



Climbing and the daily energy cost of locomotion in wild chimpanzees: implications for hominoid locomotor evolution

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Abstract

As noted by previous researchers, the chimpanzee postcranial anatomy reflects a compromise between the competing demands of arboreal and terrestrial locomotion. In this study, we measured the distance climbed and walked per day in a population of wild chimpanzees and used published equations to calculate the relative daily energy costs. Results were used to test hypotheses regarding the arboreal-terrestrial tradeoff in chimpanzee anatomy, specifically whether arboreal adaptations serve to minimize daily locomotor energy costs by decreasing the energy spent climbing. Our results show that chimpanzees spend approximately ten-times more energy per day on terrestrial travel than on vertical climbing, a figure inconsistent with minimizing energy costs in our model. This suggests non-energetic factors, such as avoiding falls from the canopy, may be the primary forces maintaining energetically costly climbing adaptations. These analyses are relevant to anatomical comparisons with living and extinct hominoids.

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Introduction

Chimpanzees present an interesting extreme among the apes in their habitual locomotor behavior. While feeding in multiple trees each day requires significant vertical climbing and arboreal travel, chimpanzees must also travel long distances on the ground, using greater day ranges than reported for any other ape except humans (Chapman and Chapman, 2000). As the morpho-

logical features associated with climbing and arboreal travel are different than those found in obligate terrestrial quadrupeds (Hildebrand, 1985), it is impossible for chimpanzees to be both classic cursors and adept arborealists. Instead, chimpanzees are caught in an evolutionary tradeoff, having a “compromised,” or generalist, morphology as described by Rose (1991) and others (see Fleagle, 1999). The competing demands of terrestrial and arboreal locomotion and the resulting behavioral and morphological adaptations have made chimpanzees a useful model for morphologists and paleoanthropologists. The goal of this study was to quantify these locomotor demands in order to

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distinguish two alternative hypotheses regarding chimpanzee locomotor anatomy.

Current evidence suggests that terrestrial travel is compromised and the daily energy cost of terrestrial travel is relatively high in chimpanzees due to morphological specializations for arboreal locomotion. The short hindlimbs and heavy distal limb segments associated with arboreal locomotion in chimpanzees (Hunt, 1991; Fleagle, 1999) have been linked to slow and energetically inefficient terrestrial travel (Hildebrand, 1985; Steudel, 1990; Minetti et al., 1994). Ecological and physiological studies of terrestrial locomotion suggest that chimpanzees are, in fact, slow and energetically inefficient on the ground. Habitual quadrupedal knuckle-walking (hereafter, simply *walking*) speeds (Hunt, 1989) for chimpanzees are 2–3 times slower than predicted by allometric scaling, and the cost of transport (energy/kilometer) is 36% greater (Taylor et al., 1982; Heglund and Taylor, 1988; but see Steudel-Numbers, 2003). These deficiencies are significant in terms of energy and time allocation; as obligate ripe-fruit specialists (Wrangham et al., 1998), chimpanzees travel long distances per day (~5 km) between food patches (Wrangham, 1977; Hunt, 1989; Herlinger et al., 2001; Chapman and Chapman, 2000) and subsequently spend a greater percentage of daily energy expenditure (DEE) on terrestrial travel than on any other activity (Leonard and Robertson, 1997). Given the high cost of terrestrial travel, why are chimpanzees morphologically “compromised” terrestrial quadrupeds?

One hypothesis suggests that arboreal adaptations serve to minimize total locomotor energy expenditure (climbing plus walking) by decreasing the energy spent on vertical climbing (*sensu* Hunt et al., 1996), a potentially costly activity. Daily locomotor energy costs are expected to be an important selection pressure in chimpanzees for a number of reasons. Optimal foraging theory (Stephens and Krebs, 1986) and life-history theory (Charnov and Berrigan, 1993) both predict that selection will favor increased locomotor energy efficiency, as this increases net energy intake and the amount of energy available for both somatic maintenance and reproduction. For species with slow life-histories and high maternal investment

such as chimpanzees (Charnov and Berrigan, 1993; Knott, 2001), increases in net energy intake are expected to have significant positive effects on fertility. Comparisons with captive animals strongly support this link; captive female chimpanzees have a significantly earlier median age at menarche and shorter interbirth interval than their wild counterparts (Knott, 2001), factors that, along with fecundability, have the largest impact on lifetime fertility (Wood, 1994). As locomotion accounts for a larger portion of the energy budget than any other activity for wild chimpanzees (Leonard and Robertson, 1997), adaptations that reduce locomotor costs potentially have the largest impact on net energy return and improved reproductive fitness. Indeed, ecological studies of chimpanzees suggest the existence of behavioral adaptations for minimizing locomotor costs; researchers have proposed that grouping and foraging decisions of chimpanzees and other primates are driven in large part by energetic factors (Wrangham et al., 1993; Janson and Goldsmith, 1995; Wrangham, 2000). Similarly, chimpanzee postcranial anatomy might be expected to exhibit adaptations for minimizing locomotor costs.

An alternative hypothesis is that the energy cost of decreased walking efficiency due to arboreal adaptations outweighs the energy saved from increased climbing efficiency. In this scenario, the energy spent on walking dominates daily locomotor energy expenditure, and chimpanzees spend more energy per day on locomotion than predicted for a more terrestrially-adapted primate. Arboreal adaptations therefore would incur an energy cost that presumably is balanced by selection for other aspects of locomotor performance. Such a tradeoff is plausible, as a range of performance variables, including access to arboreal foods, maneuverability within the canopy, predator avoidance, and avoiding falls, undoubtedly affect reproductive fitness in wild chimpanzees.

To discriminate between these two hypotheses, we present new data on the distance climbed and walked per day for a community of wild chimpanzees in Kibale National Park, Uganda, and convert these distances into energy expenditure using published equations in order to establish the relative demands of climbing and walking. We then

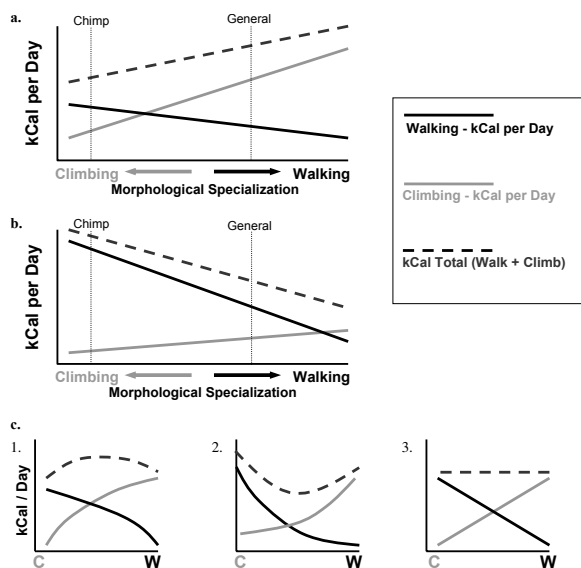


Fig. 1. Optimization models for morphological specialization and energy expenditure. a. Prediction of H1, described in text, for the relationship between morphological specialization and daily locomotor energy cost for chimpanzees. As postcranial morphology becomes more specialized for climbing, walking efficiency suffers, and thus daily energy costs for walking increase (black line). Conversely, specialization for walking leads to an increase in daily climbing costs (gray line). In this scenario chimpanzees approximate an optimal degree of specialization (Chimp) in which total locomotor energy expenditure (dashed line) is minimized. Increased specialization for walking increases total locomotor energy cost, and thus a more terrestrially-adapted primate (General) would have a higher total energy cost. b. Prediction of H2, described in text. Climbing accounts for a relatively minor portion of daily locomotor cost, and selection for minimized total cost favors increased walking specialization. c. Other cost/specialization relationships can produce 1) multiple, 2) intermediate, or 3) no energetically optimal degree(s) of specialization.

