The image of frugivorous, herbaceous, or folivorous primates moseying around cool, shady forests does not encourage the expectation of strong selection for superefficient thermoregulation. What are nonhuman primates *doing* with their efficient heat dissipation mechanism? Cursorial primates are rare.

I would like to know (1) how efficient nonhuman primate thermoregulation is compared with that of humans (I predict that the human form is more efficient, being an elaboration of the anthropoid pattern selected for improved cooling during persistence hunting) and (2) how much "use" nonhuman pri-

mates make of their enhanced sweating capacity (I predict that extensive periods of intense physical activity are rare except perhaps for *Patas*). If I am correct in these predictions, I would like to know if some other function exists for the cholinergic innervation of primate sweat glands, accounting not only for the large amount of sweat production but also for some other factor. Perhaps the efficient thermoregulatory abilities of primates are a pleiotropic effect of selection for another function, such as pheromone production, likewise effected through sweat.

by JOSEPH K. SO

Department of Anthropology, Trent University, Peterborough, Ont., Canada K9J 7B8. 7 IV 84

Carrier is to be commended for his thought-provoking theory. Citing physiological data, he argues convincingly that the human species possesses an efficient mechanism for heat dissipation and endurance running. It is safe to say that these biological attributes are uniquely human and may have played a significant role at some point in our evolution. I am less comfortable with his assertion that the success of hominids as endurance predators and the ability to outlast game animals was the primary selective force. This model is based on the assumption that hunting was the dominant mode of subsistence. As Carrier himself points out, the paleontological evidence indicates the contrary (Jungers 1982, Stern and Susman 1983). There also exists a body of data that questions the validity of the "man-the-hunter" school of thought represented by Washburn and Lancaster (1968). Cross-cultural data indicate gathering as the primary mode of subsistence in 58% of the 90 societies surveyed compared with only 25% for hunting (Martin and Voorhies 1975). Observations on hunting by chimpanzees and common baboons indicate that meat is a minor part of their diets. More importantly, primate hunting does not require great skill, strength, or physiological endurance as Carrier suggests. There is a tendency to overemphasize the importance of the predominantly male activity of hunting as a selective force in hominid evolution at the expense of the role of food gathering (Fedigan 1982, Slocum 1975). A model that accounts for only half of the human species is in my view incomplete.

Even accepting the premise that endurance was important, cooperative hunting ought to be considered. It seems that while humans can chase prey animals at speeds uneconomical for the animals, success is possible only when several hunters trail the animal from different directions. Physiological explanations, while valid and significant, are but one of many approaches to the understanding of the evolution of human social life.

by ERIK TRINKAUS

Department of Anthropology, University of New Mexico, Albuquerque, NM. 87131, U.S.A. 20 III 84

Carrier's model of hominids as bipedal endurance runners who were able to become predators without great strength or elaborate technology is well conceived and convincing. Most interestingly, its implications fit with current interpretations of the Pleistocene archeological and human paleontological records.

Archaic members of the genus *Homo* (*H. habilis*, *H. erectus*, and archaic *H. sapiens*) exhibit pronounced and consistent postcranial hypertrophy (Day 1971; Susman and Stern 1982; Susman, Stern, and Rose 1983; Trinkaus 1983, n.d.a). This implies considerable strength for these hominids. However, it primarily indicates an adaptation for habitually high levels of activity, since osteological hypertrophy is essentially a response to fatigue stress (Lanyon 1982). They must therefore have been exerting considerable effort on a regular basis, and predatory

endurance running is an excellent example of the type of activity that would promote and maintain this hypertrophy. Their associated energetic cost during this endurance running would have been accentuated by their relatively small statures and hence stride lengths (stature estimates: *H. habilis*, 150–159 cm, $N = 3$; *H. erectus*, 158–172 cm, $N = 4$; Neandertals, 166 ± 6 cm, $N = 18$), most of which are toward the lower limits of recent human ranges of variation.

