

RESEARCH ARTICLE

Determinants of climbing energetic costs in humans

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ABSTRACT

Previous studies in primates and other animals have shown that mass-specific cost of transport ($\text{J kg}^{-1} \text{m}^{-1}$) for climbing is independent of body size across species, but little is known about within-species allometry of climbing costs or the effects of difficulty and velocity. Here, we assessed the effects of velocity, route difficulty and anatomical variation on the energetic cost of climbing within humans. Twelve experienced rock climbers climbed on an indoor wall over a range of difficulty levels and velocities, with energy expenditure measured via respirometry. We found no effect of body mass or limb proportions on mass-specific cost of transport among subjects. Mass-specific cost of transport was negatively correlated with climbing velocity. Increased route difficulty was associated with slower climbing velocities and thus higher costs, but there was no statistically significant effect of route difficulty on energy expenditure independent of velocity. Finally, human climbing costs measured in this study were similar to published values for other primates, suggesting arboreal adaptations have a negligible effect on climbing efficiency.

KEY WORDS: Rock climbing, Energetics, Cost of transport

INTRODUCTION

The energetic cost of vertical climbing is critical in understanding the ecological strategies and evolutionary pressures acting on species that forage or sleep in trees and cliffs. In principle, energy allocated to locomotion cannot be apportioned to other fitness-promoting tasks such as reproduction, growth and somatic maintenance. For species that climb often, we might expect selection for behavioral or anatomical strategies to minimize climbing costs. However, while climbing energetics have been investigated in several comparative interspecific studies (e.g. Taylor et al., 1972; Full and Tullis, 1990; Hanna, 2006; Hanna et al., 2008; Hanna and Schmitt, 2011; Pontzer, 2016), few have examined the determinants of climbing cost within species, the domain in which natural selection occurs. Here, we investigated the determinants of climbing cost within a human sample.

Body size and proportions

When moving vertically, mechanical work, W , is required to raise the center of mass against gravity. Specifically, $W=Mgh$, where M is body mass (kg), g is the gravitational constant (9.81 m s^{-2}) and h is the height climbed (m). Several studies have assessed the efficiency

of climbing, defined as the ratio of W/E , where E is the metabolic energy (J) (Hanna, 2006; Hanna et al., 2008; Pontzer, 2016). These studies suggest that climbing efficiency is relatively constant at approximately 10% across a range of species, regardless of differences in body size or postcranial anatomy (e.g. Hanna, 2006; Hanna et al., 2008; Pontzer, 2016).

The similarity in efficiency across species indicates that the absolute cost of climbing (J m^{-1}) increases linearly with body mass while the mass-specific cost of transport, COT ($\text{J kg}^{-1} \text{m}^{-1}$), is independent of body size. For example, Taylor et al. (1972) compared the cost of uphill running in mice and chimpanzees and found that the mass-specific cost of ascent was the same for both taxa. Hanna and colleagues (2008), in a study of five non-human primate taxa trained to climb on vertical rope-mills, reported a non-significant trend for decreasing COT with body size, with COT scaling with $M^{-0.12 \pm 0.13}$ ($P=0.06$). In both studies, however, the lack of a statistically significant allometric relationship may reflect a modest allometric effect and the relatively restricted range of body sizes analyzed. Pontzer (2016), using a broader range of species and body size (from cockroaches to humans), found a similar allometric trend, with climbing COT scaling with $M^{-0.16 \pm 0.02}$ ($P<0.001$).

The effects of body proportions and postcranial adaptations on climbing costs have been less studied. Longer forelimbs are often interpreted as adaptations for arboreal locomotion (e.g. Fleagle, 1981; Preuschoft and Witte, 1991) and some biomechanical models suggest that an increase in arm length results in a decrease in external force on the forelimbs when climbing vertically (Cartmill, 1974; Fleagle et al., 1981; Preuschoft and Witte, 1991). If longer arms decrease the muscle forces required to maintain position on a vertical substrate, they may in turn reduce climbing COT, but the relationship between arm length and climbing costs has not been assessed.

Within the rock-climbing community, it is generally thought that a climber's 'ape index', the ratio of arm span to standing height, is positively correlated to climbing ability (Kidd et al., 2009). However, there is no significant difference in arm length between recreational climbers and non-climbers (Grant et al., 1996; Mermier et al., 2000). Further, two studies have reported a negative correlation between ape index and climbing performance (Mermier et al., 2000; Magiera et al., 2013). The relationship between climbing energetic costs and limb proportions has not been directly evaluated.

Difficulty and velocity

The effects of climbing velocity and difficulty on the energy costs of climbing are also understudied. One practical challenge to such investigations is establishing a reliable and comparable method for determining route difficulty. In rock climbing, difficulty is often rated by expert consensus with one of several widely used rating systems, such as the Yosemite Decimal System (YDS) (Kidd et al., 2009). Difficulty is affected by myriad factors, including the distance between holds, the size and shape of holds, and the angle of the wall. The effect of difficulty on climbing COT is unclear. The

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limited previous work on climbing difficulty and cost has suggested that more difficult climbs may be more costly, but these studies could not rule out effects of climber experience or the rate of ascent (Mermier et al., 1997; Bertuzzi et al., 2007). Sheel and colleagues (2003) measured the energy cost of self-rated 'easy' and 'hard' climbs for elite sport climbers and found a roughly ~10% increase in mean cost for the more difficult route. However, ascent velocities and routes varied considerably among subjects, making it difficult to isolate the factors affecting cost.

The rate of ascent (m s^{-1}), or climbing velocity, may affect the determination of climbing cost in one of two ways. First, greater climbing velocities could require faster, less efficient muscle contractions (Alexander, 1997) or impart some other mechanical or physiological effect on climbing COT. These effects would likely be observed as decreases in efficiency. Such velocity effects on climbing COT have not been examined.

Second, in climbing as with any locomotor mode, velocity will affect cost if resting or postural costs are included in the calculation of COT. As Taylor and colleagues (1982) noted in their classic comparative study of running energetics, the rate of energy expenditure during locomotion, hereafter the cost of locomotion, COL ($\text{J kg}^{-1} \text{s}^{-1}$), generally increases with locomotor velocity. Resting costs (J s^{-1}) are usually subtracted to give the net COL, hereafter COL_{net}. COT is typically calculated from COL_{net} either as the slope of the COL versus velocity trendline or by dividing COL by velocity. These two approaches give different values for COT if the intercept of the COL_{net} versus velocity relationship, termed the postural cost of locomotion, is greater than 0. The slope method is analytically convenient because it gives a value of COT, hereafter COT_{slope}, that is independent of velocity, but it ignores the postural cost of locomotion, which can be substantial. In contrast, dividing COL by velocity gives a value of COT, hereafter COT_{net}, that decreases in a semi-log manner with velocity, approaching an asymptote equal to COT_{slope}.

During running and other high-velocity locomotor modes, the difference between COT_{slope} and COT_{net} is relatively small and might be safely ignored. In climbing, which occurs at slower velocities, postural costs may represent a substantial portion of cost. From an evolutionary or ecological perspective, the postural cost of climbing, and thus climbing velocity, may be a salient aspect of climbing performance and cost.

