Limits to human locomotor performance: phylogenetic origins and comparative perspectives

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Summary

Studies of human exercise physiology have been conducted from a largely ahistorical perspective. This approach usefully elucidates proximate limits to locomotor performance, but ignores potential sources of biomechanical and physiological variation that derive from adaptation to ancestral environments. Phylogenetic reconstruction suggests that multiple hominoid lineages, including that leading to *Homo sapiens*, evolved in African highlands at altitudes of 1000–2000 m. The evolution of human locomotor physiology therefore occurred under conditions of hypobaric hypoxia. In contrast to present-day humans running on treadmills or exercising in otherwise rectilinear trajectories, ancestral patterns of hominid locomotion probably involved intermittent knuckle-walking over variable terrain, occasional bouts of arboreality and an evolving capacity for bipedalism. All such factors represent potential axes of locomotor variation at present unstudied in extant hominoid taxa. As with humans, hummingbirds evolved in mid-montane contexts but pose an extreme contrast with respect to body size, locomotor mode and metabolic capacity. Substantial biomechanical and physiological challenges are associated with flight in hypobaria. Nonetheless, hummingbird lineages demonstrate a progressive invasion of higher elevations and a remarkable tolerance to hypoxia during hovering. Upregulation of aerobic capacity and parallel resistance to hypoxia may represent coupled evolutionary adaptations to flight under high-altitude conditions.

Key words: evolution, human, hummingbird, hypoxia, locomotion, metabolic rate.

To know humans, study chimpanzees

Basal hominoids (i.e. apes, hominids and humans) appeared approximately 24 million years ago. The genus *Homo* derive from a hominoid lineage that includes the extinct australopithecines and the extant chimpanzees and gorillas (see Fig. 1). It is now well established that the closest relatives of modern humans are the chimpanzees (*Pan* spp.), with the *Homo–Pan* divergence having occurred 4.5–5.5 million years ago and the earlier separation of *Gorilla* 5.5–7 million years ago (Goodman et al., 1994). Phylogenetic reconstruction using parsimony suggests that much of hominoid evolution occurred at mid-montane elevations (Fig. 1). Key features separating humans from their hominoid relatives are an enlarged neocortex, a reduced anterior dentition, bipedalism and sophisticated interindividual (and particularly intersexual) interactions (Lovejoy, 1981). Bipedalism, of course, is the salient locomotor feature of humans, and this trait is evident in fossils of our prehuman australopithecine predecessors as early as 4 million years ago (see White, 1980; White et al., 1994; Leakey et al., 1995).

In contrast to such paleontological evidence, the behavioral origins and selective forces underlying the acquisition of bipedalism remain obscure. Such a locomotor mode clearly must have derived from the knuckle-walking behavior exhibited by our close relatives, the gorillas and chimpanzees. Significantly, the wrist morphologies of several australopithecine taxa are consistent with the evolution of bipedalism from quadrupedal knuckle-walking ancestors (Richmond and Strait, 2000). A variety of non-mutually exclusive hypotheses have been proposed for this evolutionary event, including reduced thermal load, greater locomotor efficiency and greater non-locomotor use of the forelimbs, particularly in feeding (e.g. Rodman and McHenry, 1980; Rose, 1991; Wheeler, 1991; Hunt, 1994; Isbell and Young, 1996). The discrete categorization of hominoid locomotor modes has had the unfortunate consequence, however, of obscuring potential locomotor flexibility exhibited by any given taxon. For example, otherwise upright and bipedal australopithecines may have retained some degree of arboreality, as characterizes the primarily knuckle-walking but also occasionally bipedal and arboreal chimpanzees (see Gebo, 1996; Richmond and Strait, 2000). Most importantly, such functional multiplicity is consistent with varied selective forces
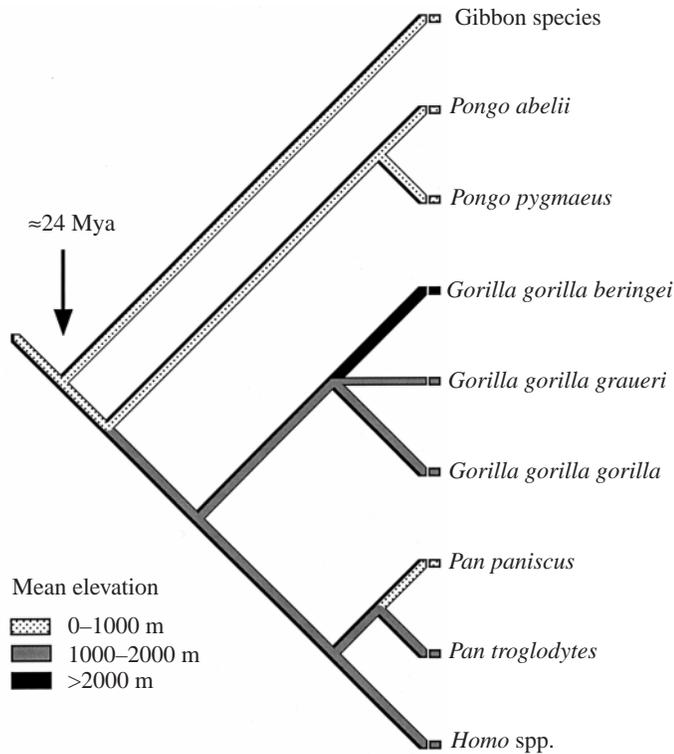
Fig. 1. Phylogeny of extant hominoid taxa, the mean of lower and upper elevational ranges for each taxon and the most parsimonious elevational reconstruction for ancestral lineages (data from various sources; see Rowe, 1996; Dudley, 2000a). The mean elevation for gibbons is derived from lower and upper distributional data for 11 species (Rowe, 1996). *Homo* spp. refers to pre-modern hominine taxa, for which elevational distributions were comparable with those of australopithecines (see Hochachka et al., 1998). Mya, million years ago.

