Locomotor Energetics in Primates: Gait Mechanics and Their Relationship to the Energetics of Vertical and Horizontal Locomotion

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Abstract

All primates regularly move within three-dimensional arboreal environments and must often climb, but little is known about the energetic costs of this critical activity. Limited previous work on the energetics of incline locomotion suggests that there may be differential selective pressures for large compared to small primates in choosing to exploit a complex arboreal environment. Necessary metabolic and gait data have never been collected to examine this possibility and biomechanical mechanisms that might explain size-based differences in the cost of arboreal movement. Energetics and kinematics were collected for five species of primate during climbing and horizontal locomotion. Subjects moved on a treadmill with a narrow vertical substrate and one with a narrow horizontal substrate at their maximum sustainable speed for 10–20 min while oxygen consumption was monitored. Data during climbing were compared to those during horizontal locomotion and across size. Results show that climbing energetic costs were similar to horizontal costs for small primates (<0.5 kg) but were nearly double for larger species. Spatio-temporal gait characteristics suggest that the relationship between the cost of locomotion and the rate of force production changes between the two locomotor modes. Thus, the main determinants of climbing costs are fundamentally different from those during horizontal locomotion. These new results combining spatiotemporal and energetic data confirm and expand on our previous argument (Hanna et al.: Science 320 (2008) 898) that similar costs of horizontal and vertical locomotion in small primates facilitated the successful occupation of a fine-branch arboreal milieu by the earliest primates.

All nonhuman primates, even those typically thought of as "terrestrial," like baboons and patas monkeys, sleep, eat, and escape predators in the trees. Living in this three-dimensional environment requires that all primates regularly climb, often doing so on vertical supports. Climbing must have been an important aspect of early primates exploitation of an arboreal niche and so it has been argued that many fundamental primate morphological features and locomotor patterns are associated with climbing (Jones, 1916; Le Gros Clark, 1950; Stern, 1976; Fleagle et al., 1981; Szalay and Dagosto, 1988; Gebo, 1996; Larson, 1998a; Hamrick,

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2001; Bloch and Boyer, 2002; Hanna, 2006; Gebo et al., 2008). In reference to the earliest primates, Larson (1998a; p 170) points out that "morphological changes enhancing limb mobility [in primates]… have been pivotal in the development of the locomotor versatility-including various forms of climbing, scrambling, and bridging behaviors-that has come to characterize arboreal primates." In later stages of primate evolutionary history, it is thought that some of the morphological changes related to climbing, such as long limbs and mobile joints, facilitated the evolution of more specialized locomotor behaviors, including suspensory locomotion and bipedality (Washburn, 1968; Conroy and Fleagle, 1972; Stern and Oxnard, 1973; Fleagle, 1976; Cartmill and Milton, 1977; Yamazaki et al., 1979; Prost, 1980; Fleagle et al., 1981; Stern and Susman, 1981; Vangor and Wells, 1983; Hirasaki et al., 1992, 1993, 1995, 2000; Larson, 1998b; Schmitt, 1998, 1999, 2003a; Richmond et al., 2001). Thus, understanding climbing is essential for understanding not only extant primate ecology, but also primate morphology and primate locomotor evolution.

The link between climbing and aspects of primate anatomy has been reinforced recently by studies showing primates that climb with a relatively high frequency have morphological specializations that facilitate specific locomotor patterns, which may in turn enhance the efficiency of vertical climbing. Morphologically specialized primates such as Asian apes, spider monkeys, and lorises exhibit longer strides than more generalized species (e.g., Hirasaki et al., 1992, 1993, 2000; Isler, 2005; Hanna, 2006). These long strides are hypothesized to be energetically advantageous during climbing (Isler, 2005; Hanna, 2006), suggesting that climbing energetics may be a key source of data for understanding climbing adaptations and the selective pressures driving anatomy and locomotor biomechanics.

In addition to exploring the link between climbing and skeletal mechanics, understanding climbing energetics also provides an exceptional case for understanding how energy and work are related in muscles. The major energetic cost of locomotion is believed to be directly related to the amount of force produced by the muscles to move the body (Fenn, 1930; Cavagna, 1964; McMahon, 1975; Alexander, 1977; Cavagna and Kaneko, 1977; Cavagna et al., 1977). During horizontal locomotion little force is produced to accomplish work in moving the center of mass vertically. This is not the case during vertical climbing, however, in which force is generated to produce net positive external work to lift the center of mass. Thus, there should be distinct differences in the relationship between energy and work during horizontal compared to vertical locomotion. Understanding the differences in the relationship between work and energy consumption in primates during various modes of locomotion provides insight into the types of selective pressures that are involved in the evolution of early primate musculoskeletal morphology.

Previous works on the energetics of primate locomotion in general are limited, and there are few data on the basic costs of climbing in primates. A seminal paper on the scaling costs of incline locomotion by Taylor et al. (1972) using mass-specific cost measures suggests that the extra cost to go uphill, over that of moving horizontally, is constant between a chimpanzee and a mouse. That is, in their study increased body mass did not increase the mass-specific cost of moving uphill. This relationship supports the idea that it costs the same amount of energy to lift 1 kg 1 m, no matter what the body size of the organism (Hill, 1950; Taylor et al., 1972; Aiello, 1992; Elton et al., 1998). On the other hand Taylor also reported that the mass-specific cost of moving horizontally is much lower in the chimpanzee than the mouse, suggesting that mass does influence locomotor costs when the work environment is more complex as is the case during horizontal locomotion. Therefore the relative cost of moving uphill is greater for the chimpanzee than for the mouse. Subsequent work examining this notion that it is relatively more expensive (compared to the horizontal cost) for large animals to go up than for small animals has been supported during incline walking by insects (Full and Tullis, 1990; Lipp et al., 2005). These insect studies indicate that larger

insects (e.g., cockroaches) incur a greater cost over that of horizontal locomotion than smaller insects (e.g., ants, which exhibit no significant difference between the cost of horizontal and incline locomotion) during incline locomotion. Clearly the data that exist so far suggest an increased cost for moving uphill for larger animals. But this is still a relatively small dataset and range of animals, and these studies do not examine purely vertical motion.

