Practice makes perfect

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Title: Practice makes perfect: performance optimisation in ‘arboreal’ parkour athletes illuminates the evolutionary ecology of great ape anatomy

Running title: Evolution of energetic ecology in great apes

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Abstract

An animal's size is central to its ecology, yet remarkably little is known about the selective pressures that drive this trait. A particularly compelling example is how ancestral apes evolved large body mass in such a physically and energetically challenging environment as the forest canopy, where weight-bearing branches and lianas are flexible, irregular and discontinuous and the majority of preferred foods are situated on the most flexible branches at the periphery of tree crowns. To date the issue has been intractable due to a lack of relevant fossil material, the limited capacity of the fossil record to reconstruct an animal's behavioural ecology and the inability to measure energy consumption in freely moving apes. We studied the oxygen consumption of parkour athletes while traversing an arboreal-like course as an elite model ape to test the ecomorphological and behavioural mechanisms by which a large-bodied ape could optimize their energetic performance during tree-based locomotion. Our results show that familiarity with the arboreal-like course allowed the athletes to substantially reduce their energy expenditure. Furthermore, athletes with larger arm-spans and shorter legs were particularly adept at finding energetic savings. Our results flesh out the scanty fossil record to offer evidence that long, strong arms, broad chests and a strong axial system, combined with the frequent use of uniform branch-to-branch arboreal pathways, were critical to off-setting the mechanical and energetic demands of large mass in ancestral apes.

Key words: energy expenditure, performance optimisation, crown hominoids, ecomorphology, arboreal locomotion

44

45 **Introduction**

46 Body size is a central feature of an animal's ecomorphology. This is particularly evident in
47 predominantly or exclusively tree-dwelling species, whose morphology must be tightly
48 interwoven with the energetic and mechanical demands of arboreal travel. The great apes
49 are an intriguing and extreme example of the interplay between body size and the
50 challenges of feeding and travelling in the forest canopy. Adult great apes are some of the
51 largest frequently or exclusively arboreal mammals, but they rely on the terminal branch
52 niche for food, the narrowest, most flexible branches at the edge of tree crowns, which are
53 laden with ripe-fruits.

54

55 A reconstruction of why large ape size evolved in such a challenging habitat has proved
56 elusive, largely because of a paucity of fossil material from late Oligocene/ early Miocene
57 anthropoids (Zalmout et al., 2010; Stevens et al., 2013). Hunt's (2016) recent synthesis of
58 the evolutionary ecology of extant apes and monkeys, however, strongly suggests that large
59 mass evolved in ancestral apes because it provided a size-related advantage in contest
60 competitions for fruit with monkeys, during the prolonged desiccation of forest cover in
61 Africa in the Miocene. However, since scaling laws generally mean that larger animals are
62 relatively weaker than smaller ones (Schmidt-Nielsen, 1984), arboreal locomotion is likely
63 to be particularly demanding for large animals (Preuschoft et al., 1992; Hunt, 1994).
64 Moreover, unlike horses and other cursorial animals, all great apes have a high proportion
65 of muscle to tendon in the limbs (Sellers et al., 2010). This enables them to counter branch
66 flexibility through powerful, muscular stabilization of the limbs (Myatt et al., 2011; Hunt,

2016), but it comes at a price. Without tendon recoil to provide much of the work involved in locomotion, arboreal travel needs to be powered almost entirely by muscular contraction, which strongly influences the metabolic cost of locomotion (Reilly et al., 2007).

Ancestral apes must therefore have evolved morphological and behavioural mechanisms to compensate for the mechanical and energetic demands associated with their large size. Field observations of living apes and monkeys provide an insight into what those mechanisms might have been. Whereas the arboreal pathways (habitual routes between resources) of individual monkeys within a group tend to be wide, ranging 25 m from the group's geographical centre (Di Fiore and Suarez, 2007; Hopkins, 2011), individual apes consistently use the same branches and locomotor behaviours to travel between neighbouring major fruit trees and when travelling long distances between trees that fruit infrequently (Mackinnon, 1974; Fleagle, 1976; Thorpe and Crompton, 2006). As well as reducing the risk of falls, repeated use of uniform branch-to-branch routes allows apes to learn about the affordances of familiar branches and lianas, which could enable them to optimize performance by matching locomotor behaviours to the mechanical properties of the arboreal supports. Unfortunately, very little is known about how large-bodied great apes might optimize their energetic performance in arboreal locomotion, because recording oxygen consumption in freely moving apes is currently impossible. However, mathematical modelling of tree-sway in wild orangutans provides tantalizing evidence to support this theory; orangutans, particularly large adult males, repeatedly sway compliant tree trunks back and forth to cross gaps in the canopy (Thorpe and Crompton, 2006). This tree-sway is an order of magnitude less costly than descending to the ground and crossing terrestrially