test the hypothesis (H1) that morphological adaptations for climbing in chimpanzees minimize total daily locomotor costs (climbing plus walking) by lowering the amount of energy spent climbing, against the alternative hypothesis (H2) that climbing adaptations do not minimize daily energy expenditure but instead incur an energy cost.

To test these hypotheses we have constructed a simple optimization model (Fig. 1), similar to that described by Seger and Stubblefield (1996) and others (see Lack, 1954; Krebs and Davies, 1993; Rose and Lauder, 1996). The model assumes that locomotor specialization for climbing decreases

energetic efficiency in walking, and vice versa. Thus, specialization for one locomotor mode increases the amount of energy per day spent on the other. To test whether chimpanzees exhibit an optimal degree of morphological specialization, we compare the energy spent walking and climbing. We then estimate the change in total locomotor cost that would result if morphological specialization (i.e., climbing or walking efficiency) were increased (Fig. 1). If chimpanzee arboreal adaptations minimize daily locomotor costs (H1), energy spent climbing must account for a significant portion of the locomotor energy costs, and increased walking efficiency should increase daily energy costs (Fig. 1a). Alternatively, if the energy spent each day on climbing is negligible relative to energy spent walking, and increased climbing efficiency increases total locomotor cost, non-energetic factors such as safety or maneuverability may be responsible for maintaining energetically costly climbing adaptations (H2) (Fig. 1b).

As the nature of the relationship between walking and climbing efficiency is not known for chimpanzees (nor for any other species), a simple tradeoff model such as the one employed here can prove inconclusive for determining the optimal degree of morphological specialization and the degree to which chimpanzees approximate it. Even simple cost/specialization curves can produce counterintuitive optimal solutions (Fig. 1c). These scenarios will be discussed below in the context of the present data; as will be shown, results are robust to assumptions regarding the nature of the cost/specialization curve.

Methods

Study site

Data were collected from field observations of habituated wild chimpanzees (*Pan troglodytes schweinfurthii*) in the Kanyawara community, Kibale National Park, Uganda. The Kanyawara area (0°30'–0°41'N and 30°19'–30°30'E) consists of rolling hills with approximately 150 m of topographical relief typical. The forest is mid-altitude (1500 m) tropical rainforest, with a

canopy ranging from 20 to 30 m (Chapman and Wrangham, 1993). The Kanyawara chimpanzee community consisted of approximately 50 individuals during the period studied. For a thorough description of the field site and history of field observations there, see Chapman and Wrangham (1993) and Wrangham et al. (1996).

Day range

Daily travel distance, or *day range*, was calculated from 200 nest-to-nest group follows from January 1998 to December 2002. While focal follows are ideal for day range analyses, the use of group follows was necessary here given the available long-term data. Individual follows were extracted from group follows for analysis. A follow was only considered *nest-to-nest* for an individual if the animal was present for the entire follow from unnesting to nesting, and was not out of sight of the assistants for more than 45 continuous minutes. All nest-to-nest follows conducted during that period were used except a) follows of seriously ill or injured animals, and b) follows that took place outside the bounds of the trail map, which were, therefore, potentially inaccurate ($N < 15$ unused follows).

Day range was measured using maps drawn in the field by field assistants, who recorded the position of the group every fifteen minutes on a trail-map of the Kanyawara range. Maps of chimpanzee follows were drawn into an ArcView 3.1 GIS map file of the Kanyawara area as a polyline theme using a mouse-driven cursor, taking care to recreate the field maps accurately. The length of these lines was then calculated in ArcView 3.1 using the *[shape]:returnlength* function. To test intraobserver reliability, a sample of ten follows was mapped twice on separate occasions. Path lengths calculated on these two occasions were highly correlated ($r^2 = 0.94$, slope = 0.99, $n = 10$), and were not significantly different ($P = 0.60$, paired 2-tailed *t*-test).

To create the ArcView 3.1 GIS map file, HP rectified the Kanyawara trail map using UTM coordinates taken in the field at over 250 trail junctions and landmarks using a Garmin 12XL. The rectified trail map and a 1:50,000 topographic

map (Ugandan Dept. of Lands and Surveys, 1977) was used to create a Geographic Information System (GIS) file for the Kanyawara area in ArcView 3.1[®]. GPS points were only used when points could be obtained with Figure of Merit values (analogous to confidence intervals) less than 10 m. A small sample of GPS points not used in rectifying the map was used to test the accuracy of the GIS file. In all cases, the points fell within 50 m of the predicted landmark or trail junction on the map; this is equivalent to the accuracy of GPS units in the field.

Climbing

HP measured the vertical distance climbed during group follows for 19 days over two months, June–July 2001. Each *climbing bout*, defined as an ascent into a tree from the ground, was recorded for all observable animals for the entirety of the group follow; data were logged for each individual separately. A *climbing follow* for an individual started with first observation or unnesting, and terminated whenever the individual was lost to the observers or nested. For each climbing bout the height climbed, species of tree, the purpose of the bout (nesting, feeding, displaying, etc.), and the amount of time spent in the tree was recorded.