acting on locomotor performance according to behavioral context. Chimpanzees, for example, are most likely to walk on two legs (either on the ground or along tree branches) when feeding, and particularly when harvesting fruits (Hunt, 1994). Those ecological circumstances that led certain australopithecines becoming predominantly bipedal relative to their knuckle-walking counterparts remain unresolved.

Within evolutionary contexts, the energetic consequences of bipedalism are not well understood. In a widely cited study, Taylor and Rowntree (Taylor and Rowntree, 1973) measured the metabolic costs of locomotion on treadmills for juvenile chimpanzees running bipedally and quadrupedally; no significant differences were found between the two locomotor modes. However, this approach may underestimate the actual costs of locomotion on naturally occurring and potentially irregular substrata, for which use of four legs may provide an energetic advantage.

Quadrupedalism can enhance cursorial maneuverability (Lovejoy, 1981), particularly in the context of vegetated terrain. A similar situation pertains in the use by humans of hiking poles to enhance balance, although concomitant energetic costs appear to be context-dependent (see Rodgers et

al., 1995; Jacobson et al., 1997; Jacobson et al., 2000). Furthermore, the juvenile chimpanzees studied by Taylor and Rowntree (Taylor and Rowntree, 1973) may not have yielded locomotor metabolic rates representative of adults (see Steudel, 1996). Bipedalism is actually an infrequent behavior in chimpanzees (Hunt, 1994), and comparison of the costs of locomotion in humans with those measured in trained chimpanzees (e.g. Rodman and McHenry, 1980) is not evolutionarily germane. Training itself may alter patterns of energetic expenditure through a reduction in kinematic variance. In summary, the energetic implications of the transition from knuckle-walking quadrupedalism to bipedalism remain speculative. Theoretical modelling of the mechanical costs of locomotion for known fossil morphologies and likely kinematic profiles (e.g. Willems et al., 1995; Kramer, 1999) may be the best method for resolving this important question.

Paleolithic athletics and the domestication of *Homo sapiens*

The reconstruction of ancestral selection regimes on humans is strongly subject to our present-day biases. In particular, modern humans are behavioral and physiological outliers relative to other extant hominoid taxa. Much of our emergence as a modern species derives from increased socialization and, indeed, from what was effectively domestication relative to our predecessors. In common with domesticated animals (see Clutton-Brock, 1999), humans have undergone dramatic changes in pelage and external appearance, with pronounced reductions in the size of the jaw and anterior teeth. Modern humans exhibit a much higher body fat content and reduced relative muscle mass than their ancestral counterparts, trends that are seen in domesticated animals generally (Allen and Mackey, 1982; O'Dea, 1991; Clutton-Brock, 1999).