Study approach

In this study, we investigated the effects of body size, limb length, route difficulty and velocity on vertical climbing costs in a sample of adult human rock climbers. Given results of previous studies (e.g. Hanna, 2006; Hanna et al., 2008; Booth et al., 1999; Taylor et al., 1972), we predicted that COL_{net} would increase linearly with velocity, but be independent of body mass. We explored the effect of arm length and route difficulty to test whether longer arms reduce climbing costs and whether greater difficulty increases costs. Finally, we examined postural cost and the effects of different analytical approaches for calculating COL and COT.

MATERIALS AND METHODS

Subjects

Twelve healthy, experienced rock climbers (9 men and 3 women) participated in this study. Institutional Review Board approval (Hunter College: 2015-0438) was obtained prior to the study, and each subject provided informed consent prior to participating. Anthropometric data including body mass, height, leg length (measured from greater trochanter to ground when subject is standing) and arm length (measured from acromion to ulnar styloid process), were all collected prior to climbing trials (Table 1). We calculated intermembral index (IMI) as the ratio of arm length to leg length and arm/height as the ratio of arm length to height. Subjects were categorized based on their self-reported experience levels from 1 (least experienced) to 3 (most experienced). Subjects were asked to refrain from eating or drinking (other than water) for 4 h prior to participation, but compliance was not verified.

Respirometry

The metabolic cost of climbing was measured using a wearable respirometry system (Cosmed k4b2). The climbers were fitted with a lightweight plastic mask covering the mouth and nose. The mask held an internal turbine to measure the flow rate of expired air and was connected to a sensor that was worn in the middle of the subject's back with a lightweight harness. The unit measured both oxygen consumption (\dot{V}_{O_2} , l min^{-1}) and carbon dioxide production (\dot{V}_{CO_2} , l min^{-1}) to calculate mass-specific metabolic rate, MR ($\text{J kg}^{-1} \text{s}^{-1}$). All participants underwent measurement of standing metabolic rate prior to climbing trials. They stood at rest for 5 min while wearing the respirometry system to collect baseline energetic expenditure data.

Table 1. Subject data

Male/female	Subject	Self-reported experience	Age (years)	Mass (kg)	Height (cm)	Arm length (cm)	Leg length (cm)	IMI	Arm/height	MR _{stand} ($\text{J kg}^{-1} \text{s}^{-1}$)	Mean velocity (m s^{-1})	Mean COL _{net} ($\text{J kg}^{-1} \text{s}^{-1}$)
Female	K3	2	25	53.7	152	51	75	68	0.34	1.77	0.14	14.08
Female	K5	1	26	61.6	165	58	85	68	0.35	1.76	0.19	11.76
Female	K7	2	32	64.8	155	53	82	65	0.34	1.82	0.15	10.52
Mean±s.d.		1.67±0.58	28±4	60.0±5.7	157±7	54±4	81±5	67±2	0.34±0.01	1.78±0.03	0.15±0.04	12.12±1.80
Male	K10	1	25	83.9	180	63	93	68	0.35	1.61	0.16	11.63
Male	K12	3	47	85.2	175	62	92	67	0.35	2.44	0.13	8.26
Male	K13	1	24	76.5	175	62	91	68	0.35	2.01	0.15	11.20
Male	K14	3	39	73.5	184	65	97	67	0.35	1.27	0.13	10.62
Male	K2	2	38	96.2	178	64	93	69	0.36	2.28	0.19	13.88
Male	K4	1	38	83.1	174	60	86	70	0.34	2.78	0.15	12.50
Male	K6	3	22	64.4	165	56	84	67	0.34	3.57	0.17	14.34
Male	K8	3	38	80.3	180	63	92	68	0.35	1.56	0.18	15.26
Male	K9	3	41	77.5	168	59	81	73	0.35	1.81	0.17	12.62
Mean±s.d.		2.22±0.97	35±9	80.1±8.8	175±6	62±3	90±5	69±2	0.35±0.01	2.15±0.71	0.16±0.02	12.26±2.13

IMI, intermembral index (ratio of arm length to leg length); arm/height, ratio of arm length to height; MR_{stand}, standing metabolic rate; COL_{net}, net cost of locomotion. Self-reported experience levels ranged from 1 (least experienced) to 3 (most experienced).

Climbing trials

Climbing trials took place at an indoor climbing gym (Gravity Vault, Chatham, NJ, USA) on a vertical (90 deg) wall with no overhangs or ledges. The section of the wall used was 2 m wide and 9.5 m high and included three routes set by experienced gym route setters and graded as 5.6 (easy), 5.8 (intermediate) and 5.10 (difficult) using the YDS (Kidd et al., 2009). The climbers wore their own light clothing, typically a short-sleeved t-shirt and shorts, and their personal climbing harness and climbing shoes during trials.

Climbers' safety was maintained by top-rope belay, common in rock climbing and familiar to the subjects. A safety rope extends from the climber's harness upward through an anchor at the top of the climb and then back down to a trained belayer on the ground (Kidd et al., 2009). Ascent by the climber creates slack in the rope, which is pulled in by the belayer through a braking device. The rope offers no upward assistance to the climber but prevents them from falling to the ground in the event of a fall while climbing. When the climber reaches the top of the climb, they release themselves from the wall and are lowered back to the ground as the belayer feeds out rope.

Each climbing trial was conducted for a minimum of 4 min (mean \pm s.d. 4.62 ± 0.93 min, range 4.26–8.41 min) in order to attain steady-state aerobic energy expenditure. For each trial, subjects climbed 4–6 laps on a given route in rapid succession. Climbers were lowered quickly between climbs (mean \pm s.d. 11.4 ± 2.5 s, range 4–20 s), to minimize breaks and to maximize the proportion of the trial spent climbing. The proportion of time being lowered (i.e. not climbing) varied between 8.2% and 24.4% of trial time (mean \pm s.d. $14.8 \pm 3.18\%$; Table S1). We visually inspected the data to confirm that the brief climbing pauses during lowering did not have an apparent effect on \dot{V}_{O_2} or \dot{V}_{CO_2} (Fig. 1). The final portion (1–2 min) of steady-state expenditure (kcal min^{-1}) was used for analyses.

The trial order was determined as follows. First, each participant climbed three trials on the YDS 5.6 route: one at their self-selected 'normal' velocity, one at a self-selected slower velocity, and one at a self-selected faster velocity. A 2 min break was taken between each trial. The 'normal' velocity trial was always conducted first. Half of the subjects were randomly assigned to perform the 'slow' trial second, whereas the other half performed the 'fast' trial second. A 4 min rest was taken at the conclusion of the YDS 5.6 route trials. Next, participants climbed one trial of the YDS 5.8 route at a self-selected 'normal' velocity. After another 4 min break, participants climbed one trial of the YDS 5.10 route at a self-selected 'normal'

velocity. In total, participants climbed five trials (three YDS 5.6 trials, one YDS 5.8 trial and one YDS 5.10 trial), and each trial consisted of 4–6 laps. Five participants were unable to complete the YDS 5.10 trial because of fatigue.