For each climbing bout, the height climbed was determined both for the initial ascent into the canopy and for vertical climbing within the canopy. For the initial ascent, height climbed was measured by first determining the vertical angles from the observer to the chimpanzee in the canopy and to the base of the tree. Next, the straight-line distance from the observer to the a) chimpanzee in the canopy, or b) trunk of the tree was measured. The vertical distance climbed was then calculated using standard trigonometric relationships (Fig. 2). The angle from the observer to the chimpanzee was measured using a standard inclinometer (Suunto), and the straight-line distance to the chimpanzee was measured using an infrared range-finder (Bushnell 500 Yardage Pro[®]), accurate to within 1 m. When the distance to the chimpanzee could not be determined using the range-finder (minimum distance measured is 19 m for this model), distance to the base of the tree was measured by pace. In rare cases, as when juveniles

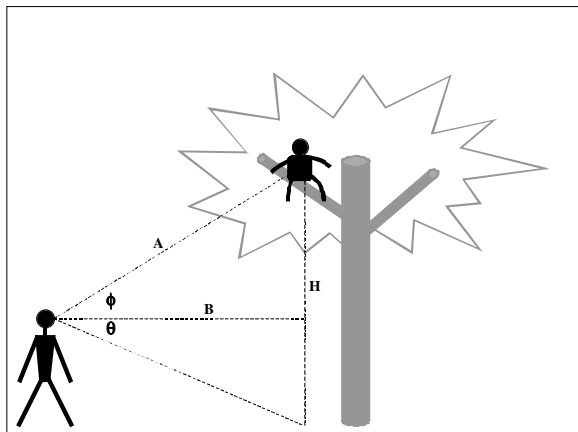


Fig. 2. Methods used for calculating the height climbed by chimpanzees. The height climbed, H , can be calculated as either $H = A \times \sin\phi + A \times \cos\phi \times \tan\theta$ or $H = B(\tan\phi + \tan\theta)$.

were playing in low bushy plants, the above methods were impractical and height climbed was estimated.

Vertical climbing *within* the canopy was estimated. Vertical displacements within the canopy were generally small (~ 5 m), and horizontal displacements in the 3-dimensional canopy, as well as undulations in the forest floor, made estimates of climbing within the canopy as reliable as trigonometric measurements. When possible (e.g., when the chimpanzee moved to a position directly above its previous position in the canopy) estimates of climbing within the canopy were compared against the distance calculated using trigonometric methods; estimates and measured distances were found to be similar.

For each climbing follow, a climbing rate (meters/hour) for each chimpanzee was calculated using the total distance climbed and the duration of the follow. As chimpanzees are more likely to be encountered during active feeding or climbing, and are more likely to be lost to observers when traveling, short observations are likely to produce artificially high rates of climbing. To eliminate this bias, only climbing follows lasting 5 hours or more were included in analyses. A total of 89 climbing follows representing 27 individuals fit these criteria; mean observation duration was 443 minutes. The sample includes 481 climbing bouts.

To calculate the mean vertical distance climbed per day, the mean rate of climbing (meters/hour) as determined above was multiplied by mean *time awake*. *Time awake* refers to the portion of the day spent out of the night-nest, and was calculated from 45 nest-to-nest follows from the long-term data. In this sample, mean time awake was 12 hours 10 minutes ($\sigma=40$ min).

Age-sex class analyses

Day ranges for each individual were extracted from the sample of 200 nest-to-nest follows, and mean day range was calculated for each individual. These individual means were then used to calculate means for each age-sex class. Climbing rates from individual climbing follows were pooled by age-sex class, and the mean calculated for each class. Age classes used were as follows: 0–2.9 years old, *clinging infant*; 3–9.9 years old, *juvenile*; 10–14.9 years old, *sub-adult*; 15 and older, *adult*. Ages for juveniles are known to within two months from long-term ecological data. Due to small sample sizes, results for sub-adults are not reported here. *Mothers* were defined as adult females with clinging infants. Clinging infants were not counted separately, as they are not independent locomotors.

Energetics

Energy expenditure was calculated from published equations derived from physiological studies of captive animals and humans. For all energetic relationships used, body mass is a primary determinant of cost. Values for adult body mass were taken from Smith and Jungers (1996) for *Pan troglodytes schweinfurthii*, which used only wild shot specimens of known body mass: males, 42.7 kg; females (and mothers), 33.7 kg. These weights are lower than those estimated from skeletal measurements for this population (Kerbis-Peterhans et al., 1993, males: 45–55 kg, $n=2$; females: ~ 40.5 kg, $n=1$) but are used here as they represent a larger sample of known body weights for this subspecies. Body mass for juveniles was taken from Pusey (1990), who used measurements of wild chimpanzees at Gombe National Park,

Tanzania (*P. t. schweinfurthii*) obtained from a spring scale placed in the forest. As energetics comparisons use pooled data for each age-sex class, it was necessary to determine a mean body mass for juveniles. A body mass of 15 kg was assigned to this class based on data presented graphically in Pusey (1990). Similarly, a body mass of 5 kg was used for clinging infants.

Daily energy expenditure

To put walking and climbing energy expenditure in the context of the total daily energy budget, we estimated the total energy expended per day, or *daily energy expenditure* (DEE), using the equation reported by Key and Ross (1999):

$$\text{DEE} = 93.3 M_b^{0.75}$$

where DEE is kCal/day and M_b is body mass in kg. This equation is based on estimated DEE for 19 species of primates including chimpanzees ($r=0.995$). As in other studies (e.g., Leonard and Robertson, 1997), Key and Ross (1999) calculated DEE for each species by summing the energy required for daily maintenance and resting with the energy required for other daily activities, including locomotion. Activity budgets were taken from the literature and converted into calories using energetic equations published by Coehlo (1974; Coehlo et al., 1979).

To account for the additional energy cost of lactation, DEE for mothers was calculated as $1.39 \times \text{DEE}$, following Oftedal (1984) and Key and Ross (1999). This method for estimating the increase in DEE due to lactation equates the necessary increase in metabolic energy expenditure to the gross breast milk energy yield, and thus is a conservative estimate.

Walking

Energy spent walking was calculated using three different equations. The first is the equation from Taylor and Rowntree (1973):

$$\text{O}_2 \times M_b^{-1} \times \text{s}^{-1} = 0.22 + 0.25 V$$

where O_2 is in ml and V is walk velocity in m/s. This equation was derived empirically from treadmill studies using two juvenile chimpanzees, mean body mass 17 kg. In applying this equation across age-sex classes, this equation cannot account for possible effects of scaling and assumes juvenile gait and mass-specific cost of locomotion are comparable to other age-sex classes. It is the only direct assessment of locomotor energetics in chimpanzees.

The second equation used to calculate the energy spent on terrestrial travel is the “Primates” equation from Taylor et al. (1982):

$$\text{O}_2 \times M_b^{-1} \times \text{s}^{-1} = 0.523 M_b^{-0.298} V + 0.345 M_b^{-0.157}$$

This equation is based on 10 species of primates, including the juvenile chimpanzees used in Taylor and Rowntree (1973); it also inappropriately includes tree shrews. The Primates equation has the advantage of including body mass as a variable.

Finally, we calculated walking energy expenditure using the general allometric equation from Taylor et al. (1982) based on 62 species.

$$\text{O}_2 \times M_b^{-1} \times \text{s}^{-1} = 0.533 M_b^{-0.316} V + 0.300 M_b^{-0.303}$$

Studel-Numbers (2003) and others have argued that the cost of locomotion reported for chimpanzees and other primates (Taylor and Rowntree, 1973; Taylor et al., 1982) is artificially high due to the use of juveniles as subjects in these physiological studies. However, it is not clear what effect age has on locomotor cost (DeJaeger et al., 2001; Frost et al., 2002), or whether other taxonomic groups in Taylor et al. (1982) were similarly biased toward juveniles. Further, locomotor costs for six of the eight non-human primate species included in Taylor et al. (1982) are greater than predicted using the general allometric equation, suggesting that primates are generally inefficient walkers. While future physiological studies may resolve this issue, here we use the general equation simply as a lower bound for daily walking cost and as a point of comparison with the predicted cost for generalized endotherms.