Using the example of modern humans to infer the locomotor capacity of ancestral hominids might therefore be analogous to using domesticated canines in the phylogenetic reconstruction of canid exercise physiology. Potentially confounding effects of domestication on anatomical and physiological characteristics clearly cannot be excluded in such cases.

Instead, physiological inferences can be drawn from the study of extant hominid taxa and from the fossil record. Foraging strategies can, in particular, provide suggestive information concerning locomotor and energetic demands on ancestral humans. Phytophagy is the dominant feeding strategy of extant apes, although low-level inclusion of animal protein is also characteristic (Milton, 1999b). This pattern probably characterized early humans up to the origins of agriculture (approximately 10 000 BCE=Before Common Era; see Diamond, 1999) and persists to the present time among hunter-gatherers who, with the exception of certain high-latitude groups, rely mostly on plant foods (Eaton and Konner, 1985; Eaton et al., 1997; Milton, 1999b; Milton, 2000). Superimposed upon foraging for somatic and reproductive plant structures was an increased tendency of ancestral hominids towards carcass-scavenging and active hunting (see

Blumenschine, 1987; Gordon, 1987). The higher caloric rewards could potentially have exceeded the increased anaerobic and aerobic costs of such activities. In turn, greater incorporation of higher-value plant products and of animal fat and protein may have facilitated energetically costly increases in brain size (Milton, 1988; Milton, 1993; Milton, 1999a; Foley and Lee, 1991; Aiello and Wheeler, 1995). Such increases occurred within the ecological context of a fairly constant vegetational mosaic of forest and grassland, albeit one characterized by greater aridity since 3 million years ago (Kingston et al., 1994; Vrba et al., 1994; deMenocal, 1995). Also, conditions of moderate hypoxia probably prevailed for much of human evolution, with concomitant implications for exercise physiology (see below).

Aforementioned foraging patterns and other contemporaneous locomotor behaviors deviate dramatically from contemporary conceptions of exercise in humans. Most hominid locomotion was probably intermittent rather than continuous and, very early in hominid evolution (i.e. from 4.5 to 3.5 million years ago), would have involved combinations of knuckle-walking and bipedal behavior. In modern humans and in other taxa, intermittent locomotion with variable exercise and rest periods reduces lactate build-up and increases overall endurance (e.g. Saltin et al., 1976). Movement over natural, irregular terrain can also dramatically alter metabolic expenditure. For example, the cost of transport increases several-fold moving on sand relative to firm substrata (Zamparo et al., 1992; Lejeune et al., 1998) and increases linearly with increasing angle of incline (see Margaria, 1976). Carcass-hauling, offspring-carrying and related locomotor behaviors similarly represent additional avenues of energetic

expenditure. Pathological conditions, including parasite and pathogen loads, gait disorders and bone breakages, may also influence locomotor performance. For example, approximately 31 % of the gibbon skeletons examined by Schultz (Schultz, 1939) exhibited repaired long bones, and the majority of baboons studied by Bramblett (Bramblett, 1967) had at least one healed fracture. Ancestral humans were clearly not exempt from such pathologies or from their concomitant effects on locomotor mechanics and energetics. Contemporary knowledge of performance limits in well-fed, trained human athletes may therefore be unrepresentative of human ancestors living and moving within natural terrains. Similarly, no experimental attention has been given to the influence of the aforementioned biotic and abiotic factors on the exercise physiology of extant hominoid taxa.