(Thorpe et al., 2007), but the orangutans' repeated use of the same tree trunks for swaying suggests they are familiar with the mechanical properties of the support. The greater use of this behaviour by adult males relative to females and adolescents also suggests that increased size can be advantageous in tree-swaying, as compliance is greater underneath a larger body mass.

The origins of large ape size seem temporally linked to the emergence of other unique great ape traits in crown hominoids, such as long arms relative to legs (high intermembral indices) and broad but shallow chests. Thus early crown hominoids (e.g. *Morotopithecus bishopi*, 16–20 million years ago [MA], *Pierolapithecus catalaunicus* [11.9 MA] and *Hispanopithecus laietanus* [9.6 MA]) were similar in weight to living female orangutans (30–40 kg) and possessed transversely broad thoraces that are distinct from the dorsoventrally deep thoraces in other stem hominoids (e.g. the habitually quadrupedal proconsulid *Ekembo nyanzae*), and extant Old World monkeys (Ward, 1993; Moya-Sola and Kohler, 1996; Moya-Sola et al., 2004; Maclatchy, 2004). Limb lengths are not preserved for *Morotopithecus* or *Pierolopithecus*, but the intermembral index for *Hispanopithecus laietanus* is consistent with that of apes rather than Old World monkeys or proconsulids (Ward, 1993; Moya-Sola and Kohler, 1996). While mobile shoulders, long arms and short legs have generally been interpreted as providing postural stability and large feeding spheres for arboreal apes (Grand, 1972), they have also been predicted to increase the efficiency of patterned arboreal locomotor behaviours, such as arm swinging and climbing vertically up tree trunks (Cartmill, 1974; Preuschoft et al., 1992, 1996). Thus

these morphological features might also allow arboreal apes to optimise their locomotor performance over time.

New research has shown that many human populations remain adept at arboreal locomotion, despite being committed terrestrial bipeds (Venkataraman et al., 2013; Kraft et al., 2014). Modern humans still share with the other apes many of the adaptations for orthograde (upright-trunked) arboreality, such as the broad, shallow chest and shoulder blades positioned on the back that allow an extensive range of motion in the shoulders (Ward, 2007; Crompton et al., 2008). This allows many rainforest hunter-gatherer communities across Asia and Africa to routinely harvest arboreal resources such as honey, fruit, nuts, seeds, rattan and palm products (Venkataraman, et al., 2013, Kraft et al., 2014). Humans' natural climbing ability is also used in sports and gymnastics, particularly by parkour athletes ('traceurs'), who 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 (Hunt et al., 1996; Thorpe and Crompton, 2006; Kelly, 2011). In the present study, we investigate the energetics of parkour athletes as an elite and tractable hominoid model traversing an 'arboreal' assault course. Reilly et al. (2007) show that animals do not necessarily use the energetically cheapest available gaits for their primary locomotor sequences and argue that locomotor costs may be driven more by ecological relevance than by the need to optimize locomotor economy. We follow this framework by quantifying the morphological, behavioural and ecological variables that influence whether the metabolic cost of locomotion can be reduced if animals are able to

take advantage of limb designs and energy-saving mechanisms that reduce muscular effort. Thus our primary hypothesis is that the parkour athletes will be able to optimise their energetic performance as they become familiar with the affordances of the course. Specifically we predict that improved energy economies will be achieved by the athletes changing locomotor behaviour in response to learning about the mechanical characteristics of the supports. We also predict that the athletes' ability to optimise performance will be influenced by their morphology; thus heavier individuals and those with relatively longer arm spans and shorter legs will be better able to work their environment to their advantage and exploit support compliance as they become familiar with it, compared to those with the converse morphologies. This experimental approach makes it possible to flesh out the scanty fossil record through quantifying the energy economies of locomotion gained by a large-bodied ape from repeatedly traversing an arboreal route, and how these gains are moderated by morphology and locomotor behaviour.