Primates provide an ideal model for filling this gap by examining the cost of actual climbing (as opposed to incline walking) and whether body size affects those costs. Primates exhibit a wide range of body masses, spanning several orders of magnitude. Additionally from the smallest 30-g mouse lemur to the large 150-kg orangutan, all nonhuman primates regularly climb, such that a functionally important scaling relationship between energetics and body mass during climbing can be determined. Unfortunately, few data exist on what the costs of climbing up a vertical support are, or how they scale, in non-human primates. Nor have any studies provided a dataset combining gait mechanics and energetic costs to examine the source of any size-based variation. In 2008, Hanna et al. did provide data on climbing by primates, showing that at small sizes the cost of climbing may not be much higher than walking. However, that paper was brief and included few details on the allometric relationships and no data on gait mechanics in the sample. The latter data are critical to understanding why small primates may differ from larger primates and other animals in experiencing no increase in cost of climbing compared to horizontal locomotion.

In contrast to the limited data on the costs of vertical climbing, there are more data available on the cost of horizontal locomotion by primates. In 1982, Taylor et al. compiled data on the cost of mass-specific horizontal locomotion from the literature for six species of primates, and directly gathered data for three more species. Taylor et al. (1982) used these data to calculate an equation to estimate the cost of horizontal transport for primates, showing that like other mammals, the cost of transport decreases with increasing body mass. Since then, few other studies have presented data on the cost of horizontal quadrupedalism for nonhuman primates. Nakatsukasa et al. (2004) published data for an additional species of primate, the Japanese macaque (*Macaca fuscata*), Sockol et al. (2007) provided additional data on the energy cost of chimpanzee quadrupedalism, Hanna et al. (2008) provided data on five additional species of primate during horizontal quadrupedalism on a simulated arboreal substrate, and O'Neill (2008) did an in depth study of *Lemur catta* metabolism during walking and running. All the data from these studies fit nicely into the regression calculated by Taylor et al. and provide more evidence to show that the mass-specific cost of horizontal locomotion in primates decreases with increasing body mass.

More recent studies have sought to explain the energy costs of locomotion in terms of kinematics and muscle function (e.g., Kram and Taylor, 1990; Roberts et al., 1998a,b; Pontzer, 2007; O'Neill, 2008). During horizontal locomotion, Kram and Taylor (1990) found that step length is inversely proportional to cost of transport such that longer step lengths are correlated with a decrease in cost of transport. Pontzer (2007) expanded on this model to include a measure of limb posture, finding that effective limb length as an indicator of step length may also be used to estimate the cost of horizontal locomotion. Both models suggest that energy consumption by muscles is the driving factor for the cost of horizontal locomotion, an idea developed by Taylor et al. (1982), elaborated on by Roberts et al. (1998a,b), and further supported by O'Neill (2008). Both step length and joint posture differences have already been reported between lemur and loris species during climbing (Hanna, 2006). Such differences in the kinematics of climbing between species may provide insight into how muscles are functioning during vertical locomotion and provide insight into the metabolic cost of climbing in primates.

Studies of climbing or inclined locomotion are aimed at understanding the relationship between energy consumption by muscles and work done by muscles in moving the center of mass vertically. During horizontal locomotion, however, there is no net vertical movement of the center of mass (the center of mass oscillates vertically but returns to the same vertical position at the end of each stride). Thus, the relationship between muscle energy use and work is obscured, and it is suggested that the work performed on the center of mass during horizontal locomotion is not the driving factor behind energy use. Rather, it is the rate at which muscles produce force that is thought to be the primary determinant of the energy cost of horizontal locomotion (Cavagna and Kaneko, 1977; Heglund et al., 1982; Kram and Taylor, 1990; Willems et al., 1995; but see Donelan et al., 2002; Collins et al., 2005; Ruina et al., 2005; Pontzer, 2007 for alternate views). There is, however, positive vertical work accomplished in lifting the center of mass during climbing, such that the primary determinant of the energy cost of climbing may be related to the magnitude of force production rather than limited to the rate of force production. Thus, climbing energetics, unlike horizontal energetics, may provide more insight into the relationship between muscle force generation and metabolic power input.

The goals of this study are three fold. First, this study seeks to understand the scaling relationship between the energetic cost of climbing and body mass in primates. Next, this study seeks to understand how the climbing costs and scaling relationship of these costs to body mass compare to the horizontal energy cost and body mass scaling in the same species. These first two goals have been briefly touched on by Hanna et al. (2008) and are presented here in greater detail. But the larger question of how the kinematics of climbing may relate to the energy costs of climbing and how this relates to muscle recruitment are addressed here for the first time as goal number three.

MATERIALS AND METHODS

Sample

To understand the energetics of climbing across primates, a taxonomically and ecologically diverse sample of species was selected for study. Subjects included four species from the Duke Lemur Center (DLC) and one species from the Center for Neotropical Primate Research and Resources at the University of South Alabama (CNPRRUSA):[1] 1) *Loris tardigradus* (DLC), 2) *Cheirogaleus medius* (DLC), 3) *Nycticebus pygmaeus* (DLC), 4) *Saimiri boliviensis* (CNPRR-USA), and 5) *Eulemur mongoz* (DLC). This sample spanned an eight-fold range in body mass (Table 1). All subjects were fully adult, healthy, and kept in semi-natural enclosures which allowed them to regularly move in a three-dimensional environment. All procedures were approved by the respective institutional animal care and use committees (IACUCs) (DUIACUC and USAIACUC).

Experimental apparatus

Individuals were habituated to climb at their maximum sustainable speed on a motor-driven, treadmill for 15–30 min (Fig. 1). The treadmill consisted of two pulleys around which a thick rubber tube (hereafter referred to as "substrate") was strung. The pulleys were situated so that the substrate was vertical. Each pulley was attached to a shaft, on the other end of which was a timing belt system. The timing belt system was driven by a timing belt such that each shaft and pulley apparatus moved at the same speed to avoid substrate slippage. The lower shaft and pulley apparatus was attached to a variable-speed DC motor.

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The diameter of the substrate varied across species because it is believed that substrate size may affect locomotor mechanics (Isler, 2004; Schmitt and Hanna, 2004), and thus, potentially locomotor energetics. Substrates were selected on the basis of species' size: *L. tardigradus, C. medius, and N. pygmaeus* climbed on a substrate of 1.12-cm diameter, while *S. boliviensis and E. mongoz* utilized a 2-cm diameter substrate. These substrate diameters correspond to preferred substrate size in the wild for most of the species (Charles-Dominique, 1974; Fleagle and Mittermeier, 1980; Hunt et al., 1996; Botz et al., 2003; Schmitt 2003b; Stevens, 2008).