Recent analyses of the archeological record (e.g., Binford 1981, 1982, 1984; Camps-Fabrer 1974; Clark 1983; Klein 1978; Oakley et al. 1977; Potts 1982; Straus 1982) suggest a similar pattern. They indicate the absence of effective hunting projectiles with hafted points prior to the terminal Middle Paleolithic (Aterian) and Upper Paleolithic and only fire-hardened wooden thrusting spears (e.g., Clacton and Lehringen spears) from earlier in the Pleistocene. In conjunction with this, Lower and Middle Paleolithic hominid-derived faunal assemblages appear to be dominated by small mammals and probably scavenged portions of medium-sized to large mammals. There is little to indicate that archaic humans were routinely hunting animals larger than themselves. This interpretation of the archeological record clearly fits with both the paleontological evidence from archaic humans and Carrier's model of endurance-running predation on smaller mammals.

It is also interesting that the earliest appearance in the archeological record of hafted projectiles that would remove the need for habitual endurance running to capture prey is associated with the appearance of early anatomically modern humans, who show a marked reduction in postcranial robusticity (Trinkaus 1983) and an increase in locomotor efficiency (as indicated by an increase in stature and hence stride length [European and Near Eastern early anatomically modern human stature estimates: 178 ± 9 cm, $N = 27$], relatively longer distal limb segments [Trinkaus 1981], and narrower pelvis [Trinkaus n.d.b]). These are combined with evidence of more systematic exploitation of a diversity of fauna and of more routine monitoring of available environmental resources. These considerations suggest, therefore, that the predatory endurance running proposed by Carrier may have been very important among archaic members of the genus *Homo*, permitting (among other things) their expansion into regions with marked seasonal variation in plant-food availability, but that it decreased in importance as logistically organized and essentially modern human hunter-gatherers emerged during the Upper Pleistocene.

Reply

by DAVID CARRIER

Ann Arbor, Mich., U.S.A. 14 V 84

In recent years there has been a tendency to emphasize the evolutionary significance of scavenging and gathering forms of subsistence of early hominids. This view is reflected in the comments of Nickels and So. Although the available archeological and paleontological evidence of early hominids is often interpreted as consistent with gathering, scavenging, and short-range opportunistic forms of hunting, the possibility of persistence hunting cannot be excluded. A scavenging and opportunistic hunting niche would impose few selective pressures and could be filled by many generalized large mammals. However, humans are not generalized mammals. Man's unique physiology and morphology cannot be easily explained by such an unspecialized subsistence pattern. If, for instance, man's exceptional capacity to dissipate heat were simply a response to general diurnal activity, as Nickels suggests, then one might expect to see similar adaptations in other large savannah mam-

mals (e.g., heavily sweating and hairless antelope). Hairlessness, transport cost independent of speed, and the capacity for superior endurance in an energetically inferior runner are features so unique that any explanation demands extreme selection. This selection, I believe, could best be provided by a diurnal endurance form of predation.

Scott's reference to Newman's (1970) thoughtful paper warrants some discussion. Newman's thesis is based on the assumption that man's exceptional thermoregulatory capacity resulted from an adaptive response to environmental heat loads. He speculates that hominids lost their hair in an ancient forest habitat before the move to open savannah. The change in habitat from shady forest to sunny savannah would greatly increase the radiant-heat load, particularly if the animals in question lacked hair. Man's enhanced ability to sweat is argued to be a response to this increased impact of radiant energy on his naked ancestors. There are two problems with this scenario. First, Newman does not provide a functional reason for the loss of hair. If the forest-dwelling predecessors of hominids lost their fur coats simply from a lack of need, why have other forest primates retained a full complement of hair? Second, man's exceptional capacity for heat dissipation is unlikely to have resulted from the imposition of the relatively minor environmental heat loads to which all large savannah mammals are subjected. It is more probable that it is a reaction to the much larger thermal loads produced during sustained exercise. Newman's paper provides many insights, but I disagree with the basic premise that hairlessness in man is largely disadvantageous and that the human capacity for sweating is an adaptive response to environmental sources of heat.

Scott raises a difficult issue for the persistence-hunting model in the seemingly large discrepancy between man's great need for water in thermoregulation and his limited ability to carry a substantial reservoir in his gut (Newman 1970). As Scott suggests, before the invention of water-carrying devices, hominids' inability to drink large quantities of water at any one time would have placed limits on the duration of hunts and the distance covered. This in turn would have limited the species of prey that could have been acquired through persistence running. Certain types of prey would have been more vulnerable than others. Hares (*Leporidae*), for example, are cursorial open-country runners that are severely limited by their inability to dissipate exercise heat loads. To facilitate passive heat loss and to conserve water, on hot days hares allow their body temperature to rise. This leaves little margin for the additional heat that must be stored during exercise. Storage of metabolic heat while running in these animals can proceed at rates more than five times the standard metabolic rate. Consequently, the core temperature of a hare pursued in the heat can reach a lethal level in a few minutes (Shoemaker, Nagy, and Costa 1976). Hares of the genera *Lepus* and *Serengetilagus* (Leakey 1965) were likely to have been easily accessible to early australopithecines on short excursions away from sources of water.

