Bridging the gap: parkour athletes provide new insights into locomotion energetics of arboreal apes

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Summary

The tree canopy is an energetically challenging environment to traverse. Along with compliant vegetation, gaps in the canopy can prove energetically costly if they force a route-extending detour. Arboreal apes exhibit diverse locomotion strategies, including for gap crossing. Which one they employ in any given scenario may be influenced by the energy costs to do so, which are affected by the details of the immediate environment in combination with their body size. Measuring energetics of arboreal apes is not tractable, thus our knowledge in this area is limited. We devised a novel, custom-made experimental setup to record the energy expenditure of parkour athletes tree-swaying, jumping, and vertical-climbing. The latter strategy was vastly more expensive indicating that when energy economy is the focus arboreal apes will prioritise routes that limit height changes. Whether tree-swaying or jumping was most economical for the athletes depended upon interactions between tree stiffness, the distance to cross, number of tree-sways required and their own mass. Updated analysis of previous inter-specific correlations suggests that whether the relative costs to vertical climb are size-invariant across primate species is complicated by details of the climbing context.

1. Introduction

Animals strive to navigate their environment efficiently since they must ensure that the energy they expend to forage does not outweigh the energy they gain from food. A classic example of solving this problem in an energy-demanding environment is provided by tree-living apes, which frequently encounter gaps in the forest canopy. To avoid taking a circuitous detour, apes may instigate one of several gap crossing strategies. While jumping and descending to cross terrestrially may be used in such situations, the most iconic gap-crossing behaviour is the tree-sway performed by orang-utans, whereby a tree trunk is oscillated to aid in reaching peripheral branches of the next tree that would otherwise be out of reach [1].

Which available gap crossing method is energetically cheapest for a large-bodied arboreal ape, and indeed which locomotion strategy is most economic when travelling through continuous forest canopy, is likely to be influenced by the interactions between properties of the animal's immediate environment such as the compliance and natural frequency of branches, along with their own size [2]. Beyond modelled estimates [1], little is known about the energetic costs of primate arboreal locomotion.

We use a novel and innovative approach to tackle this issue, including manufacturing a custom-made tree-sway support using glass fibre poles to realistically simulate the compliance of forest trees. Humans today still share many of the adaptations for orthograde arboreality exhibited by the other apes, such as a broad and shallow chest, and also shoulder blades positioned to enable extensive range of motion in the shoulders [3, 4]. Many populations of humans remain adept at arboreal locomotion [5, 6], and this includes practitioners of certain sports, most notably parkour athletes, who have elite gymnastics and athletic abilities allowing them to emulate the locomotion of arboreal apes [7]. Parkour athletes specialize in developing new techniques for moving through complex, three-dimensional urban environments whilst avoiding the ground. These involve the limbs in a wide range of joint positions, in suspension and compression, much like the locomotion of living non-human apes [2, 8].

We measured the energy expenditure of professional parkour athletes during tree-swaying, jumping and vertical climbing, and used this referential model to test previous estimates based on mechanics [1], to compare the costs of different arboreal locomotor behaviours, and to gain some empirical insight into how environmental variation and body mass can affect the relative energy costs of these behaviours.

2. Materials and methods

Empirical data

Twenty-eight parkour proponents undertook horizontal jumping, tree-sway and vertical climbing (Figure 1). Each activity involved multiple conditions designed to represent, within reason, the varying mechanical conditions experienced by arboreal apes in a forest canopy. The jumping conditions were a short and a long standing jump. The tree-sway conditions were denoted by different pole stiffnesses to represent a wide range of tree trunk stiffnesses that can be swayed to bridge canopy gaps. A ladder represents an ideal tree for climbing and 'ladder climb' is a defined locomotor code for arboreal primates [2] while a rope emulates tree vines ubiquitous in tropical rainforests and often used by apes to ascend into tree crowns [2]. During all these activities, rate of oxygen consumption (V'O$_2$) was measured via a mobile respiratory gas analyser (Oxycon mobile, Viasys) [9].

Horizontal jumping involved repeated jumping at 1.2 or 1.8 m, at 0.2 Hz. The tree-sway apparatus comprised three 5-m fibreglass poles of differing thicknesses and stiffness, held vertically by attachment to a base plate.

Each pole included foot supports 2 m from the top of the pole. Up to three different conditions were recorded for each pole, represented by different amounts of displacement (low, medium and high) as chosen by the participant. For vertical climbing, participants climbed up and down a 5-m rope. After at least 15 minutes of rest to ensure that oxygen consumption and blood lactate levels had returned to baseline, participants then climbed a vertical ladder, matching repetitions to the rope trial.