Respiratory exchange ratio

In 29 trials, the respiratory exchange ratio, RER (\dot{V}_{CO_2} produced/ \dot{V}_{O_2} consumed), exceeded 1.00, indicating some reliance on anaerobic respiration (Table S1). Studies of locomotor energetics often use RER >1.0 as an exclusion criterion for trials, with the concern being that the inclusion of any anaerobic respiration will negate measurement accuracy. Certainly, when energy expenditure is predominantly anaerobic, and metabolic demand exceeds the maximal rate of oxygen consumption, $\dot{V}_{O_{2,max}}$, O_2 consumption and CO_2 production cease to provide accurate measures of energy expenditure. However, graded exercise tests, in which the enforced workload increases in a stepwise fashion while O_2 consumption and CO_2 production are measured, clearly show that O_2 consumption and CO_2 production continue to increase in a linear manner with workload as RER rises well above 1.00 (Issekutz et al., 1962; Wasserman et al., 1973; Caiozzo et al., 1982; Edvardsen et al., 2014). Early work by Issekutz and colleagues (1962) showed that \dot{V}_{O_2} continues to increase linearly with workload up to a RER of ~ 1.15 . More recently, Edvardsen and colleagues (2014) reported a constant, linear increase in \dot{V}_{O_2} and energy expenditure with graded exercise up to a ceiling of RER of ~ 1.15 for inclined treadmill tests (Fig. S1). Further, two recent reviews of $\dot{V}_{O_{2,max}}$ criteria in humans (Nelson et al., 2010; Edvardsen et al., 2013) report mean values of RER ≥ 1.20 at $\dot{V}_{O_{2,max}}$ for men and women aged 20–50 years. We note that RER exceeded 1.20 in 3 of the trials in this dataset.

We examined the relationship between COL_{net} and climbing velocity, a measure of mechanical power output, for each subject. These variables were strongly correlated (mean $r^2 = 0.86$, range 0.58–0.98), and no subject exhibited decreased COL_{net} (which would indicate substantial anaerobic respiration) at their highest velocities or highest RER. To formally test for an effect of RER in our sample, we examined RER as a continuous variable in a linear mixed effect (LME) model, with COL_{net} as the dependent variable, velocity and RER as fixed effects, and subject as a random effect. In these analyses, RER was not a significant factor in determining COL_{net} (model coefficient \pm s.e. 0.6135 ± 2.1619 , $P = 0.78$). Finally, we repeated this analysis with RER as a categorical fixed effect (greater or less than 1.05), and again found no effect of RER (0.6805

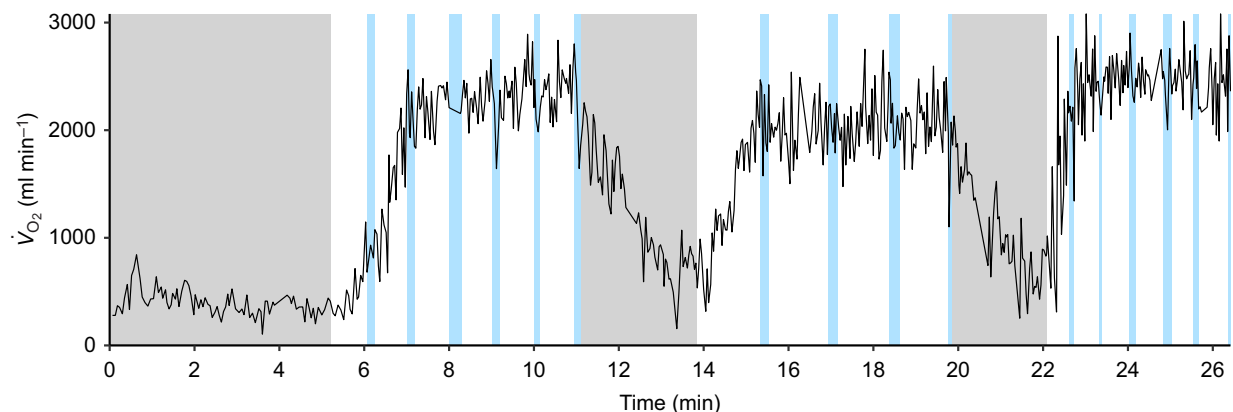


Fig. 1. Oxygen consumption during the trial. Sample trace of oxygen consumption rate (\dot{V}_{O_2}) over a set of three climbing trials at self-selected normal, slow and fast velocity in one rock-climbing participant. Gray background indicates rest periods. White/blue background indicates climbing trials; white indicates periods of ascent, blue indicates roped lowering (i.e. not climbing).

± 0.3753 , $P=0.08$). COL_{net} for trials with $RER>1.05$ trended higher, which is the opposite direction of the expected effect on COL_{net} if a substantial proportion of energy were being supplied anaerobically. We therefore concluded that the anaerobic contribution to energy expenditure in this sample was negligible and included all trials in analyses of cost. We note, however, that excluding trials with $RER>1.05$, a conservative criterion, does not affect the pattern of results reported below.

Kinematic data

For each trial, one vertical route was recorded at 30 frames s^{-1} with a Casio Exilim FX 1 camera and analyzed with the open source program Kinovea (www.kinovea.org). Contact time is the length of time for which a limb is in contact with the ground (stance phase) within one stride (Biewener, 2003). In quadrupedal animal locomotion, contact time is often measured for one representative limb such as the rear left limb (e.g. Kram and Taylor, 1990; Hanna and Schmitt, 2011; Schoonaert et al., 2016). During rock climbing trials, contact time varied significantly between different limbs and strides. In addition, because of camera placement and climbing style, there was some variation in which limbs were visible, and whether or not it was possible to measure contact time. Therefore, we measured contact time for all visible strides of each of the four limbs. For each trial, we computed the mean of pooled contact times across all four limbs and report the inverse of this mean (t_c^{-1} in s^{-1} ; Table S1). These values were used in further analyses.

Analyses

We defined MR_{stand} ($J\ kg^{-1}\ s^{-1}$) as the mass-specific metabolic rate of each participant's standing trial. For each climbing trial, we used the metabolic rate recorded during the trial, MR_{trial} , to calculate COL_{net} and COT_{net} as:

$$COL_{net} = MR_{trial} - MR_{stand}, \quad (1)$$

$$COT_{net} = COL_{net} v^{-1}, \quad (2)$$

where v is climbing average velocity ($m\ s^{-1}$) including both ascent and delay time.

We calculated two efficiency measures. We first calculated Eff_{slope} as the mass-specific work performed per meter, which simplifies to g , divided by the mass-specific metabolic energy expended per meter excluding postural costs, COT_{slope} . Second, we calculated Eff_{net} as the ratio of g to COT_{net} . Eff_{net} includes the postural cost of climbing, whereas Eff_{slope} does not.

$$Eff_{slope} = g COT_{slope}^{-1}, \quad (3)$$

$$Eff_{net} = g COT_{net}^{-1}. \quad (4)$$

To determine the effects of mass, difficulty and arm length on cost, we examined each variable as a fixed effect in a linear mixed effects model with COL_{net} as the dependent variable, velocity as a fixed effect and subject as a random effect. Statistical analyses were carried out in R (<http://www.R-project.org/>) using the *lmer()* function in the lme4 package. This approach was chosen because COL_{net} increases in a linear manner with velocity, and because COT and efficiency are derivatives of COL_{net} . Best models were evaluated using the *anova()* function, based on a log-likelihood ratio test. As true R^2 (coefficient of determination) cannot be calculated in LME models, model fit was evaluated using the conditional (R^2c) and marginal (R^2m) coefficients of determination in the R package MuMIn. R^2m assesses fits using only the fixed variables, whereas conditional fits R^2c include random and fixed

factors. Thus, an increase in R^2m , without a concurrent increase in R^2c , indicates some of the explanatory power of random effects is being subsumed into fixed effects. Throughout this text, means are