I am somewhat surprised by Scott's suggestion that nonhuman primates do not need effective mechanisms of heat dissipation. The dynamic locomotor performance of primates such as spider monkeys, langurs, and gibbons suggests that these animals commonly place very large demands on their thermoregulatory system. Because of the large accelerations against gravity, climbing and leaping from branch to branch will always require more energy than moving an equivalent distance on a continuous horizontal surface. Indeed, brachiation, the form of arboreal locomotion that could be expected to be most economical because of the possibility of passive support and the storage and recovery of energy in the pendular motion of each swing, has been shown to be less efficient than walking in spider monkeys (Parsons and Taylor 1977). Vigorous arboreal locomotion will clearly generate substantial metabolic heat loads, and dissipation of this metabolic heat is likely

to be very important in the day-to-day lives of many nonhuman primates.

Nickels and So raise the issue of the significance of foraging practices of modern hunter-gatherers to the subsistence patterns of man's ancestors. That some modern hunters run prey to exhaustion demonstrates that modern humans possess greater stamina than the animals pursued, not that man's ancestors hunted this way. Moreover, the observation that this method is not the primary hunting tactic employed by extant hominids, with their poison arrows and rifles, is irrelevant to the question of how early hominids acquired protein. There is further reason to question the value of extrapolating the practices of modern hunter-gatherers back in time to early hominids. Before the recent invention of cooking fires, much of the caloric and protein content of many plant foods used today may not have been digestible (Stahl 1984). This suggests that animal protein in some form may have been more important in the past in meeting nutritional requirements than it is at present. The presumably recent advent of greatly increased intelligence and culture makes the extrapolation of modern behavior backward in time more tenuous than is the case for nonhuman paleontology.

The question posed by Nickels of the costs and benefits of persistence hunting is critical. Running prey for extended periods in hot temperatures is an energetically expensive undertaking. If diurnal endurance predation had a significant influence on the course of hominid evolution, it must be an energetically viable strategy. The occasional use of endurance predation by modern hunters suggests that at least for *Homo sapiens* it is cost-effective, but this has yet to be measured. In addition to the caloric expenditure, this type of hunting could have been exceptionally hazardous because of the prolonged exposure to the sun's radiation, potential for dehydration, and increased exposure to the larger savannah predators. These would have represented significant obstacles to a primate employing the run-down technique and could have provided strong selection for increased intelligence, group cooperation, and precise communication.

Several of the commentators (Kapoor, Nickels, So) address the issue of the relationship between a hunting life-style and neurological functions such as intelligence and social behavior. Group cooperation plays a significant role in the hunting of all the social carnivores and modern man. With animals as intelligent and social as most of the anthropoid primates, it would be ridiculous to suggest that group cooperation would not have been important in increased hunting activity. What is really more interesting is the role that persistence hunting may have played in the evolution of human intelligence and way of life. A number of authors (Schaller and Lowther 1969, Laughlin 1968, Washburn and Lancaster 1968, Wolpoff 1980) have considered the probable influence of a shift to a predatory niche on the development of hominid intelligence and social structure. These authors and others have stressed that the shift involved much more than a change in diet. Hunting is suggested to be a way of life that has dominated the course of hominid evolution, producing modern man's intelligence, interest, emotions, communication, and basic social life.

At no point have I suggested, as So states, that primate hunting requires great endurance, skill, or strength; I have argued only that endurance running may have provided early hominids with a reliable mechanism for increasing their intake of animal protein. Nor can I agree with So's assertion that hunting by early hominids would necessarily have been a predominantly male activity. Excluding the osteological evidence of sexual dimorphism in body size (Wolpoff 1976), I see no reason to suppose that females would have been completely or partially excluded from hunting. Female members of the social carnivores regularly take an active and sometimes dominant role in hunting. Often young are left at a den site in the care of a single adult while the rest of the adults engage in hunting.