For horizontal jumping and tree-sway, the last of four minutes of $V'O_2$ data was used to calculate mean rate of energy expenditure during the activity. In the vertical climbing trials $V'O_2$ was also recorded during the subsequent period of excess post-exercise oxygen consumption, to account for anaerobic metabolism. Furthermore, blood lactate levels were taken before and after each trial. These measures were combined to calculate rate of energy expenditure [10].

See supplementary material for further details.

Model building

Based on the empirical data, models were produced to estimate and compare the energetic cost to cross a gap in the forest canopy by jumping or tree-swaying under various scenarios. Model outputs provided a 3D landscape of the energy costs of gap crossing dependent on gap distance and tree stiffness. Each model included a fixed number of tree-sways required to reach the target tree, and a fixed body mass.

The energy costs of swaying were calculated from equations derived from multiple linear regressions to predict total oxygen consumption (VO_2) per sway cycle from body mass and sway amplitude for each pole thickness separately. The sway distance required to cross a given gap was less than the actual gap due to arm reach. Standard digital analysis applied to orang-utan tree-sway videos (6 independent recordings of wild orang-utans representing both sub-species, some of which were analysed in [1]) indicated that a median of 71.6% of the exhibited reach of the animal was used to reach horizontally to the target tree or vine, with the rest of the distance made up by swaying the tree. This value was used in the model to estimate the sway amplitude required to bridge the gap assuming the mean arm span of the participants in the empirical study (158.3 ± SD 7.3 cm). Sway amplitudes of 0.4 to 0.7 m were modelled, at 0.1 m increments. For gap distances of 1.8 m, jumping cost was estimated from a prediction equation based on $V'O_2$ and body mass measured in the present study for jumps of 1.8 m. For 1.5 to 1.7 m inclusive, jumping cost was estimated given the linear relationship between jumping distance and $V'O_2$, between the recorded distances of 1.8 and 1.2 m.

3. Results and Discussion

Thorpe et al. [1] estimated the energetic cost for a model arboreal ape to cross a canopy gap based on the external (mechanical) work done. The present empirical values (Table 1) suggest that actual gap crossing costs by jumping, tree-swaying or vertical climbing are each an order of magnitude larger than the model estimates. While parkour athletes may be less energetically economical at gap crossing than arboreal apes, this marked difference in costs also holds for ladder climbing. This suggests the main explanation for the difference between empirical and model values is that the external work to move the body is a fraction of the entire metabolic cost to perform the activity. Alongside basal metabolic rate and inherent muscular inefficiency, work done that is not directly related to movement of the animal surely accounts for much of this discrepancy. This is clearly demonstrated by the vertical climbing activities; the energetic cost to descend and ascend a rope is around twice that for a ladder, despite the external work done on the body (i.e. work against gravity) being the same. Indirect energy costs for rope climbing include skeletal muscle contractions to

maintain body posture, substantial movement of body parts around the centre of mass to enable propulsion along the rope, and gripping the rope. These same factors feature in ladder climbing but clearly to a lesser extent.

Nonetheless, gap crossing can save a lot of energy compared to taking a detour and thus extending the route through the trees. Parkour athletes traversing an arboreal-like course expended around 1.2 kJ/m [7]; Table 1 indicates that the cost to sway or jump across a gap for these athletes is around 5 kJ/m, thus saving them energy if their detour to circumnavigate that gap would amount to anything more than just a few metres.

Hanna et al. [11] reported that the mass-specific metabolic costs to climb are constant across primates of differing size. For humans they used an estimate derived from rock climbing data (~68 J/kg/m). This is similar to our value for ladder climbing (Table 1; suggesting that the costs of ascent and descent during climbing are similar to each other, probably because of the aforementioned indirect energy costs), and about half that of rope climbing. Replacing the human data point in [11] with that for ladder climbing maintains a negative inter-specific relationship between cost of transport and body mass, and is highly correlated (R^2=0.97; supplementary information). This means that climbing efficiency is highly positively correlated with mass, and indicates that smaller-bodied species experience increased relative metabolic climbing costs (~two-fold). In contrast, including instead the value for rope climbing results in no inter-specific relationship between mass and climbing efficiency. However, humans may be inefficient rope climbers. The human data point is particularly influential on the slope because the dataset includes no data for non-human apes. Thus, we cannot yet conclude whether relative climbing costs are invariant across primate body sizes; the details of the climbing context (e.g. vegetation type) and the plasticity of great ape behaviour can heavily affect the metabolic costs to climb and in turn inter-specific comparisons based on size alone.