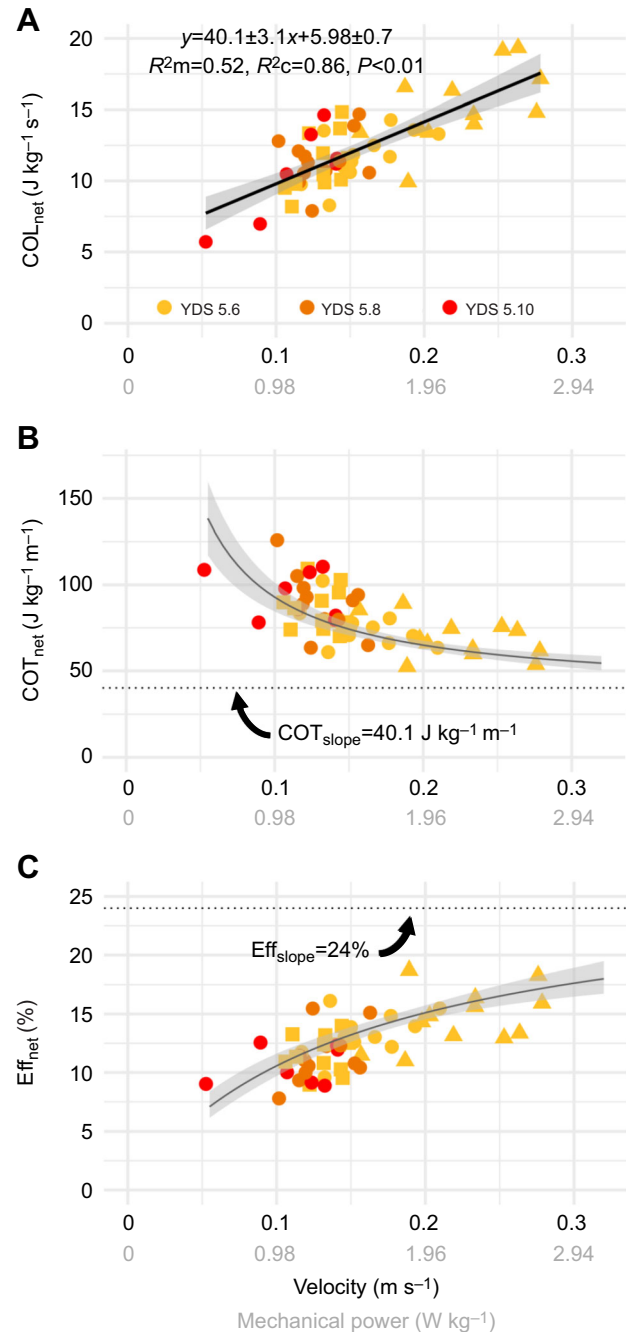


Fig. 2. Effect of velocity on climbing costs. (A) Net cost of locomotion (COL_{net}), (B) net cost of transport (COT_{net}) and (C) net efficiency (Eff_{net}) as a function of climbing velocity. Black line and grey shading represent the predicted value and 95% confidence interval for (A) COL_{net} , (B) COT_{net} and (C) Eff_{net} based on the linear model of COL_{net} as a function of velocity. Conditional (R^2c) and marginal (R^2m) coefficients of determination are shown. Symbols represent velocity categories (circles, normal velocity; squares, slow velocity; triangles, fast velocity); colors indicate route difficulty according to the Yosemite Decimal System (YDS: 5.6, easy; 5.8, intermediate; and 5.10, difficult). The horizontal line in B depicts COT_{slope} , the COT that is independent of velocity. The horizontal line in C depicts Eff_{slope} , the efficiency calculated from COT_{slope} . Gray horizontal axis values are mechanical power and are equal to velocity multiplied by g .

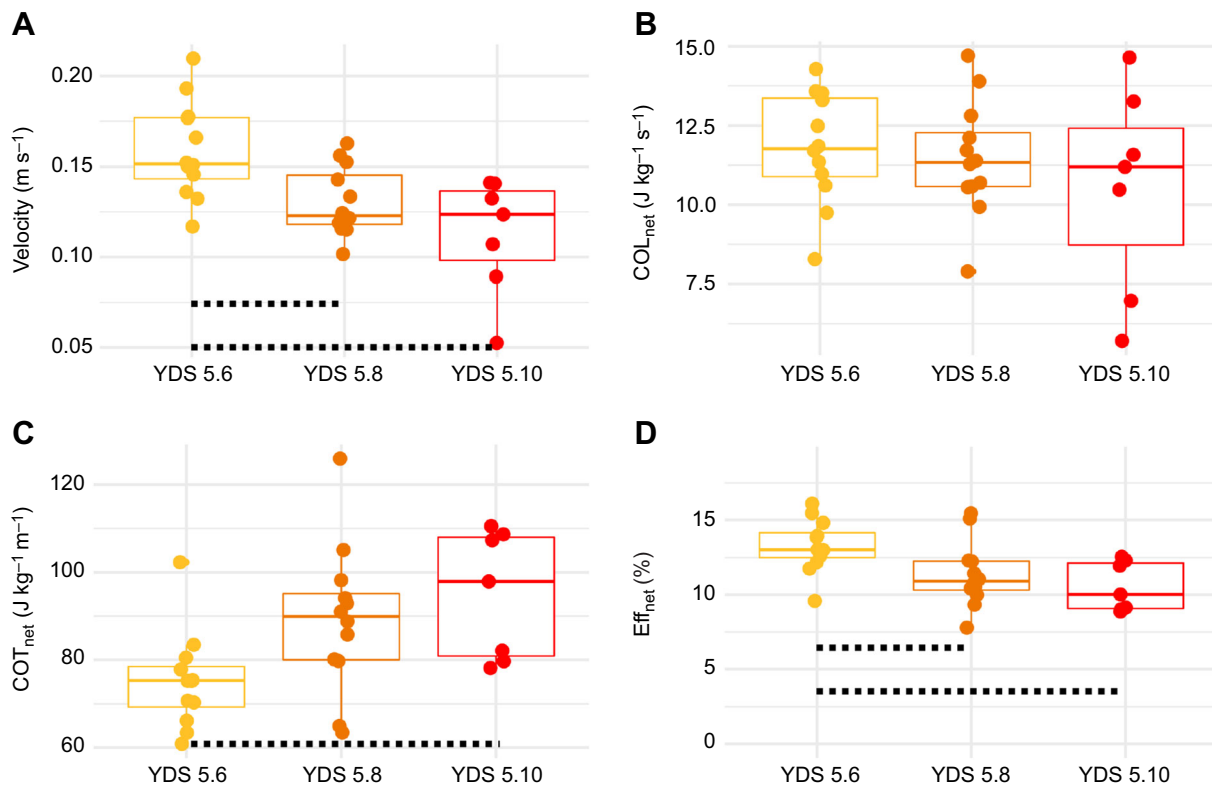


Fig. 3. Effect of route difficulty on climbing costs. (A) Velocity, (B) COL_{net} , (C) COT_{net} and (D) Eff_{net} by difficulty level during self-selected normal velocity trials. Box plots indicate medians, upper and lower quartiles and $1.5 \times$ interquartile range for individual data points (circles). Dotted lines represent significantly different pairs ($P < 0.05$, Tukey HSD test).

presented plus or minus one standard deviation, and model coefficients and intercepts are presented plus or minus one standard error.