Walking speeds were obtained from [Hunt \(1989\)](#), in which walking speeds for chimpanzees in Mahale were estimated for 306 walking bouts. Assigned speeds were as follows: males, 0.88 m/s; females, 0.78 m/s; mothers and juveniles, 0.75 m/s. We compared these data against opportunistic measurements of walking speed taken during June–July 2001; a GPS unit was used to measure walking speed while following closely behind ($\leq 15\text{m}$) an individual. Results were similar.

Time spent walking (walking speed/day range), body mass, and walking speed were used to calculate the amount of oxygen consumed (energy spent) each day on terrestrial travel using the above equations. Oxygen was converted into kilocalories as

1 liter $\text{O}_2 = 4.8 \text{ kCal}$

following [Schmidt-Nielson \(1997\)](#). Changes in energy cost due to walking up or down hills were not considered, as empirical data for chimpanzees show the increase in energy consumption required to walk uphill is matched by an equal decrease in energy expenditure walking downhill ([Taylor et al., 1972](#)).

For mothers, the cost of locomotion must be adjusted to account for the added mass of the clinging infant. The percentage increase in energy expenditure while carrying a load is directly proportional to the percentage increase in total mass presented by the load ([Taylor et al., 1980](#)). Thus, an animal running with a load equal to 20% of its body mass will use 20% more oxygen per second than it would when unloaded. To calculate the additional energy expended in carrying a clinging infant, the rate of oxygen consumption for mothers (body mass 33.7 kg) was estimated for travel using the equations above. This rate was then multiplied by the percentage increase in body mass resulting from the clinging infant (5 kg), calculated as $(5+33.7)/33.7=1.15$. This approach to estimating travel costs for mothers is similar to that used by [Altmann and Samuels \(1991\)](#).

Climbing

Estimating the energy chimpanzees spend daily on climbing is complicated by the absence of

laboratory studies on vertical climbing energetics in chimpanzees or any other non-human primate. It is necessary, then, to estimate the energy expended during climbing by equating chimpanzee climbing to either a) climbing in a similar species, or b) a similarly demanding activity for which we have physiological data for chimpanzees. Four methods are employed here.

The first three methods draw on robust physiological relationships developed in empirical studies of climbing energetics in humans. Humans are useful models for chimpanzee climbing for a number of reasons. First, while the locomotor adaptations that distinguish humans from chimpanzees are numerous and significant, humans and chimpanzees also share a number of postcranial features, such as long manual digits, a broad thorax, and a mobile shoulder joint, and these features produce climbing behaviors that are, upon casual observation, similar in some ways to experienced human climbers and chimpanzees (e.g., the forelimb is hyper-abducted, and the legs provide the majority of the force to vertically propel the body, while the arm supports much of the body weight passively through the skeleton and ligaments). Second, humans and chimpanzees are roughly similar in body mass ($\sim 40 \text{ kg}$ for adult male chimpanzees versus $\sim 65 \text{ kg}$ for adult male humans; [Smith and Jungers, 1996](#)), and so scaling effects should not significantly affect comparisons. Finally, humans are the easiest species from which to obtain physiological data, while physiological studies of non-human primates, particularly adult chimpanzees, are notoriously difficult.

We assume that the climbing adaptations described for chimpanzees (see [Aiello and Dean, 1990](#); [Hunt, 1991](#); [Fleagle, 1999](#)) and the daily practice of climbing enable chimpanzees in the wild to climb more efficiently (i.e., using less energy per meter) than even experienced human climbers. In using physiological data from humans to estimate climbing energetics for chimpanzees, we *do not* contend that chimpanzee and human climbing is in a strict sense kinematically similar, or that humans and chimpanzees use the same amount of energy to climb the same distance. Instead, we suggest that estimates of energy expenditure using a human model provide a reasonable *upper bound*,

or maximum rate of energy expenditure, for chimpanzee climbing.

Climbing has received a great deal of recent attention in the human exercise-physiology literature. Using standard open-flow systems to measure oxygen consumption, these studies have examined energy expenditure during rock climbing for a broad range of subjects from novice to elite, and over a broad range of conditions from relatively easy routes on less-than-vertical faces to extremely difficult routes on overhanging faces (Billat et al., 1995; Mermier et al., 1997; Watts and Drobish, 1998; Booth et al., 1999; Watts et al., 2000). The findings of these studies are remarkably consistent. Three robust relationships are employed here:

1. Oxygen consumption varies with climbing experience and the difficulty of the route. During climbing oxygen consumption ranges from 20–25 liters $O_2 \times kg^{-1} \times min^{-1}$ for elite climbers on moderate terrain to 30–35 liters $O_2 \times kg^{-1} \times min^{-1}$ for novice climbers on moderate terrain and elite climbers on extremely difficult terrain (Billat et al., 1995; Mermier et al., 1997; Watts and Drobish, 1998; Booth et al., 1999; Watts et al., 2000). Following this model, energy consumption during climbing in chimpanzees was calculated using these rates of oxygen consumption.
2. Oxygen consumption during moderate to difficult climbing ranges from 55 to 75% of maximal oxygen consumption, or VO_2max (Watts and Drobish, 1998; Booth et al., 1999). Experienced climbers on moderate terrain consume oxygen at 55–63% VO_2max (Watts and Drobish, 1998). Following this model, the rate of oxygen consumption for chimpanzees during climbing was modeled as 60% of the oxygen consumption rate at the VO_2max . Following Calder (1981), VO_2max was calculated as

$$O_2 \times min^{-1} = 0.47 M_b^{0.80}$$

where O_2 is in ml. This allometric relationship was derived from a treadmill study of 19 species of mammals ($r=0.72$) (Taylor et al., 1978).

3. Oxygen consumption in elite rock climbers on moderate terrain is equivalent to running at 2.6 m/sec (Mermier et al., 1997). Following this model, energy expenditure during climbing for chimpanzees was estimated as equivalent to a moderate running speed, comparable to the 2.6 m/sec figure in humans. Dynamically similar speeds (which account for differences in body size and proportion) can be calculated using a Froude number (Alexander, 1984). Froude number is a dimensionless parameter calculated as

$$Fr = U^2 (L g)^{-1}$$

where Fr is Froude number, U is running speed, L is limb length, and g is gravitational acceleration (Alexander, 1984). For the human sample in Mermier et al. (1997), 2.6 m s^{-1} is equivalent to a Froude number of 0.766, as $L=0.9$ m for a sample of that stature (Minetti et al., 1994). For chimpanzees with a leg length of 0.5 m (Shea, 1984), a Froude speed of 0.766, is equivalent to running at 1.9 m s^{-1} . Thus, energy expenditure during climbing for chimpanzees was modeled as running at 1.9 m s^{-1} using Taylor et al. (1982) and Taylor and Rowntree (1973).