Several of the points raised by Kimura require clarification: (1) It is unlikely that ancestral man could have forced prey to run at their least efficient speed. It is more probable that prey could have been driven to run intermittently and therefore inefficiently. In addition to the relevant data from humans, intermittent running has been shown to produce fatigue more rapidly than continuous running in rats (Gaesser and Brooks 1980). Intermittent running is reported to be the escape strategy used by prey animals fleeing Bushman runners (Bjerre 1960). (2) The breathing of a running quadruped is tightly coupled to the locomotor cycle, usually at a rate of one breath per stride (Bramble 1984). The breathing of conditioned human runners is typically also synchronized to the locomotor cycle. The difference is that in humans the integer ratio of stride per breath varies dramatically depending on the individual and conditions. This ability to shift ratios is exactly the mechanism suggested here to provide a cost of transport that is independent of speed in running humans. (3) The reader should be aware that donkeys are members of the horse genus *Equus*, llamas are a species of South American camel, and cattle are members of the family Bovidae.

I am intrigued by Trinkaus's alternative interpretation of the functional significance of the relatively robust bones of early hominids. If osteological hypertrophy is primarily a response to fatigue stress and hence to habitually high levels of activity, then this should be readily apparent in allometric comparisons of the bones of species that have different activity patterns. A comparative interspecies analysis of bone dimensions and locomotor performance would help clarify the extent to which this relationship can be used to estimate locomotor behavior of extinct species.

A view that seems to be held by many anthropologists is that hunting could not have been an important hominid activity until the early or mid-Pleistocene. Given the available archaeological and paleontological evidence, this is a reasonable position. However, I would like to emphasize that persistence hunting could have played a significant role in the acquisition of meat long before the first clear evidence of hominid predation. We know that the early australopithecines were fully bipedal. Although their running is likely to have been less efficient than that of *Homo*, it was probably no more costly than the quadrupedal running of their prehominid ancestors. Over the range of speeds at which measurements have been made, the cost of bipedal running is not different from the cost of quadrupedal running in chimpanzees and capuchin monkeys (Taylor and Rowntree 1973b). Instead of imposing an energetic handicap on the initial bipeds, the shift to running on two legs may have significantly increased the range of available speeds by uncoupling respiration from locomotion. It is also safe to assume that the early australopithecines were superior to the other savannah mammals in their ability to dissipate metabolic heat loads. These features could have been used effectively against certain prey animals, such as the cursorial but thermally susceptible hares. Evidence of this type of predation, if it exists, may be recognizable in the faunal assemblages associated with the early australopithecines.

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Wanted

- Correspondence and suitable bibliographic references from anthropologists interested in the ethnography of blindness, in connection with fieldwork among the blind in Israel. Please write: Shlomo Deshen, Department of Sociology and Anthropology, Bar-Ilan University, Ramat-Gan, 52100 Israel.
- Papers dealing with the lives, careers, and achievements of eminent anthropologists from any country of the world, for a volume in preparation entitled *Eminent Anthropologists: Biographical Portraits*. Papers should be no longer than 20 pages, typed double-spaced, using the footnoting rules of the *American Anthropologist*. Three clean copies plus brief résumés should be sent before September 1985 to Mario D. Zamora, Department of Anthropology, College of William and Mary, Williamsburg, Va. 23185, U.S.A.
- Manuscripts on a variety of biopolitical topics, including (1)

public-policy-related works on biomedical technologies, human ecology, health and environment, aging, food, population, and reproductive technologies; (2) the influence of biological factors on political behavior; (3) the relationship of ethology and sociobiology to the concerns of traditional political science and ethics; and (4) the relationship of biopolitics to other perspectives in the social and natural sciences, for the journal *Politics and the Life Sciences*. Data-based empirical studies are especially welcome. Please write: Thomas C. Wiegale, Editor, Northern Illinois University, DeKalb, Ill. 60115, U.S.A.

- In connection with a dissertation on incipient cultivation among Negrito hunter-gatherers, quantitative data on rice swiddens in Southeast Asia for a literature review and cross-cultural comparative study. Information is requested on published references on rice yields, swidden sizes, number of rice varieties per swidden, and percentage of burned area left uncropped. Please write: Thomas N. Headland, Bagabag, Nueva Vizcaya Province, Philippines 1505.