Comparative data

To examine whether humans exhibit a different relationship between cost and velocity from that of other primates, we included non-human primate data from Hanna (2006) and human data from Booth and colleagues (1999) (Table 2). The non-human data were collected using indirect calorimetry with five species climbing a rope treadmill. COL_{net}

was calculated from measurements reported in Hanna (2006) using the same approach as described here for human data. Because Hanna (2006) reports means for each individual, we calculated mean values for each human subject in this dataset prior to comparative analyses. The comparative human data (Booth et al., 1999) represent the mean of seven participants for a given trial. We did not include human studies that did not report climbing speeds and/or comparable COL_{net} measures removing a resting cost from a climbing metabolic rate (e.g. Bertuzzi et al., 2012; Billat et al., 1995; España-Romero et al., 2011; Mermier et al., 1997; Sheel et al., 2003; Watts et al., 2000).

RESULTS

Determinants of climbing costs

As expected, velocity was the primary determinant of COL_{net} for human rock climbers (Fig. 2A). COL_{net} increased linearly with velocity (model coefficient = $40.1 \pm 3.1 \text{ J kg}^{-1} \text{ m}^{-1}$, d.f. = 44.9, $P < 0.001$) with a postural cost (y -intercept) of $5.98 \pm 0.7 \text{ J kg}^{-1} \text{ s}^{-1}$ (d.f. = 36.8, $P < 0.001$). Note that this postural cost was over and above the cost of standing, MR_{stand} ($2.06 \pm 0.18 \text{ J kg}^{-1} \text{ s}^{-1}$; Table 1). $\text{COT}_{\text{slope}}$ is given by the slope of the COL_{net} versus velocity regression ($40.1 \pm 3.1 \text{ J kg}^{-1} \text{ m}^{-1}$) and excludes postural cost (Fig. 2B). The resulting $\text{Eff}_{\text{slope}}$ was 24% (95% confidence interval, CI, 21–29%) (Fig. 2C) and approaches the theoretical maximum efficiency for muscle (Hill, 1922). By definition, $\text{COT}_{\text{slope}}$ and $\text{Eff}_{\text{slope}}$ are independent of speed. In contrast, COT_{net} decreased with climbing velocity (Fig. 2B). At the highest velocities observed in this study (0.28 m s^{-1}) predicted COT_{net} was $61.5 \text{ J kg}^{-1} \text{ m}^{-1}$. Conversely, Eff_{net} , which includes postural cost, increased as a function of velocity (Fig. 2C). While mean Eff_{net} was $12.5 \pm 2.4\%$, the highest Eff_{net} among trials in this study was 19% (Table S1).

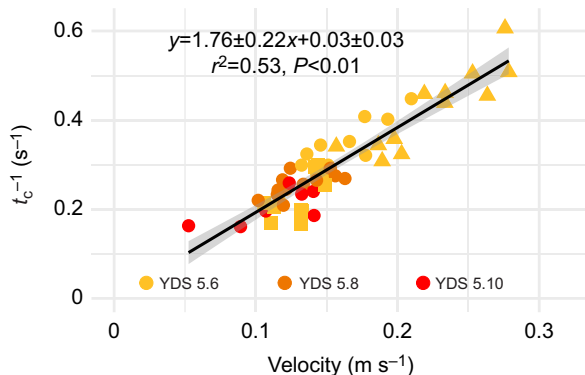


Fig. 4. Relationship between contact time and velocity. Velocity and inverse contact time (t_c^{-1}) were collinear. The black line depicts the results of a general linear model. The gray area represents the model 95% CI. Symbols represent self-selected velocities (circles, normal velocity; squares, slow velocity; triangles, fast velocity); colors indicate route difficulty (see Fig. 2).

Table 2. Mean energetic cost of climbing (COL_{net}) in humans and non-human primates

Study	Taxon	Climb type	COL _{net} (J kg ⁻¹ s ⁻¹)	Velocity (m s ⁻¹)
Hanna, 2006	<i>Loris tardigradus</i>	Rope	5.80±1.05	0.07
		Rope	8.60±3.18	0.08
		Rope	4.65±0.35	0.07
		Rope	12.05±0.07	0.19
		Rope	9.83±1.40	0.13
This study	<i>Homo sapiens</i>	5.6	11.81±1.76	0.16
		5.8	11.47±1.90	0.13
		5.10	10.56±3.20	0.11
		5.10d	7.63±0.53	0.05
Booth et al., 1999	<i>Homo sapiens</i>	Treadwall	6.93±0.34	0.13
		Treadwall	8.54±0.30	0.17
		Treadwall	10.12±0.43	0.20
		Treadwall	10.12±0.43	0.20

Climb type values refer to Yosemite Decimal System grades. COL_{net} data are means±s.d.; velocity data are means. Note, the velocities for Hanna (2006) are preferred speeds selected by the animals. The velocities for Booth et al. (1999) were enforced by study design (not selected by participants). Means for the present study presented in this table were calculated using self-selected normal speed trials with fast and slow trials excluded.

Anthropometric variables did not affect climbing costs. In LME models with velocity and subject as factors, neither body mass (model coefficient=−0.04±0.04, $P=0.31$) nor arm length (model coefficient=−0.14±0.10, $P=0.22$) was a significant factor when included in the model (Table S2). Similarly, other expressions of limb length, including IMI (model coefficient=7.15±26.57, $P=0.79$) and arm/height (model coefficient=−104.63±144.77, $P=0.23$) were not significant factors for COL_{net} (Table S2). Self-reported climbing experience was also unrelated to COL_{net} (0.33±0.55, $P=0.56$). Note that anthropometric variables and experience were not collinear with velocity (Table S3).

Likewise, route difficulty had no significant effect on COL_{net} independent of velocity. In LME models controlling for velocity and subject, and including difficulty as an ordinal variable, difficulty level was not a significant predictor (YDS 5.8, $P=0.178$; YDS 5.10, $P=0.207$; Table S2). However, route difficulty significantly correlated with velocity. When controlling for individual subjects as a fixed factor, and including only self-selected ‘normal’ speed trials, velocity varied significantly as a function of difficulty level (repeated measures ANOVA: $F_{2,17}=19.4$, $P<0.01$). At self-selected normal velocities, subjects climbed the easiest route (YDS 5.6) the fastest (0.16±0.03 m s⁻¹), the intermediate route (YDS 5.8) more slowly (0.13±0.02 m s⁻¹), and the hardest route (YDS 5.10) the slowest (0.11±0.03 m s⁻¹) (Fig. 3A). Subsequently, mean COL_{net}, COT_{net} and Eff_{net} did vary with difficulty. Climbing more difficult routes was more costly and less efficient, but only because the rate of ascent was slower (Fig. 3B–D).