Finally, as a fourth method of modeling climbing energy expenditure independent of the human climbing literature, energy expended was calculated as a multiple of basal metabolic rate (BMR). Following James and Schofield (1990) and FAO/WHO/UNU (1985), the rate of energy expenditure during a given activity can be described as a multiple of BMR. These studies report a value of $5.5 \times BMR$ for “heavy work”, the most energy-expensive category of work. Assuming (generously) that climbing is equivalent to “heavy work” for chimpanzees, energy expended in climbing was estimated at $5.5 \times BMR$, where BMR is calculated using the Kleiber (1961) equation for resting metabolic rate

$$O_2 \times min^{-1} = 0.113 M_b^{0.75}$$

Here, O_2 is in *liters* of oxygen. Previous work has shown that hominoids do not depart significantly

from this relationship (Kurland and Pearson, 1986; Leonard and Robertson, 1994, 1997).

All four of the above methods for estimating energy expenditure produce a mass-specific rate of oxygen consumption with which to calculate the energy expended during climbing. Oxygen was converted to kCal as for walking. For mothers, the rate of energy expenditure was increased by 15% to account for the mass of the infant as for walking. Time spent climbing was calculated from mean climbing velocity and the total distance climbed per day.

Climbing velocity was measured using video recording of four climbing bouts (two adult males, one mother, one juvenile) taken in Kanyawara during June–July 2001, using the video display to time the ascent. Mean climbing velocity for these observations was 0.5 m s^{-1} . This figure is similar to that measured by Isler (2003) for captive male bonobos (0.7 m s^{-1} , $\sigma=0.3$, $n=2$ individuals) and both male and female gorillas (0.7 m s^{-1} , $\sigma=0.1$, $n=1$ male and 1 female), though less than she reports for captive female bonobos (1.2 m s^{-1} , $\sigma=0.4$, $n=2$). Given the similarity of the estimate from Kanyawara chimpanzees and most other captive apes, 0.5 m s^{-1} was used in these analyses. It should be noted that an increase of $0.1\text{--}0.2 \text{ m s}^{-1}$ (in line with speeds of captive apes) will slightly decrease estimates of energy expenditure, as time spent climbing will be decreased.

Minimum mechanical work

Simply calculating the mechanical work performed to lift a chimpanzee into the canopy is informative but insufficient for estimating energetic costs of climbing. The work performed can be calculated using the standard equation for work, $W=F d$, where W is work in joules, F is force in newtons, and d is displacement in meters. Converting force into its equivalent expression $\text{mass} \times \text{acceleration}$ yields, $W=M a d$. In displacing the body vertically as in climbing, the mass is the mass of the body, M_b , and the acceleration during steady climbing is the acceleration of gravity, g . Thus the equation gives $W=M_b g d$ for calculating the mechanical work required to lift the body into the canopy.

Using this equation, the work performed to lift an adult male chimpanzee with a body mass of 42.7 (Smith and Jungers, 1996) 100 m is 41.9 kJ, or 10.0 kCal. However, the energy spent to walk 100 m over level ground at 0.5 m s^{-1} , using the equation from Taylor and Rowntree (1973), is 14.2 kCal, or 142% of the energy required as estimated by the work equation. Simply calculating the amount of physical work required to lift the body mass of the chimpanzee significantly underestimates the energy spent climbing. This finding has important implications for studies that apply mechanical equations directly to locomotor behaviors to estimate energy costs (e.g., Warren and Crompton, 1998)—specifically, that values of locomotor energy expenditure for vertical climbing are likely to be underestimated.

Results

Day range and climbing

Day range and distance climbed per day are shown in Table 1 for each age-sex class. Mean day range (standard error) for Kanyawara males was 2.4 (0.04) km/day, versus 2.0 (0.15) for adult females, 1.9 (0.14) km/day for mothers, and 1.9 (0.15) km/day for juveniles. Mean day ranges for Kanyawara chimpanzees were less than those published at other sites (Table 1), but showed similar sex differences in ranging such that males traveled significantly further than individuals in the other classes ($P<0.05$, Student's two-tailed t -test between classes assuming unequal variance).

Mean distance climbed per day was more variable, perhaps owing to smaller sample size. Males climbed, on average 104 (7.2) m/day, adult females 117 (26.6) m/day, mothers 96 (10.6) m/day, and juveniles 134 (13.3) meter/day. These figures may seem low given the importance of climbing for chimpanzees, but they are perhaps less surprising when considering the average crown height of this forest (20–30 m) and the number of feeding bouts per day (3–5). Values may be slightly lower in this sample due to the importance of the relatively low-crowned *Uvariopsis* tree in the sample (mean height climbed for 257 bouts in *Uvariopsis* was

Table 1
Vertical climbing per day and day range for Kibale chimpanzees

Class	Kibale–Kanyawara Community							Gombe		Taï (by community)					
	Climbing (m/day)			Day range (km)				Mean	N^c	North		Middle		South	
	Mean	(S.E.)	N^a	Mean	(S.E.)	N^b	(fws.)			Mean	N^c	Mean	N^c	Mean	N^c
Adult males	104	(7.2)	37	2.4*	(0.05)	13	(736)	4.6*	93	3.7	205	2.1	125	4.3	147
Adult females	117	(26.6)	3	2.0	(0.16)	11	(112)	3.2	41	3.6				4.1	
Mothers	96	(10.6)	19	1.9	(0.12)	12	(165)								
Juveniles	134	(13.3)	23	2.0	(0.12)	16	(229)								
Total	113	(5.7)	82	2.1	(0.06)	52	(1242)	3.9	134	3.7	205	2.1	125	4.2	147

Values for Gombe (Wrangham, 1977) and Taï (Herbinger et al., 2001) are given for comparison. Means (with standard errors) are reported for each age-sex class analyzed. Sample sizes used to calculate error are as follows: N^a , number of climbing follows; N^b , number of individuals (number of follows); N^c , number of focal follows.

*Indicates mean is significantly greater than that for all other classes.

9.1 m, $\sigma=4.0$). However, while half of all climbing bouts were in *Uvariopsis* trees, the effect of lower crown height was largely offset by the higher rate of climbing bouts per hour observed when chimpanzees foraged in *Uvariopsis* groves. Climbing rate (meters/hour) for a follow and the proportion of *Uvariopsis* trees climbed during that follow were not significantly correlated ($r=0.16$, $P=0.13$, $N=89$, LSR).