A section of the substrate on which the subjects climbed in place was enclosed in a metabolic chamber (Fig. 1). It is worth noting that the subjects stayed in place in this experiment and thus no net work was done on the center of mass. However, as the substrate rotated downward, the animals climbed in place and resisted downward motion, thus doing internal work to maintain the center of mass position. In so doing they incurred metabolic costs. Moreover, subjects in this study used similar postures and gait patterns as reported for free climbing by Hanna (2006). We still describe our data as "climbing" or "horizontal" values because the animals use the same postures and gait parameters they use during free climbing or horizontal walking (Hanna, 2006) and we assume that the cost of transporting the center of mass is constant across body size (the theoretical cost of transporting the center of mass vertically would be 9.8 J kg^{-1} m^{-1}). We do not add in this value to our data, however, since we have no comparable theoretical value to add to the horizontal data.

The height of this chamber was adjusted to the stride of each species to ensure steady locomotion. Each chamber had a hole in the top and bottom of it through which the substrate ran. These holes were packed with insulative filters to reduce air leakage. Two additional holes, outfitted with PVC drain covers, were located at the top and the bottom of each chamber. The holes allowed air to be drawn through the chamber. The top hole was attached, via an air hose, to a standard open-flow calorimetry system (Sable Systems®; Las Vegas, NV), consisting of a personal computer for O_2 concentration data collection and analysis software (Datacan V, Sable Systems, Las Vegas, NV), an oxygen analyzer, digital flow-meters, and desiccants for both water and CO_2.

Video recording and analysis

All climbing sequences were video-recorded for speed and spatio-temporal gait analysis using one or two video cameras. The locomotor experiments were videotaped using different methods and equipment for the nocturnal species (*Loris, Nycticebus, and Cheirogaleus*) compared to the diurnal species (*Eulemur, Saimiri*). For two of the nocturnal species (*Loris and Cheirogaleus*), one analog camera (AG-450; Panasonic, Secaucus, NJ) recorded video images at 60 frames per sec under infrared lights. Shutter speed for this camera was set at 1/1,000 of a second. The camera was set lateral to the substrate within the chamber. For Nycticebus, two synchronized cameras were used (AG-450; Panasonic, Secaucus, NJ, and a digital infrared security camera, CCTV style), both filming at 60 frames per sec with infrared lights. The Panasonic camera was set at a shutter speed of 1/1,000 of a second. Both cameras were set up perpendicular to each other. For the diurnal strepsirhine species, two synchronized video cameras were used (HD-D5100; Panasonic, Secaucus, NJ) at 60 frames per sec with shutter speeds of 1/1,000 of a second. Only one of these cameras could be used for *Saimiri* due to the size of the room. Professional quality lights were focused on the treadmill chamber. Both cameras were set up perpendicular to the substrate and to each other. In all cases, the video images were passed through a video mixer (Videonics; Focus Enhancements; Campbell, CA). When two cameras were used, both images were mixed during the experiment with a video effects editor so that they were displayed side by side on one screen. Speed of the substrate was used to measure climbing speed. Substrate speed was determined with a stopwatch six to ten times throughout an experiment, at equal intervals.

The substrate was marked with a piece of tape to aid in this process. Using the time for one complete rotation of the substrate (from marker to marker), and the length of the substrate, speed was determined in meters per second. The exact same system and methods were used to collect data on horizontal locomotion. The only difference is that the treadmill was rotated 908 counterclockwise so that the movement of the substrate was parallel to the ground. Like the climbing data, these represent the first data ever data collected on metabolic costs of multiple species of primates during locomotion on relatively narrow substrates.

Step length

Using frame-by frame playback on a VCR of the video recordings of each experiment (an oxygen consumption recording experiment lasting on average 20 min), 30 values for contact time were collected (measured as frames in which the limb is in contact with substrate and converted to seconds). Those data were compiled to produce one value for average contact time per experiment for comparison with the metabolic data. This value was determined for the left hindlimb, only, as the hindlimbs provide the greatest contribution to propulsion during both horizontal locomotion (Kimura et al., 1979; Demes et al., 1994) and climbing (Hirasaki et al., 1993; Hanna and Schmitt, in press). The number of frames the hind-foot was in contact with the substrate during a stride was counted in order to determine contact time for ten strides in a row. This value was then divided by 60 (because the filming rate was 60 f s^{-1}) to yield the contact time in seconds. This process of collecting ten strides for contact time analysis was repeated three times, at even intervals throughout the middle of the oxygen plateau period, yielding three independent sets of ten contact time values. The average of these values was calculated. Following determination of contact time, step length was calculated according to Kram and Taylor (1990), where step length (L_c) equals the product of speed and contact time (t_c).

Open-flow respirometry

Oxygen content of the air was monitored and recorded using O_2 software (Datacan V, Sable Systems, Las Vegas, NV). Prior to air entering the oxygen analyzer, CO_2 and water vapor were removed with desiccants. In addition, the main flow rate through the chamber was monitored and recorded. The sampling frequency for recording data was 2 Hz. Before and after each climbing session, a baselining procedure described by Lipp et al. (2005) was performed. Oxygen consumption rate was calculated using the initial equation from Withers (1977) modifying it to include a nitrogen calibration (Fedak et al., 1981) and applying a correction for slight differences in flow rate between animal experiment and nitrogen calibration.

Withers (1977) presented the following equation:

$$\dot{V}O_2 = \frac{\dot{V}E \cdot \left(F_{I_{O2}} - F'_{E_{O2}}\right)}{1 - F_{I_{O2}} + RQ \cdot \left(F_{I_{O2}} - F'_{E_{O2}}\right)}$$

(1)

where $\dot{V}_E$ is the main flow rate out of the chamber or mask (STP), F_{IO2} is the fractional concentration of O_2 entering the mask, F'_{EO2} is the fractional concentration of O_2 leaving the mask after CO_2 has been removed, and RQ is the respiratory quotient. The respiratory quotient is a ratio of the amount of carbon dioxide produced to the amount of oxygen consumed, and is a good indicator of which fuels are being metabolized (e.g., proteins, fats, or carbohydrates), (Brooks et al., 1996).