Both [1] and the empirical findings of the present study concur that vertical climbing is an order of magnitude more energetically expensive than tree-swaying or jumping, underlining the substantial costs for an ape to climb directly against gravity. This suggests that when focussing on energetic economy, arboreal primates will aim to move through the trees in ways that limit their changes in height above the forest floor. When they do accept noteworthy losses in height to make progress this likely indicates morphological limitations and/or an overriding focus on safety in terms of limiting the risk of injury from falling.

Our models indicate that the energy expended to sway or jump is greatly affected by the details of the local environment (gap distance, branch stiffness), and the mass and reach of the animal (Figure 2). Larger animals can experience greater energy savings by jumping instead of tree-swaying than can smaller animals. Yet smaller individuals are more inclined to jump. For heavier individuals the threat of injury, e.g. due to a breaking branch, overrides the opportunity to save energy. Some populations of orangutans spend more time on the ground than previously believed [12]. The high relative energy cost of climbing up and down emphasises the nutritional importance of terrestrial-based foods and the value of social and fleeing opportunities available on the ground.

Our study brings into question well-held beliefs about how the costs of climbing scale with body mass and demonstrates the importance of ecological context in understanding performance.

Table 1. Estimates of energy costs to bridge a canopy gap based on equations in [1] and on empirical measurements.

	Thorpe et al. (2007) [1]			Present study		
Body mass (kg)	75.3					
Height from ground (m)	4.0					
Gap distance (m)	1.8					
Sway distance (m)*	0.67					
No. half tree-sway cycles**	6					
Stiffness of tree (N m^{-1})	925	1485	1922	925	1485	1922
Work to sway (kJ)	0.26	0.41	0.53	3.30	3.54	4.07
Work to jump (kJ)	0.7			5.2		
				Rope		Ladder
Work to vertically climb (descend and ascend) (kJ)	3.0			36.6		18.3

Body mass is the study participant mean; height from ground is at the participant centre of mass during tree-swaying; gap distance is the higher of the two jump distances tested in the study; sway distance is the calculated distance required to sway accounting for reach; no. half sway cycles is the average of those presented in [1]; tree stiffness values are those of the three tree-sway poles.

* Orang-utan reach was not accounted for in [1].

** [1] calculates the energy cost to tree-sway based on half cycles, e.g. 6 half tree-sway cycles represents 3 full tree-sways.

Figure 1. Horizontal jumping (A); pole swaying (B); climbing a ladder (C) and a rope (D). Photographs by Lewis Halsey.
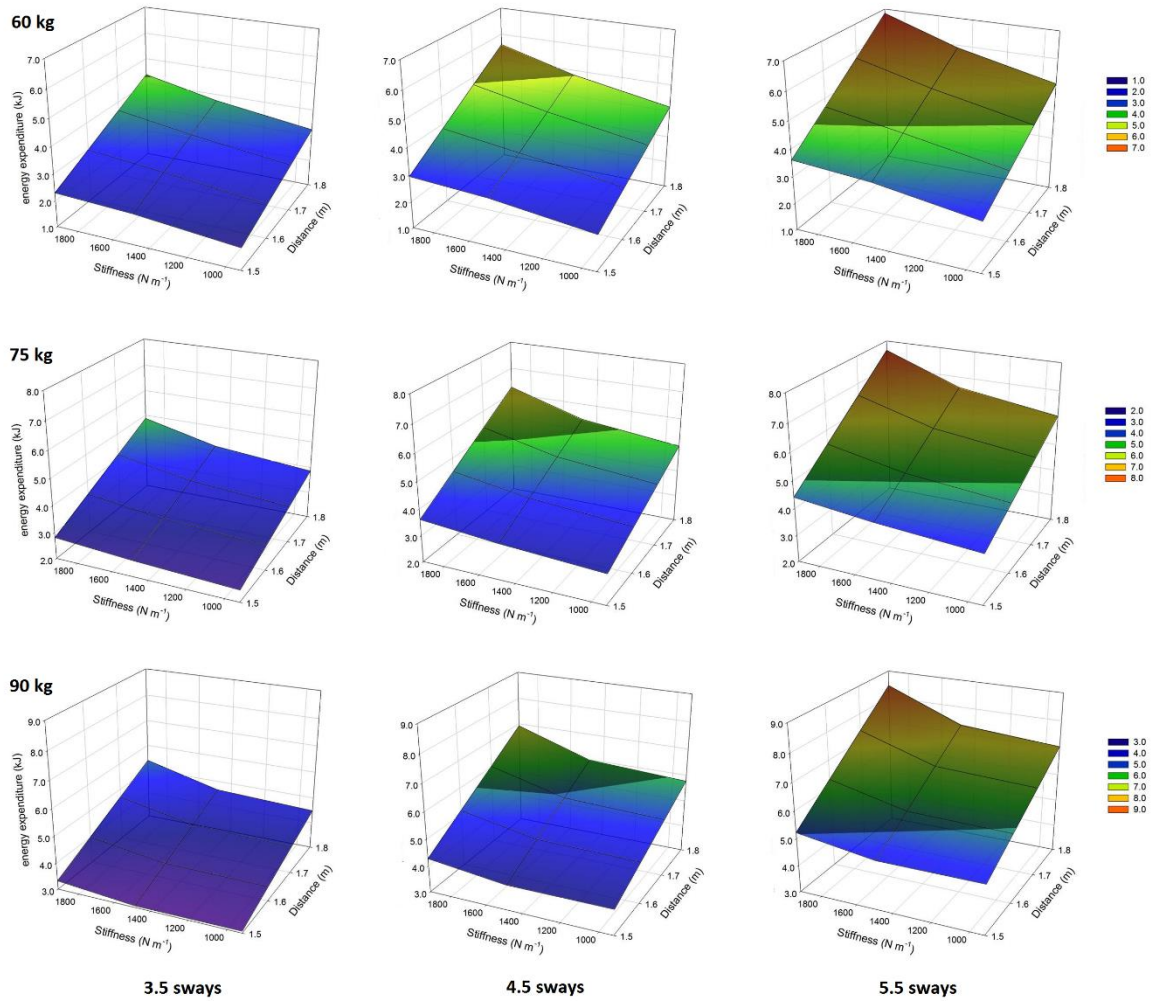
Figure 2. The modelled energy cost for an arboreal ape to cross a canopy gap of typical distance by either jumping or tree-swaying. Each panel displays an energy cost landscape: energy expenditure is on the y axis, supported by a colour scale. This landscape is related to tree stiffness and gap distance, and represents a unique combination of ape body mass (60, 75 or 90 kg) and number of sways (3.5, 4.5 or 5.5). The area of each landscape grey-shaded indicates the tree stiffnesses and gap distances where jumping to cross the gap is energetically cheaper than tree-swaying. The range on the y axis differs for each body mass to maximise resolution. View the figure in colour for full clarity.