Energetics

Estimates of daily energy spent walking and climbing are shown in Fig. 3 for each of the methods described above, excluding the general equation for walking cost. Results are consistent across methods: mean energy cost of terrestrial travel averaged 221 (range of estimates 193–249) kCal/day for males, 156 (141–171) kCal/day for females, 183 (165–200) kCal/day for mothers, and 73 (72–73) kCal/day for juveniles. Estimated energy spent climbing was an order of magnitude lower: mean cost for males was 22 (17–30) kCal/day; females, 21 (16–26) kCal/day; mothers, 19 (15–25) kCal/day; and juveniles, 11 (8–13) kCal/day. For ease of comparison, we averaged estimates from each method (excluding the general equation for walking), and used the mean for subsequent analyses. Mean energy spent on walking and climbing and estimated daily energy expenditure (DEE) is shown in Table 2, with the

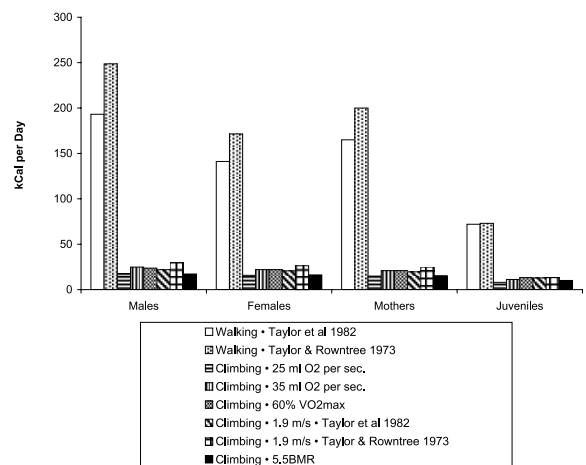


Fig. 3. Estimates of energy expended (kCal) per day for walking and climbing in Kibale chimpanzees. Methods are described in the text.

estimated cost from the general equation for walking included for comparison.

Climbing accounted for less than 2% of DEE for all age-sex classes. In contrast, walking accounted for 10–14% of DEE (Fig. 4). As the majority of DEE is spent on basal metabolic function, the energy costs of walking and climbing are perhaps best understood in the context of other non-BMR activities, such as feeding and resting. When BMR and, for mothers, the cost of lactation are subtracted from DEE, walking accounted

Table 2
Estimated energy expenditure per day (kCal) for Kibale chimpanzees

Class	DEE	Climbing	CI	Walking	CI	General endotherm
Males	1558	22	(14–35)	221	(180–267)	135
Adult females	1305	21	(8–40)	156	(124–194)	99
Mothers	1814	19	(11–32)	183	(183–223)	115
Juveniles	711	11	(6–17)	73	(64–82)	54

Values for climbing and walking are means of estimates from the methods described in the text. Confidence interval (CI) is calculated as described in the text. Daily Energy Expenditure (DEE) for mothers includes the energetic cost of lactation. General endotherm values for walking are estimated using the general endotherm equation from Taylor et al. (1982).

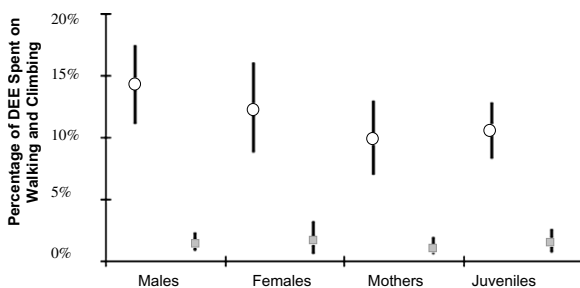


Fig. 4. Energy spent on walking and climbing per day in Kanyawara chimpanzees as a percentage of Daily Energy Expenditure (DEE). Open circles and gray squares indicate mean estimates for walking and climbing, respectively. Bars indicate confidence intervals for the mean, calculated as described in the text.

for 43–57% of total energy expenditure, while climbing accounted for only 6%.

Calculating the error for estimates of energy expenditure is difficult, as estimates of error are absent from much of the supporting literature (e.g., Taylor and Rowntree, 1973; Taylor et al., 1982). To estimate the standard error for energy expenditure, the 95% confidence limits were calculated for the mean distance climbed and walked per day. These values were then used to calculate the minimum and maximum estimated energy cost of walking and climbing using the methods described above. This interval was then extended by $\pm 5\%$, the mean margin of error for estimates of energy expenditure calculated from the climbing literature reviewed here (Mermier et al., 1997; Watts and Drobish, 1998; Booth et al., 1999; Watts et al., 2000). Confidence limits are given in Table 2 and shown in Fig. 4. These confidence limits support the relatively high cost of walking

when compared to climbing: the *minimum* estimates for walking cost are 3–5 times greater than *maximum* estimates for climbing.

Discussion

Methods for estimating energy costs

Given the methods used to calculate climbing energy expenditure and concerns over the validity of the equations used to calculate walking energy costs in chimpanzees (Studel-Numbers, 2003), it is useful to investigate potential sources of bias in these estimates of energy expenditure. First, the time period used to measure climbing may not have been representative of year round chimpanzee climbing behavior. While additional studies are needed to validate these data, the small number of fruit trees visited each day (approximately 3–5 based on Kanyawara data) and the range of crown heights available in the forest (15–35 m) suggest an average of 95–135 m/day is reasonable. Rough estimates from other sites support this: estimates for total height climbed per day in Gombe are similar to figures for Kanyawara (Wrangham, unpub. data). Further, the sample includes feeding bouts in different tree genera and, as shown above, climbing rates do not correlate with tree type, suggesting that these results are robust to differences in season.

Second, the methods used to estimate energy expenditure during climbing might be argued to underestimate energy spent climbing in chimpanzees. However, the human-based models used likely *overestimate* energy expenditure; the actual

energy cost of climbing is likely to be even lower than reported here. Furthermore, even at the predicted maximal rate of aerobic energy expenditure, $VO_2\text{max}$ (Calder, 1981), climbing would only account for 3% of DEE, significantly less than energy spent walking.

Finally, because the chimpanzees used to estimate locomotor energy expenditure were juveniles (Taylor and Rowntree, 1973), energy expenditure for terrestrial travel may be overestimated (Steudel-Numbers, 2003). However, the general equation for endotherms from Taylor et al. (1982) produces similar results (Table 2): mean estimated energy spent walking, though significantly decreased, is still 5–6 times greater than energy spent climbing.

Hominoid ranging ecology

Among chimpanzee populations, these results do not appear to be unique to Kanyawara. Day ranges and activity budgets from other chimpanzee sites (Gombe: Wrangham, 1977; Mahale: Matsumoto-Oda, 2002; Tai: Boesch and Boesch-Achermann, 2000; Herbinger et al., 2001) (Table 1) suggest similar patterns of locomotor energy expenditure. As day ranges in Gombe, Mahale, and Tai are greater than those shown here for Kanyawara, chimpanzees in these sites presumably show an even greater disparity in the amount of energy spent on terrestrial travel and climbing.