Fedak et al. (1981) improved upon Withers' (1977) calculation using a nitrogen calibration technique that corrects for the drying of water vapor and removal of carbon dioxide from the sample prior to gas analysis. They also assumed that F_{IO2} is equal to 0.2094, $F_{IO2} - F'_{EO2}$ is equal to 0.01, and RQ is ~1. These assumptions yield the following equation:

$$\dot{V}O_2 = \left(\frac{0.2094\dot{V}^*_{N_2}}{0.8} \right) \left(\frac{\Delta C}{\Delta C*} \right)$$

(2)

In this equation, "ΔC and $\Delta C*$ refer to the deflection of the analyzer during measurement and calibration, respectively" (Fedak et al., 1981, 776). Using this equation yields a maximum error of 9% (maximum of 8% error for animal produced water vapor and maximum of 1% RQ related error) (Fedak et al., 1981). This study uses a modified version of the Fedak equation that takes into account the actual change in oxygen concentration after drying and removal of carbon dioxide (instead of assuming it is 0.01) and accounts for error caused by differences in flow rate between animal experiment and calibration:

$$\dot{V}O_2 = \dot{V}^*_{N_2} \left(\frac{0.2094}{0.7906 + RQ\left(\frac{\Delta C}{100}\right)} \right) \left(\frac{\Delta C}{\Delta C*} \right) \left(\frac{\dot{V}_E}{\dot{V}^*_E} \right)$$

(3)

In Eq. (3), $\dot{V}O_2$ is the oxygen consumption rate in L min^{-1}, $\dot{V}^*_{N_2}$ is the flow rate of the nitrogen during the nitrogen dilution, in L min^{-1}, RQ is the respiration quotient, ΔC is the change in oxygen concentration during an animal experiment in percentage, $\Delta C*$ is the change in oxygen concentration during an animal experiment in percentage, $\dot{V}_E$ is the main flow rate through the chamber during a nitrogen experiment on L min^{-1}, and $\dot{V}_E$ is the main flow rate through the chamber during an animal experiment in L min^{-1}. Equation (3) still has the possibility of yielding 9% error, although this is unlikely as the 8% error caused by animal produced water-vapor would only occur if the animal saturated the air stream when it was 40°C (Fedak et al., 1981). The term $\left(\dot{V}_E / \dot{V}^*_E \right)$ in the equation used for this study was added to Fedak et al.'s (1981) equation in order to more accurately estimate oxygen consumption. Fedak et al.'s (1981) equation does not require that the main flow rate exiting the chamber $\left(\dot{V}_E \right)$ be monitored because they assume that $\dot{V}^*_E = \dot{V}_E$. However, if this is not the case and the two flow rates differ, even minutely, then error is introduced. The error caused by differences in main flow rate between animal experiment and nitrogen calibration would cause changes in the deflection of oxygen content, ΔC or $\Delta C*$. $\Delta C/\Delta C*$ accounts for differences in oxygen deflection due to differences in flow rates, although these differences may not be linear. Thus, by adding this additional flow rate ratio term, the equation used to calculate oxygen consumption in this study yields greater accuracy. Finally, because RQ is typically between 0.7 and 1.0 during walking and running, the respiration quotient was held constant at 0.8 (Griffin et al., 2004).

After calculating the oxygen consumption rate based on these parameters, it was converted to metabolic rate assuming a conversion factor of 20.1 J ml^{-1}O$_2$ (Brooks et al., 1996):

$$MR = \dot{V}O_2 \times 335$$

(4)

where MR is in J s^{-1} and $\dot{V}O_2$ is in L min^{-1}. When appropriate, mass-specific metabolic rate was calculated as MR/M_b, where M_b is body mass in kg.

Mass-specific cost of transport (COT) was also calculated using the observed speed for each experiment. That is:

$$COT = \frac{MR}{M_b \times V}$$

(5)

where COT is the cost of transport in $J\ kg^{-1}\ m^{-1}$, M_b is body mass in kilograms, and V is speed in $m\ s^{-1}$.

Experimental protocol

The habituation period for each subject lasted between three weeks and three months. During this period, subjects were encouraged to climb (or move horizontally on) the substrate treadmill with food rewards given through the top hole of the metabolic chamber. The habituation period was considered over when a subject could climb the substrate at their maximum sustainable speed for 15–30 min. After the habituation period, each individual performed at least two valid oxygen consumption trials (Table 1). Trials in which the individual got off the substrate for more than 10 s, or got off the substrate more than five times, were discarded. Food rewards were still offered, although these rewards never exceeded 10% of their regular diet (by mass). Only one climbing (or horizontal) session per day per individual was permitted.

Data treatment

Initially, intraspecific variation in cost of transport and speed were examined using Mann Whitney U or Kruskal Wallis, depending on the number of subjects in each species. These nonparametric tests were used because of the small sample for each individual. Significance levels were adjusted for multiple comparisons using a sequential Bonferroni adjustment (Rice, 1989). Where warranted, species means and standard deviations were calculated for each variable from the two or three individual means. Data grouped by species were tested for normality by graphical methods, and all passed. Thus, further analyses were calculated using parametric tests.

First, the log of metabolic rate during climbing was examined against speed using least-squares linear regression (Sokal and Rohlf, 1995) for each species to determine whether speed affected the metabolic cost of locomotion, as it has been found during horizontal locomotion (Taylor et al., 1982). Log-log regressions of the cost of locomotion (and efficiency) versus body mass have been presented elsewhere (Hanna et al., 2008). That study found that the mass-specific cost of transport did not decrease with body mass during climbing, but neither did the mass-specific cost of horizontal locomotion, at least significantly. Because it is well known that the mass-specific cost of horizontal transport does significantly decrease with body mass (Taylor et al., 1982; Alexander, 2003; Steudel-Numbers, 2003), Hanna et al.'s analysis of their horizontal data was likely impacted by a small interspecific sample ($n = 5$). To accommodate this statistical problem, intraspecific comparisons of the cost of transport between locomotor modes were calculated in this study, instead.

Cost coefficient—During horizontal locomotion, it has been found that the energy used by muscles is proportional to the total volume of muscle is active, but is inversely proportional to contact time (e.g., Kram and Taylor, 1990; Roberts et al., 1998; Griffin et al., 2003; McGowan et al., 2006). It is well accepted that the mass-specific active muscle volume is the same in both large and small mammals (Alexander et al., 1981; Biewener, 1990; Kram and Taylor, 1990; Roberts et al., 1998a), such that muscle shortening velocity

(as measured by contact time or step length) is one of the major determinants of horizontal locomotor cost. This relationship is often described by the equation:

$$c = \frac{MR}{W_b} \times L_c$$

(6)

where MR is the metabolic rate in J m^{-1}, W_b is the body weight in N and L_c is the step length (m). In this equation, the "cost coefficient," c (J N^{-1}), expresses the relationship between body-weight-specific energy cost and the rate of force generation. We examined this relationship during horizontal locomotion and climbing to determine whether there is a proportional relationship during climbing. A linear regression of kinematic variables relative to speed was calculated, including the cost coefficient described by Kram and Taylor (1990).