Material and methods

The study was approved by the University of Birmingham Ethics Committee and all athletes provided written, informed consent for their participation. We measured the impact of variation in morphology and locomotor behaviour on the rate of oxygen consumption ($\dot{V}_{O_2}$, ml O₂ min⁻¹) of 19 elite male parkour athletes (aged 18–35 years) as they repeatedly traversed an arboreal-like assault course of 103 m horizontal length in a gymnasium at the University of Birmingham, U.K (from January to March 2012). The athletes traversed the course four times with a rest of at least 15 minutes between each trial. The course consisted

of a range of generic gymnasium apparatus such as vaulting horses, raised blocks, high bars, wall bars, and areas filled with loose foam blocks to emulate the range of mechanical conditions present in an arboreal pathway, rather than the exact structure of the forest canopy. Thus parts of the course incorporated support compliance, irregularity and discontinuity to reflect the conditions experienced during gap crossing between tree crowns, while others were rigid and predictable to reflect the phases between bouts of gap crossing when even large-bodied apes may walk into and out of the core of a tree along thick boughs (full details of the course route and types of challenge are presented in the Supplementary Online Material [SOM]). It was also designed to allow a range of locomotor solutions to each obstacle and the parkour athletes were instructed to complete the course ‘wasting as little energy as possible’. The course was co-designed by the researchers and the lead athlete from EMP Parkour, who did not subsequently take part in the experiment.

Fig. 1. Typical locomotor behaviours exhibited by the athletes. A) forelimb swing, B) vertical climb, C and D) pronograde scramble, E) brachiation, F) forelimb swing

Before their first trial, the athletes were shown around the course to familiarise them with the general route to be taken, the obstacles to be traversed, and the few ‘rules’ to be followed, such as not touching the ground and not using the edges of certain obstacles. They were then allowed two minutes to further look around (but not touch) the course. This ensured that athletes were relatively naïve concerning the mechanical properties of the supports for their first trial, while being clear about the general route.

The $\dot{V}_{O_2}$ of the athletes was measured via a mobile respiratory gas analyser (Oxycon mobile, Viasys, Germany). Immediately prior to each course attempt the athletes were required to undertake a low-intensity 5minute graded warm up on a rowing machine, where for the first minute they performed a stroke once every 5 s, then once every 4 s, and once every 3 s for the final three minutes. Within a minute of completion of the rowing, they started the course. This procedure ensured aerobic metabolism was primary throughout each trial. We were able to confirm that, while traversing the course, the athletes were mainly metabolising aerobically. This was known because measures of their respiratory exchange ratios were almost always below 1 and otherwise below 1.1, and rating of perceived exertion (RPE) scores were almost always below 16 and otherwise below 17 (Scherr et al., 2012). Measures of $\dot{V}_{O_2}$ are considered to be an accurate representation of rate of energy expenditure during mainly aerobic activity. The athletes had at least 15 minutes of rest before undertaking the next iteration of the course and reported being fully recovered each time. Mean RPE scores did not differ between iterations 1 and 4 of the course.

The athletes were also video-recorded at 25 frames per second (DCR-SR90, Sony, Japan) to allow subsequent identification of locomotor behaviours. From this, two measures were calculated: a) the proportion of locomotor behaviours that were changed between each athlete's 1st and 4th trials (see SOM Figure S1) and b) whether the athletes profiled as 'leapers', employing predominantly patterned gaits such as leaping, brachiation and vertical climbing, or as 'scramblers', exhibiting predominantly unpatterned clambering gaits. Separation of the athletes into patterned and unpatterned locomotor profiles was based on the fact that they clearly employed one of these locomotor strategies rather than combining the two types of locomotion (see SOM Figure S2).