Scaling Mount Olympus: evolution at altitude

Phylogenetic reconstructions suggest that the genus *Homo* evolved not in the African lowlands but rather at altitudes in the range 1000–2000 m (Hochachka et al., 1998). At 1500 m, oxygen partial pressure is approximately 83 % of the sea-level value. Although this difference is unlikely to impose absolute constraints on oxygen uptake, such a reduction in oxygen availability is easily sufficient to induce acclimation responses (see Winslow and Monge, 1987; Levine and Stray-Gunderson, 1997) and ultimately to yield evolutionary adaptation. Moderate hypoxia was, therefore, the norm during much of human evolution. Perhaps more importantly, progressive colonization of higher elevations considerably predates the human lineage and originates within the basal hominoids
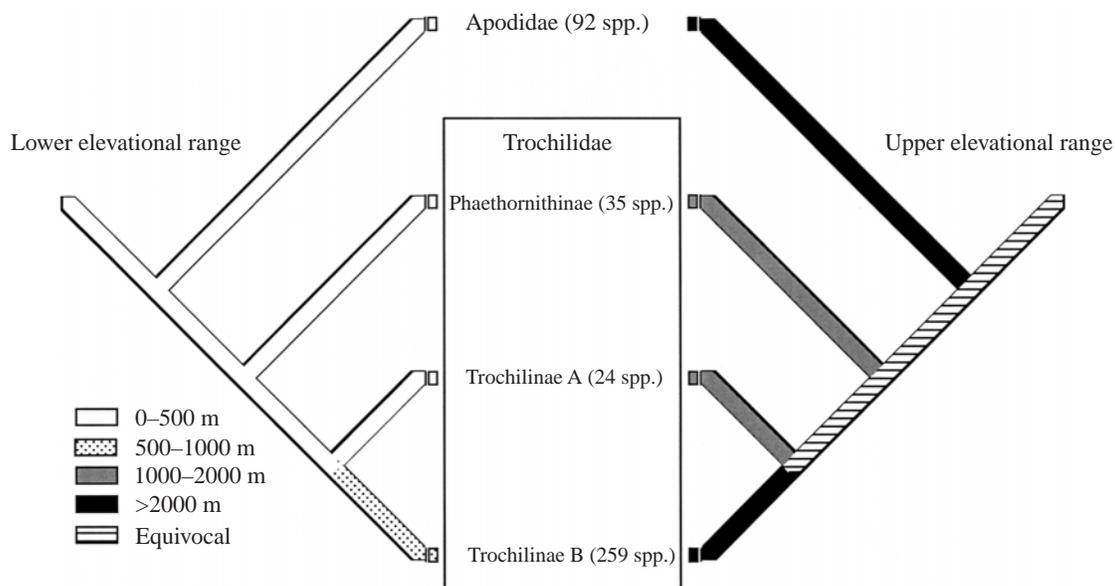

Fig. 2. Phylogeny of major hummingbird (Trochilidae) lineages in relation to mean interspecific values for lower and upper elevational distribution. The relationships of subfamilies and other groupings within the hummingbirds derive from analyses of Zusi and Bentz (Zusi and Bentz, 1995), Bleiweiss et al. (Bleiweiss et al., 1997) and Gerwin and Zink (Gerwin and Zink, 1998). Values for elevational distributions are from del Hoy et al. (del Hoy et al., 1999), as are data for the outgroup family Apodidae, the swifts.

(Fig. 1). This phylogenetic observation therefore corroborates the hypothesis of Hochachka et al. (Hochachka et al., 1998) that altitude-tolerance is ancestral for humans.

Hypobaric hypoxia is known to reduce maximal aerobic power in modern humans (see Cerretelli and Hoppeler, 1996; West, 1996), whereas any number of ecological scenarios for ancient hominids are consistent with selection for enhanced aerobic capacity. It is therefore not surprising that the physiological traits underlying hypoxia-tolerance in modern humans are similar to those associated with greater endurance (Hochachka et al., 1998). More generally, atmospheric oxygen availability interacts with morphological and physiological factors underlying internal gas transport to constrain aerobic capacity. Athletic training in humans, for example, is known to increase the maximum rate of oxygen uptake, and yields correlated increases in the mass, myoglobin content and capillary density of skeletal muscles, together with increases in cardiac stroke volume. For birds and mammals, maximum cardiac output is a strong predictor of aerobic capacity for any given level of atmospheric oxygen availability (e.g. Bishop, 1997; Bishop, 1999). At least in humans, however, a variety of transport conductances supplemental to cardiac output also influence aerobic capacity, particularly at the lower oxygen partial pressures of higher elevations (see Jones and Lindstedt, 1993; Wagner, 1996a; Wagner, 1996b).