Contact time, t_c , was collinear with velocity. We found that the inverse of contact time (t_c^{-1}) was positively linearly correlated with climbing velocity (Fig. 4), as has been previously reported for running (e.g. Roberts et al., 1998). As climbing velocity increases, the average time any limb is in contact with the support decreases. However, unlike studies of running cost (e.g. Kram and Taylor, 1990), t_c^{-1} was not a better predictor of COL_{net} than velocity. In LME models with velocity and subject as factors, t_c^{-1} was not a significant factor. Further, an LME model using t_c^{-1} and subject as factors did not explain as much of the variance in COL_{net} as a model of velocity and subject (Table S2).

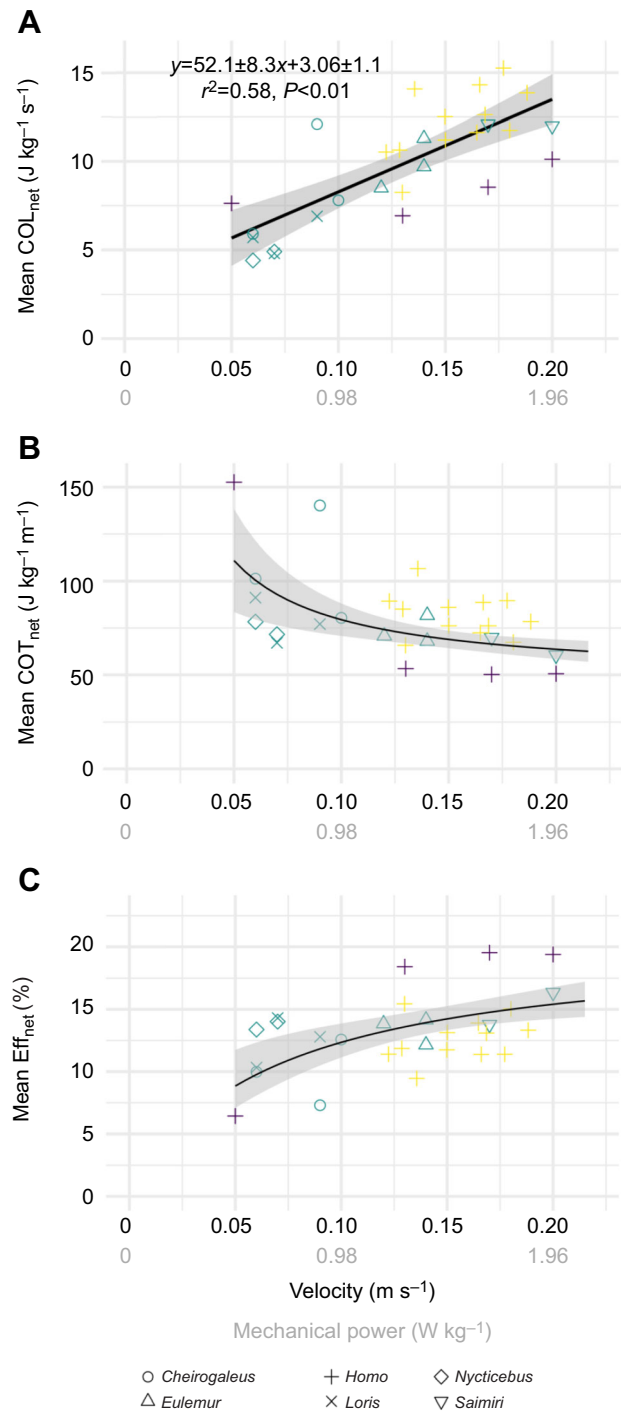


Fig. 5. Comparison of effect of velocity on climbing costs in humans and non-human primates. (A) Mean COL_{net}, (B) mean COT_{net} and (C) mean Eff_{net} as a function of mean climbing velocity. Each point from Hanna (2006) (green) and this study (yellow) is the mean for an individual. Each point from Booth et al. (1999) (purple) is the mean of seven participants for a given trial. Different shapes represent the different genera. Gray horizontal axis values are mechanical power and are equal to velocity multiplied by g .

Comparison with non-human primates

In comparing data from this study and those collected by Hanna (2006), Hanna et al. (2008) and Booth et al. (1999), we found that COL_{net} did not differ between humans and non-human primates in analyses including velocity (Fig. 5, Table 2). There was no effect of group (human versus non-human) on COL_{net} in a general linear

model with velocity as a factor (ANCOVA: $F_{1,26}=1.222$, $P=0.28$). However, there was an effect of study on COL_{net} with velocity as a factor (ANCOVA: $F_{2,25}=5.65$, $P=0.01$). *Post hoc* pairwise comparison with Bonferroni correction showed that this study had a significantly higher intercept or postural cost (0.11 ± 0.03) than that of Booth et al. (1999) (0.80 ± 0.87). Other pairwise comparisons were not significant.

DISCUSSION

The energy cost of climbing in humans is well predicted by the mechanical work required for ascent. Across a sample of subjects ranging from 53.7 to 96.2 kg and 1.52 to 1.84 m height, we found no evidence for allometric effects of body size or proportion on COL_{net} , COT_{net} or efficiency. These results are consistent with interspecific comparisons reporting similar COT_{net} for climbing across a broad range of species (Taylor et al., 1972; Full and Tullis, 1990; Hanna et al., 2008). The efficiency of human climbing is similar to that of other species, including non-human primates. Indeed, mass-specific climbing costs for humans are essentially identical to those of arboreally adapted primates when accounting for velocity (Fig. 5).

Velocity

Our results show that velocity is the primary determinant of COT_{net} and COL_{net} . In this study, climbers significantly decreased their climbing costs by increasing their velocity. For each additional 0.05 m s^{-1} of velocity, the model predicts a $1.73\text{ J kg}^{-1}\text{ s}^{-1}$ increase in metabolic rate (Fig. 2A). Conversely, COT_{net} is lower at faster speeds, as the effect of postural cost is reduced (Fig. 2B). The decrease in climbing costs as a function of speed matches the model of Tosi et al. (2011). In this model, they suggest that climbing energy costs decrease with speed, and that climbing speed derives from minimizing both work per unit length (COT_{net}) and power (COL_{net}) (Tosi et al., 2011).

Measurements of COL_{net} and COT_{net} in the present study are consistent with those reported previously for rock climbers (Table 2), particularly when accounting for velocity effects. Booth et al. (1999) reported higher costs for outdoor climbing than for indoor, climbing-treadmill trials. They also suggested that the difference in cost was related to climbing velocity, with the slower outdoor trials requiring more ‘static work’ to maintain position on the wall. The results here support that explanation, with strong agreement in cost values with those of Booth et al. (1999).

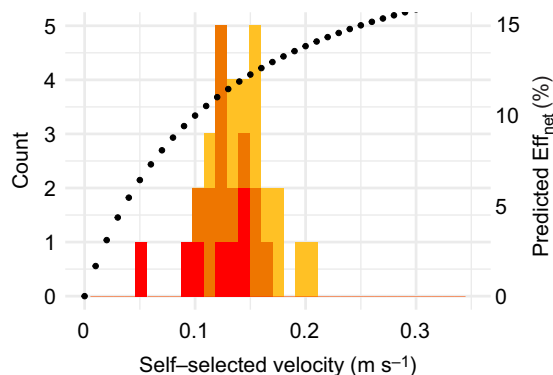


Fig. 6. Relationship between velocity and ecological efficiency. The histogram shows self-selected normal climbing velocity and the dotted line indicates estimated ecological efficiency for human rock climbers in this study. Bar color indicates route difficulty as in Fig. 2. See Discussion for analysis of ecological and muscular efficiency.