Differences in the distances climbed and walked per day among age classes suggest possible effects of body size on locomotor behavior. Juvenile chimpanzees used the shortest day ranges of all age-sex classes, but also climbed the greatest distance per day. This is similar to differences demonstrated by Doran (1992), which showed that terrestrial quadrupedalism accounted for a smaller proportion of locomotor bouts for juveniles than for adults. Further work on the effects of size on locomotor performance may determine whether this difference is attributable to the differential effects of body mass on the cost of arboreal versus terrestrial locomotion.

Comparisons with other apes suggest the pattern of locomotor energy expenditure seen in

Kanyawara chimpanzees is similar to that in bonobos and lowland gorillas, but different from that in orangutans and mountain gorillas. Bonobos share broadly similar locomotor activity budgets with chimpanzees, with some differences in the amount of climbing within the canopy (Doran, 1992, 1993). While a lack of day range analyses for bonobos prevents direct comparisons, it is likely that climbing accounts for a similarly small proportion of DEE. Similarly, reported day ranges for lowland gorillas (western: 1.5–2.5 km, Doran and McNeilage, 2001; eastern: 0.8 km, Yamagiwa et al., 1996) suggest terrestrial locomotion may account for a considerable proportion of DEE, especially in western populations. In contrast, the shorter day ranges of orangutans (0.5 km, Rodman and Mitani, 1986) and mountain gorillas (0.5 km, Watts, 1996) suggest overall locomotor costs are likely much lower than in chimpanzees, with climbing accounting for a higher percentage of DEE in orangutans.

Testing optimization models

Does the “compromised” anatomy of chimpanzees minimize total locomotor energy expenditure by lowering climbing costs? Applying estimated costs to the simple tradeoff model described above provides a useful tool for investigating this issue (Fig. 5). The high cost of walking relative to climbing, and the significant decrease in locomotor cost expected with increased walking efficiency, cause us to reject H1, i.e., that chimpanzee anatomy minimizes daily locomotor costs. Lowering the energy cost of walking to those predicted for a general endotherm (Taylor et al., 1982) would decrease daily locomotor costs by over 35% and non-BMR energy expenditure by 20% (see Fig. 5). Even when chimpanzees are assumed to be as efficient as general endotherms (Steudel-Numbers, 2003), walking dominates daily locomotor costs, selecting for increased walking efficiency (Fig. 5). Therefore, the data presented here support the alternative hypothesis (H2), i.e., that morphological specializations for arboreal locomotion do not minimize total locomotor energy expenditure, but instead incur a significant energy cost (Fig. 1b).

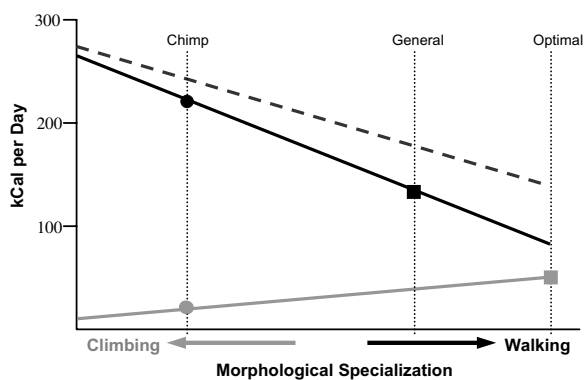


Fig. 5. Data for walking and climbing energy costs for chimpanzees applied to a simple tradeoff model. Circles: daily energy cost for walking (black circle) and climbing (gray circle) for an adult male chimpanzee (Chimp), calculated as described in text. Squares: Predicted daily energy costs for walking (black square), using the general endotherm equation (Taylor et al., 1982), and climbing (gray square), assuming climbing requires maximal aerobic energy expenditure ($VO_2\text{max}$). Increasing walking efficiency to that expected allometrically (General) significantly decreases total costs, and total cost is minimized at some hypothetical maximum walking efficiency (Optimal), where climbing cost is maximized. Total cost increases with increased climbing specialization.

It is important to note that the nature of the cost/specialization curve is unknown. We have presented the data here in the simplest case, with a linear cost/specialization function, and the degree of “morphological specialization” used in our model is difficult, if not impossible, to quantify. However, while more complex relationships can produce different results, the 10-fold disparity in walking and climbing costs suggest these results are robust to most plausible tradeoff models. Future studies on the relative costs of climbing and walking for other species may test whether the tradeoff model employed here for chimpanzees is valid.

Evidence for selection pressures on chimpanzee anatomy

While tests of optimality in the current environment are not conclusive tests of selection (Reznick and Travis, 1996), results of this study strongly suggest that chimpanzee anatomy is not selected to minimize locomotor costs. Instead, non-energetic

factors such as maneuverability within the canopy, predator avoidance, phylogenetic inertia, and/or climbing safety may be critical in shaping chimpanzee locomotor anatomy.

The importance of access to or maneuverability within the canopy is difficult to quantify or test. Food resources in the terminal branches of the canopy, unavailable to a less agile climber, may provide important energy gains. However, non-arboreal species, including human foragers (Yanamamo: Chagnon, 1997: 61; San: Lee, 1993: 29; Hadza: Jones and Marlowe, 2002) and bears (*Ursus thibetanus*: Nowak, 1991: 1086; *U. americanus*: Nowak, 1991: 1087), as well as more terrestrially adapted primates such as baboons (Rowell, 1966), commonly exploit arboreal resources, suggesting much of the food available in the canopy would be available to chimpanzees without energetically costly arboreal specializations. Further, most fallback foods for chimpanzees, the critical resources during fruit-poor times, are terrestrial (Wrangham et al., 1998). If maneuverability within the canopy is an important pressure shaping chimpanzee anatomy, the additional energy gains (relative to those available to non-arboreal species) during fruit-rich periods must be shown to offset the year round cost of maintaining climbing adaptations.

Predator avoidance, commonly cited as a primary factor influencing grouping decisions in primates (van Schaik, 1983; Boesch, 1991; Isbell, 1994; Janson and Goldsmith, 1995) is difficult to assess as a selection pressure on chimpanzee anatomy. Events such as predation, though rare, may exert strong selection for climbing fast in order to escape predators. However, if chimpanzees are most vulnerable to predators on the ground, as suggested by some accounts (Boesch and Boesch-Achermann, 2000: 31–33), deficiencies in terrestrial locomotor performance may suggest predation is not a primary factor. Locomotor studies of juveniles, the most vulnerable age class, suggest chimpanzees are significantly slower than comparably-sized mammals: maximum sustained running speeds (Taylor and Rowntree, 1973) are at least 2–3 times slower than predicted by allometric scaling (Heglund and Taylor, 1988; Garland, 1983). Behavioral adaptations such as grouping

may compensate for these performance constraints (Isbell, 1994).