RESULTS

Metabolic results

A total of 60 climbing experiments and 38 horizontal locomotion experiments satisfied the criteria listed above. Table 1 indicates the number of valid climbing and horizontal experiments for each subject, and the speed range utilized by each subject and species. Intra-specific variation in speed and cost of transport was negligible; thus, future analyses grouped data for all subjects of a species together. Speed was not significantly correlated with metabolic rate in any species except *L. tardigradus* (Table 2). Based on the narrow speed ranges used by each species (Table 1), this correlation was ignored in further analyses

As indicated by Hanna et al. (2008), the cost of climbing is statistically constant relative to the decrease in the cost of horizontal transport compared to body mass (−0.119 and −0.750, respectively) (Fig. 2, Table 3). The slopes of these costs of transport compared to body mass, however, are not significant. It is well known that the cost of transport during horizontal locomotion decreases significantly with body mass in primates (Taylor et al., 1982; Alexander, 2003; Steudel-Numbers, 2003). Thus, the interspecific analysis presented here and by Hanna et al. (2008) may be limited due to the small sample size ($n = 5$ species). Future studies should expand this sample and include more anthropoids.

The comparison of the intraspecific cost of transport across locomotor modes showed that the difference in cost between vertical and horizontal locomotion increases with body mass (Table 3). Within species, primates larger than 0.5 kg exhibit a significant difference between the cost of climbing and the cost of horizontal locomotion, with climbing being more expensive. On the other hand primates smaller than 0.5 kg exhibit statistically equivalent costs of climbing and horizontal locomotion.

Spatio-temporal characteristics—There were no significant contact time or step length differences between locomotor modes in each species, although most species tended to use longer contact times during climbing (Table 4). Additionally, during horizontal locomotion the relationship between step length and body mass increases with a slope of ~0.25 (Fig. 3), similar to the slope of 0.30 found by Kram and Taylor (1990). During climbing, however, the slope of this relationship is 0.047 (Fig. 3). This relationship between step length and body mass is not significant during horizontal locomotion or during climbing.

Cost coefficient—During both climbing and horizontal locomotion, the cost coefficient is essentially constant across body weight (Fig. 4). The mean cost coefficient during horizontal locomotion is 0.111 J N^{-1}(±0.050 s.d.), slightly less than that found by Kram and Taylor

(1990) for a wider range of body masses (mean cost coefficient of 0.183 J N^{-1}). During climbing, the mean cost coefficient is 0.148 J N^{-1} (±0.045 s.d.).

Effects of Loris tardigradus—The relationship between oxygen consumption rate and speed for the slender loris deviates from the rest of the sample dramatically (Table 2). Step length and contact time are related to speed, thus we examined these parameters in *L. tardigradus*. This species exhibits a relatively long step length and long contact time, previously reported by Hanna (2006) for climbing on a rigid pole. These long step lengths and contact times affect additional relationships in this study as well. If *L. tardigradus* were removed from the analysis of the effect of step length on climbing mechanics and energetics, step length increased regularly with body mass during climbing, but cost of transport still did not. The unusual position of the slender loris relative to other primates and the strong effect of step length on these data, as is discussed further below, highlights a clear relationship between limb length, contact time, muscle volume recruitment, and climbing energetics.

DISCUSSION

The goals of this study were three fold: 1) to test hypotheses about the scaling of the energetic cost of climbing with body mass in nonhuman primates, 2) to examine how this previous relationship compares to the cost of horizontal locomotion in primates, and 3) to examine the potential influence of limb movements (specifically step lengths) on metabolic costs.

It is worth noting, before moving deeper into the discussion, that in this study climbing animals were moving on a rope treadmill, which can influence results and data interpretation (e.g., van Ingen Schenau, 1980; Minetti et al., 1999; di Prampero et al., 2005). While moving on a treadmill, there is no net movement of the center of mass. Thus, no external work was accomplished during these experiments, either on the vertical or horizontal treadmill. On the other hand, the metabolic data collected here represent a measure of the energy cost required to accomplish internal work to maintain the position of the center of mass, and the external work required to move the center of mass relative to the substrate (maintain a steady position against the downward motion of the treadmill) (Minetti et al., 1999). As such, the data collected in this study may represent an underestimate of the true metabolic cost (and total work required) of climbing. This treadmill bias is certainly a very interesting topic and deserves further examination, but is beyond the scope of the current study. The discussion that follows incorporates an understanding of the limitations of treadmill-based studies of locomotion.

The results of this study suggest that: 1) unlike horizontal locomotion, the mass-specific cost of climbing does not consistently decrease with body mass at the same rate, 2) compared to horizontal locomotion, it is more costly for large primates to climb, and finally, 3) there are both theoretical and empirical reasons for arguing that spatio-temporal aspects of climbing help explain some portion of the cost of climbing. All of these are discussed in detail below.

These results support several previous ideas. First, data showing that cost of transport during climbing is constant across body mass (Fig. 2) support the idea that it costs the same amount of energy to lift 1 kg 1 m regardless of the body size of the organism (Hill, 1950; Taylor et al., 1972; Aiello, 1992; Elton et al., 1998). This is an important pattern to recognize and although this relationship has been described before, demonstrating it through studying the energetics of treadmill climbing is still valuable because climbing represents work done without options of energy saving mechanisms often involved in walking and running.

Second, the comparison between climbing and horizontal costs of locomotion support Taylor et al.'s (1972) argument that it is relatively more expensive for large animals to climb compared to smaller animals. The results presented here significantly expand the range of animals for which data are available and provide data during vertical climbing rather than incline locomotion. Finally, the data presented here combine metabolic cost data and data on kinematics. These data lead to new possibilities for further investigation. In this article, relying on theoretical and empirical data during walking (Roberts, 1998a,b) and running (Kram and Taylor, 1990) we raise the possibility that the length of the stride exhibited by primates with a high frequency of climbing in their repertoire has a strong effect on the costs of climbing.

Muscle recruitment volume and costs of climbing

These three conclusions lead to a deeper understanding of primate anatomy, behavioral choices, and locomotor evolution. For example, these data show that during hand-over-hand climbing large primates (and probably other animals as well) do not appear to use energy saving mechanisms, such as elastic energy storage (Alexander, 1977, 1980) or inverted-pendulum mechanics (Cavagna et al., 1977), that are available when moving horizontally. These mechanisms reduce muscular work needed to accelerate and decelerate the center of mass of larger animals. This is a factor that leads to a decreasing cost of horizontal locomotion (Fig. 2). Since these mechanisms are unavailable during vertical climbing, those costs are size invariant. Thus, it is very expensive (both absolutely, and relative to the horizontal cost of locomotion) for large primates to climb in a hand over hand manner compared to small primates. This pattern serves as a possible explanation for the observation that larger primates tend to spend more time moving on terrestrial supports compared to smaller primates (Table 1 in Gebo, 1996).