Our results are also consistent with those reported by España-Romero and colleagues (2011) and Bertuzzi and colleagues (2007), which found lower energy costs of ascent (similar to COT here, but without resting costs removed) associated with faster climbing velocities. Notably, our analyses indicate that velocity effects are sufficient to explain the apparent effect of route difficulty on cost: harder routes incur a greater COT because they are ascended more slowly (Fig. 3). In contrast, Sheel and colleagues (2003) reported greater costs of ascent for more difficult routes without any difference in climbing velocity. The reasons for this discrepancy between studies with respect to route difficulty are unclear, but it is possible that the difficulty becomes a factor only with exceptionally difficult climbing. The ‘hard’ routes in the study by Sheel and colleagues (2003) had a mean rating of YDS 5.11c, considerably more difficult than the most difficult route in the present study (YDS 5.10). We hypothesize that, at extreme levels of difficulty, the postural costs of rock climbing might be elevated as a result of the challenge of maintaining position. Additional studies, examining a broader range of climbing routes and difficulties, are needed to test this hypothesis.

Muscular (Eff_{slope}) and ecological (Eff_{net}) efficiency

The efficiency of human climbing extrapolated from the slope of the COL_{net} versus velocity plot (Eff_{slope} , Fig. 2C) was 24%, consistent with efficiencies reported by Minetti and colleagues (2002) for human walking ($22\pm6\%$) and running ($24\pm1\%$) up steep ($\geq 15\%$) inclines. This efficiency represents the incremental metabolic cost for each meter of ascent, and can be considered the ‘muscular efficiency’ of human climbing. The muscular efficiency of human climbing is consistent with the theoretical efficiency of human muscle (Hill, 1922) and empirically measured efficiencies of ~ 20 – 30% for isolated human muscle fibers (He et al., 2000). Together, observations from this study and previous research suggest human muscle efficiency remains within a narrow range across tasks and contexts.

It is notable, however, that the observed efficiencies for climbing trials in this study (Eff_{net}), as shown in Fig. 2C, were considerably lower than the extrapolated muscle efficiency. Because of the postural costs of climbing, observed efficiencies (Eff_{net}) never exceeded 19% (Fig. 2C). Thus, we can distinguish an ‘ecological efficiency’ of climbing, Eff_{net} (Fig. 2C) from the muscular efficiency of climbing. The ecological efficiency of climbing reflects the actual metabolic cost of ascent and may therefore be ecologically and evolutionarily salient when considering climbing behavior and postcranial adaptations. Adaptations to reduce the postural cost of climbing would improve the ecological efficiency of climbing without necessarily affecting muscular efficiency (i.e. the slope of the COL_{net} versus velocity relationship). For example, Full and Tullis (1990) suggested that cockroaches are able to maintain position on vertical substrates passively, which could reflect selection to minimize climbing postural costs and improve ecological efficiency.

The relationship between velocity and ecological efficiency has the potential to affect climbing ecology and behavior for animals in the wild. As the velocity of ascent approaches 0, so does the ecological efficiency of climbing. All other considerations being equal, the relationship between velocity and ecological efficiency would predict that an animal should choose to climb quickly in order to minimize cost. Indeed, in this study, rock climbers favored velocities at which efficiency is at least 10% (Fig. 6). Examining the self-selected climbing velocities in wild animal populations or in human foragers who regularly climb is a promising area of further research into climbing optimization. The trade-off between velocity

and efficiency could be used to interrogate the importance of energy cost relative to other parameters such as safety.

Postcranial anatomy

As reported by Hanna and colleagues (2008), we found no significant difference in climbing costs between humans and other primates (Fig. 5). The large variation in body size (<1 kg in non-human primates to >60 kg in humans), limb proportions (IMI ranging from approximately 68 in humans to greater than 100 in the other primates), and other anatomical traits (e.g. grasping foot, digit length and curvature) across this sample clearly supports the conclusion that postcranial anatomy does not affect climbing costs, at least among primates. Critically, in this controlled study of human rock climbers, we did not find an effect of limb length or body mass (Table S2). The similarity in climbing costs between humans and other primates may suggest that arboreal adaptations are products of selection for safety in the canopy. Indeed, falls from the canopy are a potentially powerful selective pressure and an important source of morbidity and mortality in both human foragers (Kraft et al., 2014) and non-human primates (Pontzer and Wrangham, 2004; Carter et al., 2008; Pontzer, 2017).

The lack of postcranial anatomy effects on climbing costs both here and in broad comparative analyses does not completely rule out an effect of postcranial traits on climbing cost. At least two possibilities warrant further investigation. The first is that there is an effect of limb length on climbing costs which is too small to be detected by the present study. This is supported by the fact that in the present study, the range of variation in IMI was small (65–73; Table 1). Moreover, the effects of arm length and the ratio of arm length/height, while not statistically significant, were negative, suggesting a possible effect on cost.

The second possibility is that post-cranial traits have an indirect effect on climbing costs by affecting climbing speed. While Hanna and Schmitt (2011) found no evidence for an effect of limb length or step length on locomotor costs, Halsey and colleagues (2017) found that athletes with greater arm spans were able to increase velocity and decrease locomotor costs when they trained on an obstacle course. Arboreal adaptations could enable non-human primates to climb faster, which the results here indicate will reduce cost. The relationship of limb length and other postcranial traits to climbing energy expenditure therefore warrants further study to determine whether there may be relatively small but ecologically salient effects.

Primates are well suited for examining the determinants of climbing locomotor costs, as they are proficient climbers spanning a large range of body sizes and limb proportions. Further, their study may hold important implications for human and primate evolution, considering more broadly the limb proportions of non-human apes and fossil hominins. Still, broadening the study of climbing costs to other taxonomic groups might bring greater anatomical diversity to bear on the question of climbing efficiency. Previous studies of vertical climbing energetics have been largely restricted to primates and insects (Pontzer, 2016), and the inclusion of other clades may help advance current understanding of climbing performance, ecology, and evolution. For example, a diverse set of reptile species, including lizards and snakes, regularly engage in climbing (e.g. Clemente et al., 2013; Krause and Fischer, 2013; Byrnes and Jayne, 2014) and the energy cost of their vertical ascent would broaden current understanding the anatomical and kinematic determinants of climbing energetics.