References

1. Thorpe S.K.S., Crompton R.H., Alexander R.M. 2007 Orangutans use compliant branches to lower the cost of locomotion. *Biol Lett* **3**, 253-256.
2. Thorpe S.K.S., Crompton R.H. 2006 Orangutan Positional Behavior and the Nature of Arboreal Locomotion in Hominoidea. *Am J Phys Anthrop* **131**, 384-401.
3. Crompton R., Vereecke E., Thorpe S. 2008 Locomotion and posture from the common hominoid ancestor to fully modern hominins, with special reference to the last common panin/hominin ancestor. *Journal of Anatomy* **212**, 501-543.
4. Ward C.V. 2007 6 Postcranial and Locomotor Adaptations of Hominoids. In *Handbook of paleoanthropology* (pp. 1011-1030, Springer.
5. Kraft T.S., Venkataraman V.V., Dominy N.J. 2014 A natural history of human tree climbing. *J Hum Evol* **71**, 105-118.
6. Venkataraman V.V., Kraft T.S., Dominy N.J. 2013 Tree climbing and human evolution. *Proceedings of the national academy of sciences* **110**(4), 1237-1242.
7. Halsey L., Coward S., Crompton R., Thorpe S.K.S. In Press Practise makes perfect: performance optimisation in 'arboreal' parkour athletes illuminates the evolutionary ecology of great ape anatomy. *J Hum Evol*.
8. Hunt K.D., Cant J.G., Gebo D.L., Rose M.D., Walker S.E., Youlatos D. 1996 Standardized descriptions of primate locomotor and postural modes. *Primates* **37**(4), 363-387.
9. Halsey L.G., Coward S.R., Thorpe S. 2016 Data from: Bridging the gap: parkour athletes provide new insights into locomotion energetics of arboreal apes. Dryad. (
10. Scott C., Leary M., TenBraak A. 2011 Energy expenditure characteristics of weight lifting: 2 sets to fatigue. *Applied Physiology, Nutrition and metabolism* **36**, 115-120.
11. Hanna J.B., Schmitt D., Griffin T.M. 2008 The energetics cost of climbing in primates. *Science* **320**, 320.
12. Ashbury A.M., Posa M.R.C., Dunkel L.P., Spillmann B., Atmoko S., van Schaik C.P., van Noordwijk M.A. 2015 Why do orangutans leave the trees? Terrestrial behavior among wild Bornean orangutans (Pongo pygmaeus wurmbii) at Tuanan, Central Kalimantan. *Am J Primat* **77**(11), 1216-1229.