In addition to potentially climbing less often, large primates often use other forms of locomotion to ascend. Orthograde suspensory locomotion (Hunt et al., 1996), certain forms of which may take advantage of pendulum mechanics and potentially conserve energy (Parson and Taylor, 1977; Bertram et al., 1999; Chang et al., 1997, 2000), can be used to ascend. Additionally, pulse climbing (Hunt et al., 1996), is commonly used by cercopithecids (Hunt, 1992; DeSilva, 2008) and may offer elastic energy savings to primates that utilize it.

The constant energy consumption across body mass in primates reported in this study raises interesting questions that relate to gait characteristics and muscle volume recruitment. The consideration of how stride time and muscle volume recruitment effect climbing costs is based on theoretical and empirical work collected on nonprimate mammals. Several lines of evidence lead us to argue that muscle volume recruitment will change with size and substrate orientation. For example, during incline locomotion, and presumably climbing, some studies have found that the rate of force production is increased relative to that during horizontal locomotion (Roberts et al., 1997; Wickler et al., 2005). The rate of force production is influenced in part by step length or contact time. On the other hand, other studies have found that shortening velocities decrease between horizontal and incline locomotion (McGuigan et al., 2009) and others have found that contraction velocity does not increase even under loaded conditions (McGowan et al., 2006). Therefore, since contact time was not significantly different between horizontal locomotion and climbing in each species in this study, it is possible that contraction velocities are not increased during climbing (although there is a definite trend toward increased contact time in the smaller species). However, it is well accepted that muscles increase work production during incline locomotion compared to horizontal locomotion (Roberts et al., 1997; Daley and Biewener, 2003; Galbaldon et al., 2004; Higham et al., 2008; McGuigan et al., 2009), although the proximate cause of the increased work is under debate (e.g., increased force production or

increased strain). We do not have the data to speculate how work may or may not be increased between horizontal locomotion and climbing in this study. But, since there are no significant changes in contact time (although all species trended towards an increase in contact time), the difference in metabolic cost between locomotor modes within species must be explained by differential muscle force production and/or muscle volume recruitment. Thus, we predict that large primates in this study recruit a greater mass-specific volume of muscle during climbing compared to during horizontal locomotion, and that this phenomenon is the proximate cause of the grater mass-specific energy cost in large primates during climbing.

Loris tardigradus

In addition to the differences that large primates must be experiencing, we also suggest that *Loris tardigradus* presents a special case during both horizontal locomotion and climbing in terms of how muscles are consuming energy. Lorises have relatively long limbs and this appears to translate into long muscle fibers relative to other primates (Hanna, unpublished data). Because *L. tardigradus* uses such long contact times during both horizontal locomotion and climbing, their rate of force production should be much lower than other small primates. Thus, we should expect to see *L. tardigradus* utilize less energy than *C. medius* and possibly even *N. pygmaeus*. As indicated by Figure 2, however, *L. tardigradus* uses approximately the predicted amount of mass-specific energy during horizontal locomotion and a similar mass-specific energy during climbing as other species. Thus, *L. tardigradus* does not appear to gain any energetic benefit due to slower rates of muscle contraction.

Previous work on horizontal locomotion has revealed principles which support this hypothesis. For example, Roberts et al. (1998b) have shown that turkeys and dogs produce similar forces and consume the same amount of energy to run (Roberts et al., 1998b). Turkeys, however, use a larger volume of muscle to run than dogs, despite the fact that turkeys and dogs recruit a similar cross-sectional area of muscle. Roberts et al. explained this phenomenon as being due to the longer muscle fibers of turkeys. The similar energy consumption phenomenon between turkeys and dogs was explained as the "greater volume [of muscle] appears to offset the economy of slower rates of force generation" (Roberts et al., 1998b; p 2753). We suggest a similar mechanism is at work during both horizontal locomotion and climbing in *Loris tardigradus*, such that the mass-specific volume of muscle recruited offsets any differential economy that these primates get due to slower contraction velocities. This potential relationship between metabolic cost and muscle recruitment volume remains speculative but fits the data presented here and theoretical expectations. Further study with electromyography data would be necessary to test these hypotheses.

Climbing and primate origins

In addition to adding to our understanding of metabolic constraints on climbing in primates and opening up new areas for research, the data presented here also have bearing on the pathways of primate locomotor evolution. The origin of primates has long been associated with the exploitation of a complex three-dimensional arboreal environment with thin flexible branches (Jenkins, 1972; Cartmill, 1972, 1994; Lemelin, 1999; Lemelin and Schmitt, 2007). If this represents a significant adaptive shift for early primates, one might speculate that this shift was associated with significant costs because of the increased amount of climbing added to the locomotor repertoire of basal primates. However, the data presented here suggests that if this shift occurred at a small body size, then there would be no increased metabolic cost by adding climbing to their locomotion. Thus, at a small size early primates could easily expand the range of areas in which they moved and foraged allowing them to exploit a potentially open ecological niche. We do not know how large early primates were

and this remains an area of healthy debate. There is considerable reason to argue that early primates were small and spent time moving and foraging on thin flexible (Jenkins, 1972; Cartmill, 1972, 1994; Kay and Cartmill, 1977; Lemelin, 1999). This is consistent with the size of other early arboreal mammals including plesiadapiformes (Bloch et al., 2007; Silcox et al., 2007). However, arguments by Soligo and Martin (2006) regarding claw loss in the primate lineage suggest that early primates may have been larger (as much as 1,000 g). In the latter case it does seem that additional climbing would raise overall metabolic costs for early primates. Offsetting such costs in a relatively large primate ancestor would have required an increase in caloric intake from either new food sources or more food volume that would perhaps be available in this arboreal niche. However, if the early primate ancestors were small it is not necessary to invoke a model that requires increased caloric intake. The initial entry into the arboreal milieu could have been achieved with no increases in the costs of locomotion.