While phylogenetic history must constrain locomotor morphology, it seems unlikely that climbing adaptations in chimpanzees are simply a result of phylogenetic inertia, held over from a more arboreal ancestor. The high energetic cost of terrestrial travel (Taylor et al., 1982), presumably due to specializations for climbing, suggests these traits would be under negative selection if other pressures did not maintain them. Demonstrating this formally will require biomechanical analyses linking specific climbing adaptations such as heavy distal limb segments, short hindlimbs, and humeral torsion, to increased cost of transport, slower walking speeds, or some other negative impact on walking performance. Classic considerations of limb design support these links (Hildebrand, 1985), with some empirical support from other species (Studel, 1990; Minetti et al., 1994; but see Studel, 1994; Taylor et al., 1974; Studel and Beattie, 1995).

In contrast to maneuverability, predation, or phylogenetic inertia, strong evidence suggests climbing safety is an important factor in shaping chimpanzee anatomy. Chimpanzee mortality is high in adults relative to human foragers (Hill et al., 2001), and adult mortality is likely to have significant negative impacts on fertility in a long-lived, high parental-investment species such as chimpanzees. Evidence of skeletal trauma in chimpanzees and other apes (Schultz, 1969; Jurmain, 1997; Lovell, 1990; Carter et al., in prep.), along with observations of falls (Goodall, 1986), underscore the importance of falls in contributing to morbidity and mortality. Morphological and behavioral studies suggest a number of adaptations for preventing falls. The long, curved phalanges of chimpanzees (Latimer, 1991), the importance of maintaining a point of support through arm-hanging (Hunt, 1991), and the use of diagonal sequence gaits (Cartmill et al., 2002) support the proposition that chimpanzees and other primates are adapted primarily to avoid falling from the canopy. In light of the energetics data shown here, such evidence suggests an interesting tradeoff between climbing safety and walking efficiency. Future biomechanical analyses linking specific

traits to climbing safety or the cost of walking will provide a means of testing this hypothesis.

Applications to hominoid evolution

The significant locomotor costs associated with the locomotor anatomy of chimpanzees and the importance of climbing safety may aid in reconstructing locomotor performance in extinct hominoids. First, these results suggest climbing efficiency is an unreliable predictor of locomotor ecology for early hominins. Thus, within the ongoing debate regarding arboreal behavior in *Australopithecus afarensis*, analyses focusing on muscle function and skeletal traits as related to vertical climbing ability (Latimer and Lovejoy, 1989; Stern and Susman, 1981, 1983, 1991) or the amount of time spent on vertical climbing (Latimer, 1991; Ohman et al., 1997) in this species might not provide the best measures of arboreal behavior. Chimpanzees do not climb prohibitive distances each day, and early hominins, if semi-arboreal, would presumably have climbed even less as they inhabited more open habitats. Thus, vertical climbing proficiency would probably not have been a critical aspect of arboreal performance for these early hominins. Instead, traits important for avoiding falls from the canopy may be more useful measures of locomotor performance and behavior in extinct hominins. For example, Hunt (1991, 1994, 1996) has argued that similarities in the chimpanzee and *A. afarensis* shoulder and arm reflect selection for maintaining a point of support (and reducing mechanical stress in the thorax) during feeding via arm-hanging postures, with the shorter phalanges of early hominins (Latimer, 1991; Alba et al., 2003) reflecting the use of smaller diameter branches for support. Conversely, Latimer (1991) has argued that shorter phalanges reflect decreased selection pressure on climbing safety due to less arboreal foraging. More biomechanical analyses, focusing on the relationships between specific morphological traits and aspects of performance related to climbing safety, are necessary to test these competing hypotheses.

Second, the significant energetic cost of walking for chimpanzees provides some support for efficiency-based arguments for the evolution of

bipedalism (e.g., Rodman and McHenry, 1980). Assuming the chimp-human last common ancestor was similar to chimpanzees in its locomotor anatomy and ecology, the high proportion of DEE spent on terrestrial travel would presumably lead to strong selection for decreased walking costs. Changes in forest structure or preferred habitat that increased the distance between food patches or decreased the probability or severity of falls would magnify this effect. Morphological traits conferring greater energy efficiency might therefore be expected to significantly increase fitness for early hominins, especially as drier climatic conditions led to a more patchy distribution of resources. While the energetic cost of transport for early hominins such as *A. afarensis* remains a topic of considerable debate (Stern and Susman, 1983; Berge, 1991; Preuschoft and Witte, 1991; Ohman et al., 1997; Crompton et al., 1998; Stern, 1999; Kramer and Eck, 2000), our data suggest there may have been strong selection for increased energy efficiency.

Similarly, the daily locomotor costs for chimpanzees may be informative in interpreting postcranial adaptations in Miocene apes. Some Miocene species (e.g., *Sivapithecus* spp.) have been shown to possess a combination of traits associated with suspensory locomotion, such as powerful grasping hands, and terrestrial locomotion, such as a lack of humeral torsion and curved humeral shafts (Rose, 1984, 1986, 1989, 1994; Pilbeam et al., 1990; Spoor et al., 1991; Larson, 1998; Madar et al., 2002). Assuming an arboreal ancestral condition, the mosaic of terrestrial and suspensory traits in Miocene apes may reflect selection for decreased cost of transport and maintained safety in the canopy. Such adaptations might be expected given the high walking costs and fall-related mortality seen in extant chimpanzees. Again, further biomechanical analyses are necessary to test these hypotheses.

Conclusion

Chimpanzees exhibit a number of postcranial adaptations for arboreal locomotion. New data presented here on the distance climbed and

walked each day and the relative costs of walking and climbing, suggest that these adaptations incur a significant net energy cost. Chimpanzees spend roughly ten times more energy walking than climbing, a figure inconsistent with minimizing daily energy costs via increased climbing efficiency in the optimization models considered here. Evidence from other sites suggests that this pattern of energy expenditure is common to all chimpanzees, and perhaps bonobos and lowland gorillas as well.

It is important to note that tests of energetic optimization are not direct tests of the selection pressures that have shaped chimpanzee anatomy. Demonstrating that a given trait is or is not “optimal” in its current environment does not provide conclusive evidence of the underlying dynamic evolutionary or ontogenetic processes that created it (Gould and Lewontin, 1979; Reznick and Travis, 1996). However, these analyses of daily locomotor demands provide a useful framework for investigating selection pressures on chimpanzee anatomy. Of the possible factors considered here, climbing safety (avoiding falls), more than maneuverability, predator avoidance, or phylogenetic inertia, appears to be the most likely selective pressure shaping chimpanzee anatomy. Future analyses focusing on the specific performance demands on chimpanzee locomotion will refine our understanding of chimpanzee anatomy. Similarly, greater focus on morphological traits linked to the specific, competing demands of terrestrial efficiency and climbing safety may allow us to better test hypotheses regarding locomotor adaptations in fossil hominoids.

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