Limitations

This study included a moderate range of body sizes within our human sample, but only a narrow range of limb proportions. Also,

climbing energy cost data are available for only a small number of non-human primate species, and those studies used a somewhat different protocol: non-human primates climbed a rope treadmill rather than a static wall, and their resting costs were measured while lying down or sitting, rather than standing. Thus our approach may underestimate human postural costs relative to those of other primates, because we subtracted a larger base cost to calculate COL_{net} . This underestimation of human postural costs should be of the order of $\sim 0.5 \text{ J s}^{-1}$, the difference between sitting and standing expenditure (Ainsworth et al., 2011), too small to affect the large overlap of confidence intervals for postural costs between humans and non-human primates. These limitations constrain our ability to detect the effects of locomotor anatomy on climbing cost and efficiency. It is possible that the effects of anatomy on climbing costs and/or differences between humans and other primates were too small or variable to be detected in our analyses. Second, a substantial number of trials resulted in RER values >1.00, and it is possible that the contribution of anaerobic metabolism affected our results. The observation in this study that climbing readily resulted in $RER > 1.00$ is itself notable, reflecting the nature of metabolic demand in this activity, at least in humans. Our analyses indicate that RER was not a significant factor in our results, but future studies might design climbing trials at lower velocities to avoid this issue. Finally, we examined a relatively narrow range of climbing conditions (e.g. vertical wall, indoors) and relatively short route ($\sim 10 \text{ m}$) that necessitated repeated lowering between ascents. Additional measures from longer and more varied routes could further elucidate the effects of route conditions on climbing cost.

Conclusion

We found that climbing mass-specific COT is independent of body mass in an intra-species sample, consistent with previous work (Hanna et al., 2008; Taylor et al., 1972). We further found that climbing experience is not associated with variation in COT. COT increased and net efficiency decreased with difficulty, but this effect was attributable to the slower climbing velocities used during harder climbs. We found no effect of difficulty independent of velocity. We therefore identify self-selected climbing velocity in ecologically relevant settings as a promising metric to further test hypotheses of climbing optimization. The similarity in climbing COT across species and substrates (e.g. treadmill: Booth et al., 1999; tread-rope: Hanna et al., 2008; and rock wall: Booth et al., 1999, and present study) suggests the ecological context of climbing (e.g. cliffs or trees) and anatomical adaptations for climbing have a negligible impact on energy cost. Integrating energetic costs with other aspects of performance, such as safety, may be a fruitful direction for future work investigating the evolutionary pressures shaping climbing morphologies and behaviors.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: E.E.K., H.P.; Methodology: E.E.K., H.P.; Formal analysis: E.E.K.; Investigation: E.E.K., H.P.; Data curation: E.E.K.; Writing - original draft: E.E.K.; Writing - review & editing: E.E.K., H.P.; Supervision: H.P.; Funding acquisition: E.E.K., H.P.

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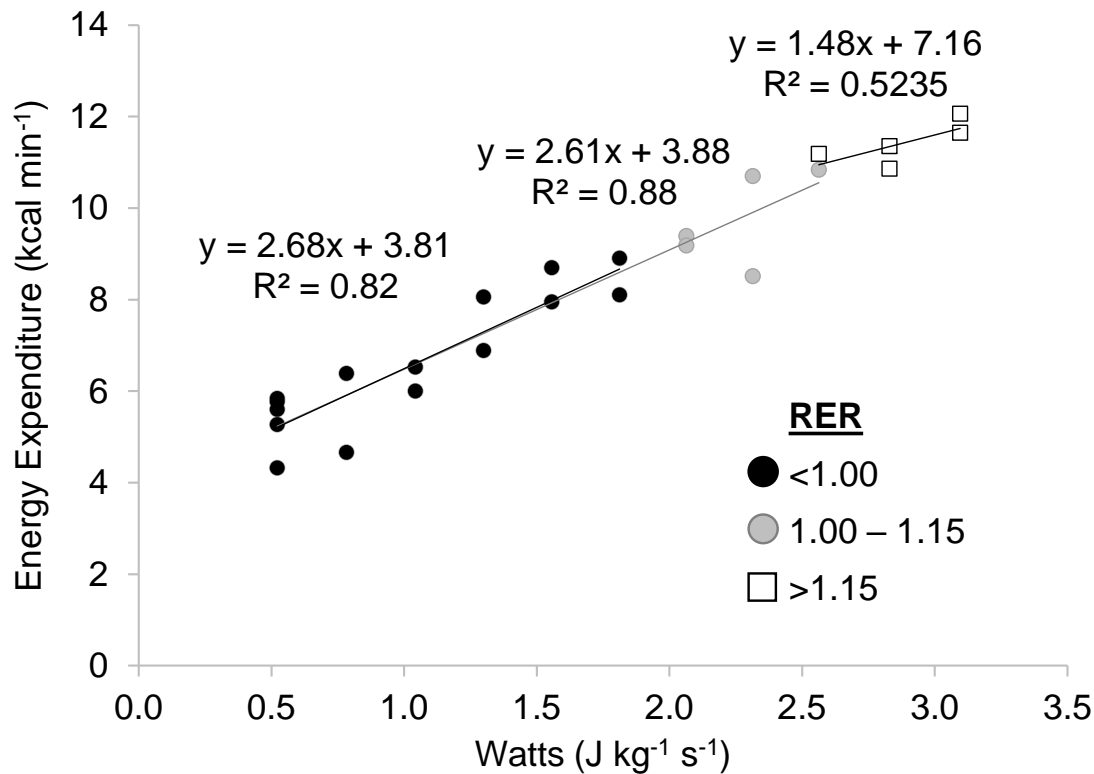


Fig. S1. Energy expenditure as a function of work. Energy expenditure, calculated from VO_2 and VCO_2 using the Weir equation, plotted against workload for a human subject in a graded exercise test reported in Table 3 of Evardsen et al. 2014. The subject maintained a constant running speed (4.8 kph) while the incline of the treadmill increased from 4% to 20%. Once the treadmill reached 20%, speed was further increased to 5.3 kph and then to 5.8 kph. Workload (Watts) reflects the rate of ascent, $\text{speed} \times \sin\theta$, where θ is treadmill incline angle. The first minute of the test is excluded from this analysis. As can be seen from the plot, energy expenditure continues to track workload above $\text{RER}=1.00$, up to $\text{RER}=1.15$.

Table S1

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Table S2. Tested COL_{net} linear mixed effect models. Selected model is bolded.

Model	R ² _m	R ² _c	AIC
lmer (COL_{net} ~ velocity + (1 subject))	0.52	0.86	187
lmer (COL _{net} ~ t _c ⁻¹ + (1 subject))	0.29	0.59	232
lmer (COL _{net} ~ velocity + mass + (1 subject))	0.53	0.86	192
lmer (COL _{net} ~ velocity + imi + (1 subject))	0.52	0.86	180
lmer (COL _{net} ~ velocity + arm + (1 subject))	0.54	0.86	189
lmer (COL _{net} ~ velocity + height + (1 subject))	0.53	0.86	192
lmer (COL _{net} ~ velocity + difficulty + (1 subject))	0.54	0.86	188
lmer (COL _{net} ~ velocity + experience + (1 subject))	0.51	0.86	188

Table S3. Correlation tests between velocity and potential explanatory variables of COL_{net}.

Variable	Type of test	Correlation coefficient	Significance
Experience	Spearman's	$\rho = -0.08$	p = 0.54
Difficulty	Spearman's	$\rho = -0.51$	p < 0.01
Inverse contact time	Pearson's	r = 0.73	p < 0.01
Body mass	Spearman's	$\rho = 0.05$	p = 0.70
Arm length	Spearman's	$\rho = 0.02$	p = 0.91
Height	Spearman's	$\rho < 0.01$	p = 0.95
IMI	Spearman's	$\rho = 0.29$	p = 0.08