Acknowledgments

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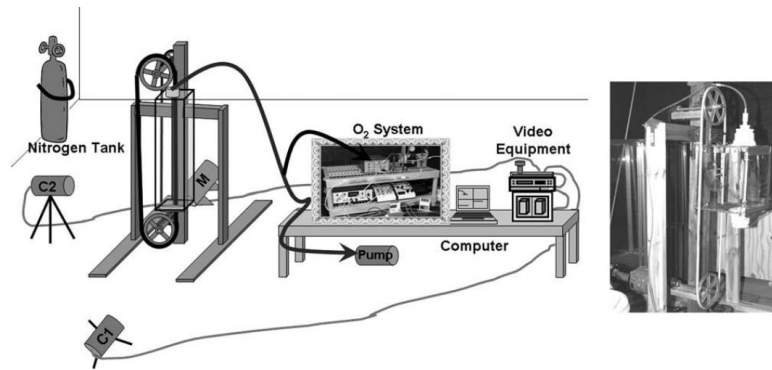
Fig. 1.
A schematic of the setup with a treadmill and oxygen analysis system. O_2 system indicates the oxygen analysis electronics. Air was drawn through the metabolic chamber, out the top past the subject's head, and into the oxygen analysis system. The oxygen analysis equipment fed data into the laptop computer. During the trial the four channels are displayed on the laptop screen while data are being recorded. *M* indicates the variable speed motor used to run the treadmill, and C1 and C2 indicate the video cameras. Video equipment consisted of, from top to bottom, a video mixer, a VCR, and a TV. Video data were fed into the mixer such that the two views were displayed side by side on the TV. Data from the mixer were fed into the VCR, and then from the VCR into the TV to ensure the image on the TV was the exact same as that being recorded. Photo shows a *L. tardigradus* climbing in the metabolic chamber.
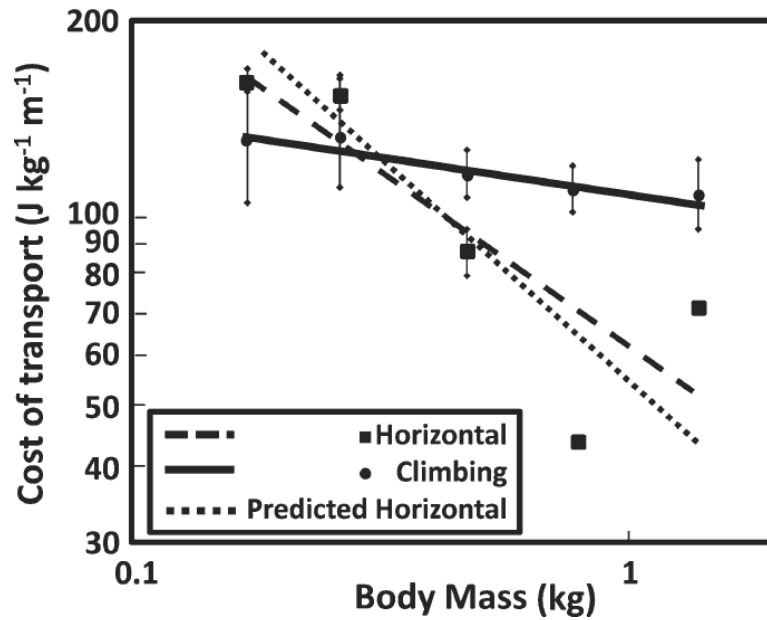
Fig. 2.
Graph of the cost of transport compared to body mass during horizontal locomotion and during climbing. The regression equation best describing COT_{horiz} is $COT_{Horiz} = 51.5M_b{}^{-0.750}$ ($r = 0.843$; $P = 0.073$); the regression equation best describing the cost of climbing is $COT_{climb} = 107.4M_b{}^{-0.119}$ ($r = 0.858$; $P = 0.063$) (Hanna et al., 2008). Note that neither slope is significant, probably due to the small sample size. The predicted COT_{horiz} line of best fit was added in for comparison purposes. The predicted COT_{horiz} was calculated for each individual using the equation: $V_{O2}/M_b = 0.300M_b{}^{-0.303} + 0.533M_b{}^{-0.316}V$, from Taylor et al. (1982). Speeds and body mass were those observed in this study. Note that the actual COT_{horiz} line of best fit is very similar to the predicted COT_{horiz}.
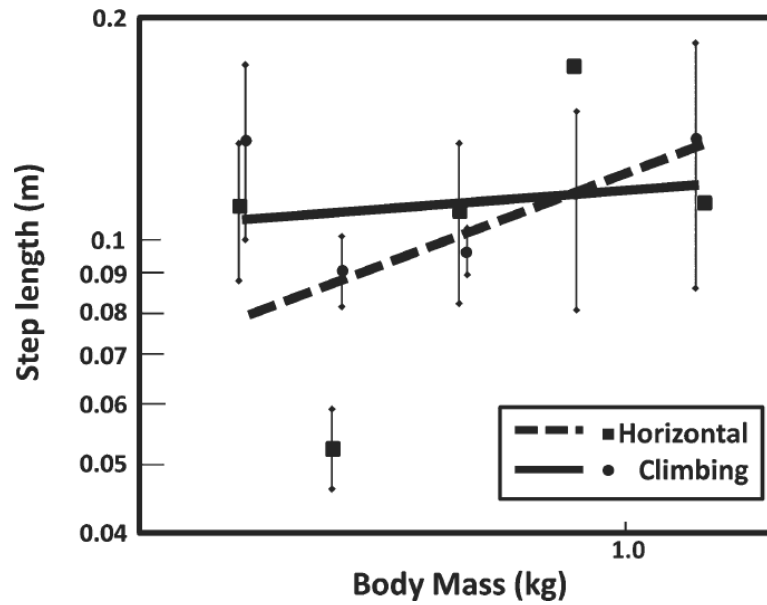
Fig. 3.
Graph of step length versus body mass during horizontal locomotion and climbing. Each point represents a species mean, and the lines represent ± 1 standard deviation. The data are plotted on log-log axes because Kram and Taylor (1990) found a linear relationship between these two variables when logged. The equation for horizontal locomotion is: $\log Lc_{Horiz} = -0.907 + 0.24 \log M_b$ where Lc_{Horiz} is step length and M_b is body mass. Although the slope of the line for horizontal locomotion is 0.245, close to the value of 0.30 found by Kram and Taylor (1990), the slope is not significantly different from zero ($P\ 5\ 0.403$). The equation for climbing is: $\log Lc_{Climb} = -0.937 + 0.047 \log M_b$ where Lc_{climb} is step length and M_b is body mass.
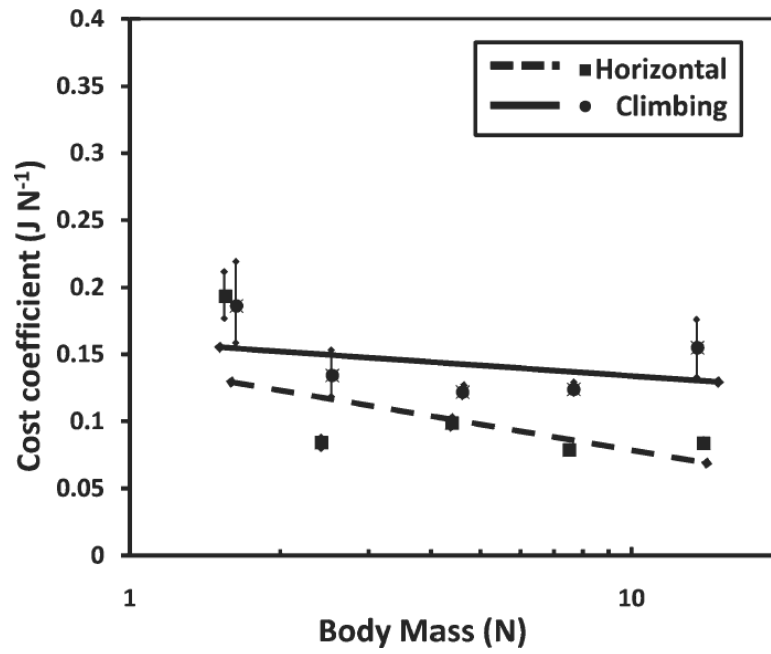
Fig. 4.
Graph illustrating the constant relationship between the cost coefficient and body mass during horizontal locomotion and climbing. Each box represents a species mean and the bars indicate ± one standard deviation. Notice that the slopes of both comparisons are almost zero (−0.083 and 0.019; horizontal locomotion and climbing, respectively).