The following morphometric data were collected from each participant: height (178.7 ± 7.5 cm), mass (73.9 ± 8.1 kg), hip height (height of the anterior superior iliac spine (102.3 ± 4.9 cm), right arm length (distance between the acromion process and the centre of the webbing between the thumb and index finger; 60.2 ± 4.9 cm) and arm span (distance between the webbing between the thumb and index finger on the left hand and the corresponding location on the right hand: 156.9 ± 7.1 cm). The webbing between the fingers was used, rather than finger tips, to reflect the distance from the shoulder at which an object may be grasped.

Statistical analysis

General linear repeated measures models with least-squares difference (LSD) post hoc pairwise comparisons were conducted to test for differences between course trials one to four in

the time taken to complete the course, rate of oxygen consumption ($\dot{V}_{O_2}$) during the course, and total oxygen consumed (VO_2) to complete the course. A general linear model (GLM) and a multiple linear regression (MLR) were then employed to explore the behavioural and morphological factors, respectively, that influenced the change in $\dot{V}_{O_2}$ between the athletes' 1st and 4th trials. The GLM included the change in time taken to complete the course and the two behavioural measures (change in the number of different locomotor behaviours [mode and submode – see SOM Figure S1] used between the 1st and 4th trials and whether the athletes profiled as leapers or as scramblers). The final MLR, obtained from both backwards and forwards stepwise methods, included the change in time taken to complete the course, along with two morphological variables (hip height and arm span). Analysis was performed using SPSS v19. Data figures were generated using R (R Development Core Team, 2011) and the 'beeswarm' package (Eklund, 2011). Multiple tests indicated that each model was robust. In each case the independent variable was approximately normally distributed, plots of the regression standardised residuals against the regression standardised predicted values offered little evidence of heteroscedasticity, and the partial plots also did not suggest heteroscedasticity. For the MLR there was no evidence of multicollinearity since variance inflation factors all suggested that the regressions were not biased, tolerance was always about 0.5 and each predictor variable had its variance loading on different eigenvalues. The Durbin-Watson value suggested strong independence of the residual terms, and there were no obvious patterns of over or under-dispersion, or non-homogeneity of variance. The Cook's distance values for all data points were well below 1, the Mahalanobis distances were all below 9 and the centred leverage values were

acceptable, indicating that that no data points were excessively influential. The collinearity statistics reported variance inflation factors below 4, suggesting no cause for concern. Case-wise diagnostics indicated no values with standardized residuals greater than 2.

Results

To test the validity of our model and course design, we first compared the locomotor behaviour of the parkour athletes on the course to published data for the other great apes. Our aim in the study was to present a large bodied-ape with similar mechanical challenges to those experienced in wild arboreal habitats, and to quantify the morphological attributes and behaviours that facilitated performance optimisation. Thus, it was not our purpose to specifically replicate non-human great ape locomotion. Nevertheless, the range of locomotor behaviours employed by the parkour athletes incorporated many of the behaviours exhibited by non-human apes in response to similar mechanical challenges (Fig. 1, Table 1), such as leaping, arm-swing, brachiation, and both pronograde (horizontal trunk) and orthograde (upright trunk) clambering (Hunt et al., 1996; Thorpe and Crompton, 2006). Even though the course contained much less environmental variation than the habitats in which data were collected for the other species (because all our athletes followed the course whereas the data for the other great apes is based on animals ranging freely in broad geographical areas), the results show that all of the core locomotor modes (families of biomechanically-linked types of locomotion) typical of great apes were exhibited by the athletes. Torso-pronograde suspension, ride and bridge were not exhibited by the athletes, but current data suggest they may be specific to orangutans (Thorpe and Crompton, 2006, Thorpe et al., 2009). Frequencies did, of course, differ, with the athletes' locomotion

dominated overall by bipedalism, and leaping and jumping; the last was often used in situations where wild great apes would use vertical climbing and descent.