One approach to identifying general constraints on aerobic capacity is to examine taxa with unusually high metabolic rates. Hummingbirds (family Trochilidae) are known for their extreme levels of oxygen consumption during flight (Suarez, 1992; Suarez, 1996), but less appreciated is the extent to which this group also comprises mostly mid-montane specialists. Hummingbirds are most typically found in the elevational range 1000–2500 m, and relationships among the major trochilid lineages suggest progressive colonization of higher altitudes (Fig. 2; see also Bleiweiss, 1998a). Flight at such elevations requires substantial compensatory responses to reductions in both air density and oxygen partial pressure (see Faraci, 1991; Dudley and Chai, 1996). In ruby-throated hummingbirds (*Archilochus colubris*), substantial resistance to hypoxia has been demonstrated in experimental studies of hovering flight in hypodense and hypoxic gas mixtures (Chai and Dudley, 1996). Ruby-throated hummingbirds sustain hovering flight at oxygen partial pressures corresponding to elevations of approximately 4000 m, even when simultaneously challenged aerodynamically by air densities two-thirds the sea-level value. Flight failure in such gas mixtures clearly derives from reduced oxygen supply rather than from the aerodynamic limits that pertain in contexts of greater oxygen availability (see Chai and Dudley, 1995; Chai et al., 1996).

One obvious underpinning to such impressive performance is the particularly large heart found in hummingbirds relative to other birds (see Bishop, 1997). Moreover, the hypoxia-tolerance of hovering ruby-throated hummingbirds by no means represents the maximum physiological capacity among the trochilids. Mechanical power expenditure during hovering
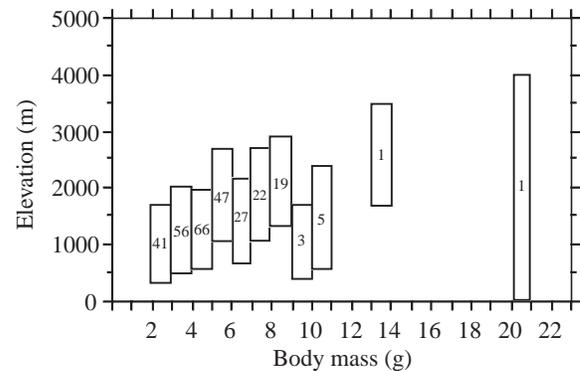

Fig. 3. Elevational range in relation to body mass for extant hummingbird species. Within each size class, the box plot delineates mean interspecific values for the lower and upper elevational range, as given for each species by del Hoy et al. (del Hoy et al., 1999). The numbers within any given box indicate the number of species for the particular size class. Interspecific linear regressions relating body mass to minimum, mean and maximum elevation are highly significant ($P<0.001$ for each variable), although the variance in elevational distribution that can be attributed to body mass alone is less than 10 % in each case.

flight tends to increase with increasing body mass and with decreasing air density (see Dudley, 2000b). Although previous workers have concluded that hummingbird body mass is independent of elevation (Feinsinger et al., 1979; Bleiweiss, 1998b), analysis of the entire known fauna shows that heavier hummingbird species also tend to be found at higher elevations (Fig. 3). As an extreme example, the giant Andean hummingbird (*Patagona gigas*) has a body mass of 20–22 g and is capable of hovering at elevations near 4000 m. Moreover, this species vertically lifts an extraordinary 140 % of its body weight at such altitudes (D. Altshuler and R. Dudley, unpublished data). The respiratory and cardiovascular performance of this species hovering in hypobaria represents an exciting target for future investigations of the limits to vertebrate metabolic capacity in the face of hypoxic and energetically challenging conditions.

Knuckle-walking into the future

A sparse fossil record precludes detailed analysis of our ancestral locomotor abilities, and the currently slow rate of specimen recovery suggests no immediate improvement in this situation. Phylogenetic reconstruction of ancestral hominoid physiology using data from extant taxa represents a useful alternative to inference based on limited osteological remains. Somewhat surprisingly, neither hypoxic responses nor maximum aerobic capacities have been measured in our hominoid relatives, although the application of comparative methods could potentially reveal evolutionary trends in hominoid locomotor physiology. Historical patterns of hypoxic exposure are of more than scientific interest given modern-day implications of residence and training under conditions of variable oxygen availability for enhancing athletic

performance (e.g. Levine and Stray-Gunderson, 1997). In hummingbirds, a wealth of morphological, physiological and ecological diversity (del Hoy et al., 1999) presents fertile ground for studying the upregulation of aerobic capacity within the natural context of hypobaria.

Finally, the ability to simulate elevational gradients in the laboratory and to decouple the effects of variable air density from those of oxygen availability (see Dudley, 2000b) suggest that both short-term and evolutionary responses to hypobaria can be studied in diverse animal taxa, even including primates.

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