TABLE 1

Sample size (i.e., number of experiments during which valid data were collected) for climbing metabolic rate (MR), cost of transport (COT), and speed ranges utilized during climbing, for each individual and species (body mass in kilograms)

Species	Climbing MR (N)	COT$_{climb}$ (N)	Speed$_{climb}$ max-min (m s^{-1})	Horizontal MR (N)	COT$_{horiz}$ (N)	Speed$_{horiz}$ max-min (m s^{-1})
L. tardigradus	16	12	0.114–0.041	8	8	0.092–0.045
A (0.157)	7	5	0.081–0.041	2	6	0.076–0.060
B (0.172)	4	2	0.072–0.071	NA	NA	NA
C (0.171)	5	5	0.114–0.068	6	2	0.092–0.045
C. medius	18	16	0.112–0.042	14	13	0.114–0.043
A (0.241)	6	4	0.076–0.042	5	5	0.072–0.047
B (0.276)	4	4	0.111–0.076	4	4	0.071–0.043
C (0.260)	8	8	0.112–0.049	5	4	0.114–0.053
N. pygmaeus	9	9	0.079–0.047	8	8	0.076–0.049
A (0.447)	5	5	0.079–0.053	4	4	0.076–0.060
B (0.492)	4	4	0.067–0.047	4	4	0.073–0.049
S. boliviensis	8	8	0.213–0.152	4	4	0.334–0.231
A (0.744)	4	4	0.188–0.152	NA	NA	NA
B (0.821)	4	4	0.213–0.158	4	4	0.334–0.231
E. mongoz	9	9	0.157–0.110	4	4	0.160–0.140
A (1.340)	2	2	0.151–0.135	4	4	0.160–0.140
B (1.346)	5	5	0.157–0.110	NA	NA	NA
C (1.460)	2	2	0.123–0.117	NA	NA	NA

TABLE 2

Pearson product-moment correlation coefficients and significance values of oxygen consumption rate (ml O_2 $kg^{-1} s^{-1}$) compared to speed (m s^{-1})

Species	Pearson product-moment$_{climb}$	Significance values$_{climb}$	Pearson product-moment$_{horiz}$	Significance values$_{horiz}$
L. tardigradus	**0.71**	**0.01**	**0.933**	**0.001**
C. medius	0.391	0.134	0.366	0.242
N. pygmaeus	−0.08	0.838	0.737	0.037
S. boliviensis	0.434	0.283	0.948	0.051
E. mongoz	0.548	0.126	0.070	0.930

Bold values indicate significance at an alpha level of equal to or less than 0.05, after sequential Bonferroni adjustment.

TABLE 3

Mean cost of transport for climbing compared to horizontal locomotion (J kg^{-1} m^{-1}), by species, ±1 standard deviation (SD)

Species	COT$_{climb}$ (±SD)	COT$_{horiz}$ (±SD)	COT ratio[a]	T-test probability[b]
L. tardigradus	131.64 (26.17)	159.79 (0.37)	1 (0.82)	0.125
C. medius	134.97 (26.99)	156.23 (8.31)	1 (0.86)	0.2989
N. pygmaeus	110.48 (9.48)	86.94 (7.60)	1 (1.27)	0.019
S. boliviensis	104.60 (8.28)	43.81 (15.12)[c]	2.39	**0.001**
E. mongoz	109.10 (14.08)	71.17 (9.97)[c]	1.27	**0.001**

[a]COT ratio is COT$_{climb}$/COT$_{horiz}$. Ratio is indicated as 1 if the *t*-test was not significant, although the calculated ratio is given in parentheses.

[b]Bold values indicate significance after sequential Bonferroni adjustment. Degrees of freedom were based on the number of subjects for each species.

[c]Data were collected for only one subject during horizontal locomotion. Thus the standard deviation and degrees of freedom are calculated based on the number of experiments for that subject.

TABLE 4

Comparison of mean contact time (in seconds) and step length (in meters) for each species during horizontal locomotion and during climbing

Species	Contact time$_{horiz}$ (±SD)	Contact time$_{climb}$ (±SD)	T-test probability[a]	Step length$_{horiz}$ (±SD)	Step length$_{climb}$ (±SD)	T-test probability[a]
L. tardigradus	1.687 (0.253)	1.841 (0.172)	0.5787	0.112 (0.025)	0.136 (0.035)	0.5471
C. medius	0.835 (0.024)	1.228 (0.295)	0.1497	0.052 (0.007)	0.090 (0.010)	0.0564
N. pygmaeus	1.661 (0.275)	1.714 (0.278)	0.8657	0.110 (0.026)	0.096 (0.007)	0.3194
S. boliviensis	0.593 (NA)[b]	0.615 (0.132)	NA	0.172 (NA)[b]	0.116 (0.035)	NA
E. mongoz	0.740 (NA)[b]	1.028 (0.367)	NA	0.113 (NA)[b]	0.137 (0.052)	NA

SD indicates 1 standard deviation.

[a]No comparisons were significant after sequential Bonferroni adjustment. Degrees of freedom were based on the number of subjects for each species.

[b]Data were collected for only one subject during horizontal locomotion. Thus the standard deviation and degrees of freedom are calculated based on the number of experiments for that subject.