INSERT TABLE 1 HERE

Raw data are provided in Table 2. We found that, with greater familiarity of the course, the athletes tended to complete it more quickly; Figure 2A shows that time taken to complete the course decreased significantly with each trial (for example, a mean of 8% between trials 1 and 2, $p = 0.023$; 7% between trials 2 and 3, $p = 0.011$; and 17% overall i.e. between the 1st and 4th trials, $p < 0.001$). Conversely, while $\dot{V}_{O_2}$ consequently increased with each trial (Fig. 2B), these increases were very small (2% between trials 1 and 2, $p = 0.035$; 0% between trials 2 and 3, $p = 0.761$; and overall by a mean of 3%, $p = 0.064$). As a result, VO_2 (a function of $\dot{V}_{O_2}$ and time) decreased with each trial (by 6% between 1 and 2, $p = 0.123$; then 8% between 2 and 3, $p = 0.003$; and overall by 15%, $p = 0.001$). In summary, the increases in $\dot{V}_{O_2}$ were small despite large reductions in the time taken, indicating that the athletes were improving their energetic economy to traverse the course as they became more experienced at it.

INSERT TABLE 2 HERE

Fig. 2. Time taken and oxygen consumed to complete the course on each of four attempts. Each data point is for an individual parkour athlete ($n = 19$). The thick horizontal bars amongst the data points are means, and the whiskers represent 95% confidence intervals. Percent values of change and p values are presented for pairwise comparisons between course attempts as indicated. A) time taken; B) rate of oxygen consumption; C) total oxygen consumption. The presence of horizontal lines above the graphs indicate where significant differences exist in the performance measures between different trials (* $p < 0.05$; ** $p < 0.01$, *** $p < 0.001$). Note that the y axis for each panel does not reach 0.

To identify how the athletes were able to optimise their performance, we explored the factors that influenced the change in $\dot{V}_{O_2}$ (mean: 97.6 ml O₂ min⁻¹; standard deviation: 215) between the athletes' first and fourth trials. We found that the change in time taken to complete the course, and athlete arm span and hip height combined to explain the change in $\dot{V}_{O_2}$ between the athletes' first and final trials (Table 3). There was no evidence that body mass was a predictor variable. In most instances, the athletes completed the fourth trial faster than the first. Since (as described earlier) this was on average associated with only a very small increase in $\dot{V}_{O_2}$ (Fig. 3A), our results indicate that the increased $\dot{V}_{O_2}$ was attenuated through energetic savings. Athletes with longer arm spans and, to a lesser extent, shorter legs were particularly able to attenuate the increase in $\dot{V}_{O_2}$ (Fig. 3B and C). This indicates that long arm spans and short legs improved the athletes' capacity to find energy

306 savings around the course and thus minimise the increase in rate of energy expenditure
307 associated with completing the course in a shorter time. There was no evidence to suggest
308 that the locomotor behaviour profile of each athlete (leaper or scrambler) or the proportion
309 of locomotor behaviours that they changed between the first and fourth trials influenced
310 their ability to attenuate the increase in $\dot{V}_{O_2}$.

311

312 INSERT TABLE 3 HERE

Fig. 3. Partial regression plots showing the relationships between the change in $\dot{V}_{O_2}$ between course iterations 1 and 4 and the significant explanatory variables. A: change in time taken to complete the course between iterations 1 and 4; B: arm span; C: hip height, in each case while controlling for the other significant factors. $n = 19$; each data point is for a unique athlete. For changes in rate of oxygen consumption ($\dot{V}_{O_2}$), higher values indicate that the increase in $\dot{V}_{O_2}$ between course iterations 1 and 4 was greater. For changes in time (panel A), lower values indicate that the athlete reduced their time taken to complete the 4th iteration compared to the 1st iteration by a greater amount. Thus for example in panel A, high y values, indicating that an athlete exhibited a large increase in $\dot{V}_{O_2}$ between course iterations 1 and 4, tend to be associated with low x values, which indicate that the athlete went much quicker on the 4th compared to the 1st iteration. Because partial regression plots show the effect of adding another variable to a model already populated with predictor variables, the panels herein should be interpreted qualitatively rather than quantitatively.

Discussion

Energy is a fundamental currency of life, required for all physiological and behavioural processes including growth and reproduction, and larger animals typically require more energy on a daily basis than do smaller animals (Nagy, 2005). Arboreal great apes are both large and live in an energetically challenging environment. A number of studies have indicated they display energy-saving adaptations in their locomotion (Pontzer et al., 2010; Thorpe et al., 2007). Yet to date there have not been any studies into how their morphology

and locomotor strategies provide economic efficiencies when moving around their forest habitat.

Our hypothesis that the athletes would be able to optimise their performance as they became familiar with the course was supported. However, this was not achieved entirely as we predicted. Our results offer tantalising experimental evidence that re-using the same branch-to-branch arboreal pathway just once can make a difference to energy expenditure for large bodied apes and re-using it several times may facilitate substantial energy savings. However, contrary to our prediction, the energetic benefit of route familiarity did not lie in changing locomotor behaviour at a gross level (SOM Figure S1) in response to learning about the mechanical characteristics of the supports. Nevertheless, it is likely that the athletes may have refined their behaviour at the more subtle level of hand and foot placements, stride lengths, and push off and landing forces to increase the smoothness of motion, reduce unnecessary movement and attenuate energy loss to compliant supports. Similarly, humans walking on complex terrain are able to modify foot placement to maximally harness the passive mechanical forces inherent in steady-state bipedal gait, despite the irregular stride lengths and velocity changes associated with uneven terrain (Matthis and Fajen, 2013). It is also possible that the athletes would improve their energetic economy further with continued exposure to the course both through additional refinement of their locomotor behaviour (the fact that some athletes took longer in the fourth trial than the first may suggest they were still testing ways to reduce their energetic cost) and as their muscles became habituated to the specific types of locomotion required.

Our other prediction, that performance optimisation would be linked to morphological variation between the athletes, was supported. Athletes with longer arm-spans and shorter legs were particularly able to find energetic economies to attenuate the increase in $\dot{V}_{O_2}$ associated with completing the course more quickly (Figs. 3B and C). Long arms and short legs allow living apes to harness passive mechanical forces to save energy in patterned gaits. Longer arms, for example, enhance pendulum-length in steady-state brachiation and magnify impulse in leaping, while shorter legs reduce the body's moment of inertia during arm swinging behaviours (Cartmill, 1974; Preuschoft et al., 1992, 1996), although long legs might be more beneficial during landing to allow impact forces to be absorbed over a longer period (Preuschoft et al., 1996). However, in the present study it was arm span, rather than arm length, that facilitated the largest energy savings. The mechanics of unpatterned gaits are little understood because mechanical modelling is restricted to locomotor modes that can be viewed as static systems or are broadly cyclic. However, they are generally perceived to be less beneficial for obtaining energy savings than patterned gaits. We suggest that the benefit of an elongated arm span (more so than only long arms) is that it greatly enhances reach in bridging and reaching manoeuvres, which will enhance the efficacy of both patterned and unpatterned gaits. This explains why the athletes' locomotor profiles as leapers or as scramblers (SOM Figure S2) were eliminated in the modelling process.

From an evolutionary perspective, our results imply that natural selection for increased arm span and decreased leg length in ancestral arboreal apes travelling and feeding in the forest

canopy along consistent routes could have been significantly enhanced because of their impact on the animal's energy costs. To find such strong associations within a single species with limited morphological range – the level at which selection would occur – indicates the energetic benefits that can be accrued from minor morphological variation and is fundamental to understanding the processes through which morphology changed in hominoid evolution. To our knowledge, the present study provides the first experimental evidence that directly tests the energetic benefits accrued by the evolution of key great ape morphological adaptations.

Despite large variation in the body masses of the parkour athletes (58–89 kg), their weight was not a predictor of gains in energy economy, indicating that heavy and light athletes did not differ in their ability to find energetic savings with course familiarity. This counters our hypothesis that heavier individuals would be better able than lighter individuals to work their environment to their energetic advantage, and may indicate that a threshold exists above which greater body mass does not facilitate an increased ability to utilise support compliance. While it also confirms that the statistically significant effect of arm span in this study is not simply a proxy for body size, the two are likely to be coupled. In all mammals, the thorax and the rest of the axial system provides the foundation for the production of mechanical work by the limbs (Schilling, 2011). The demands on the axial system in arboreal apes are particularly high because they require high mobility and high grip forces to manoeuvre the body in complex three-dimensional forest habitats (Myatt et al., 2011), which results in forearm flexor muscles that are nearly four times as large as in cursorial species (Alexander et al., 1981). This suggests that, as well as being under direct selection

pressure for contest competitions with monkeys, large ape body size was to some extent also an evolutionary trade-off in the selection for the broad thorax and long powerful forelimbs. Maintaining short hindlimbs would have helped minimize the increases in body mass associated with elongating the arm span.

Finally, we speculate that the implications of our study may extend beyond hominoid body mass and postcranial morphology. The energetic savings accrued by the athletes were reliant on repeated use of the same supports along their route and such behaviour could have had significant repercussions for the evolution of ape intelligence. The small size of monkeys results in minimal branch deflection under their weight, which increases the range of route choices available and results in a low risk of falls (Cartmill, 1974). In addition, they often follow geographical features such as rivers and ridges (Di Fiore and Suarez, 2007, Hopkins, 2011) and some species cover 50% of their home range every five days or less (Milton, 2000). The requirement to remember detailed route information is therefore low. In contrast, most supports deflect under an ape's large mass and may break; the dangers from falls are greater for larger animals (Cartmill, 1974) and even non-fatal falls incur a high cost through injury or time spent recovering. Nevertheless, observations of wild adult apes suggest they rarely fall or retrace their steps (Thorpe and Crompton, 2006). Thus, we suggest that to ensure that selected supports will take their weight and that they do not reach dead ends forcing detours, apes must have evolved the ability to plan suitable, indeed optimal, routes either in real time or in advance (Chappell and Thorpe, 2010; Tecwyn et al., 2013). Either option is cognitively demanding. However, we suggest that developing tree-to-tree, branch-to-branch routes in advance that are remembered, refined,

passed down the generations and only slightly modified in real time in response to forest dynamics such as tree falls or growth is less cognitively demanding than each individual independently innovating new routes every time those routes are travelled. Moreover, it is less risky because supports are familiar; it incurs a lower time cost than looking ahead to plan and, as we have shown, it is more energetically efficient since route familiarity facilitates energy savings. Thus, while enhanced intelligence must have been functionally coupled to large size over evolutionary timescales, the use of arboreal pathways would have mitigated the cognitive load of such demands on individuals. Whilst there is limited fossil evidence available for brain size in ancestral apes, the cranial capacity is measureable for the mid-Miocene *Hispanopithecus hungaricus* (Alba, 2010). The encephalisation residual (an indicator of general intelligence) of *H. hungaricus* falls within the great ape range, and contrasts with Old World monkeys and *Proconsul*, indicating that increases in ape intelligence did co-occur with large size and long arm spans.

Hunt's (2016) synthesis of the evolutionary ecology of extant apes and monkeys suggested that large ape mass was selected for because it provided a size-related advantage in contest competitions for food with monkeys. Our results expand this hypothesis to suggest that large mass evolved as part of a multifactorial functional trait complex (Cheverud, 1982) in which selection for long, strong forelimbs, broad chests and a strong axial system, enhanced intelligence and the frequent use of uniform branch-to-branch arboreal pathways were critical to off-setting the mechanical and energetic demands of large mass. Increased stability, decreased rates of fatigue and enhanced safety are other factors of likely importance during arboreal locomotion. Whilst all of these will inherently influence the

metabolic cost of locomotion, these relationships are not yet fully understood (Reilly et al., 2007). Our study thus provides novel empirical evidence to aid reconstruction of the mechanisms through which the most distinctive and unique anatomical features of ancestral apes were distinguished from those of monkeys and stem hominoids.

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LGH and SKST designed the study. LGH and SRLC collected the data. LGH and SKST analysed the data. LGH prepared the figures. SKST wrote the manuscript with input from LGH. All authors contributed to the paper and gave final approval for publication.

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573 **Table Legends**

574 Table 1. Comparison of arboreal (off ground) locomotion in the parkour athletes' final trial
575 compared to other hominoids (modified after Thorpe and Crompton, 2006).

576

577 Table 2. Athlete morphometric and time-energy data from the present study.^a

578

579 Table 3. Final model from a stepwise multivariable regression analysis to explore the factors that
580 influenced change in the rate of oxygen consumption between the 1st and 4th iteration of the course (
581 *n* = 19)^a.

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