

## Practice makes perfect

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

3

4 **Running title:** Evolution of energetic ecology in great apes

5

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21

22 **Abstract**

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

41

42 **Key words:** energy expenditure, performance optimisation, crown hominoids,  
43 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,

67 2016), but it comes at a price. Without tendon recoil to provide much of the work involved  
68 in locomotion, arboreal travel needs to be powered almost entirely by muscular contraction,  
69 which strongly influences the metabolic cost of locomotion (Reilly et al., 2007).

70

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

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

95

96 The origins of large ape size seem temporally linked to the emergence of other unique great  
97 ape traits in crown hominoids, such as long arms relative to legs (high intermembral  
98 indices) and broad but shallow chests. Thus early crown hominoids (e.g. *Morotopithecus*  
99 *bishopi*, 16–20 million years ago [MA], *Pierolapithecus catalaunicus* [11.9 MA] and  
100 *Hispanopithecus laietanus* [9.6 MA]) were similar in weight to living female orangutans  
101 (30–40 kg) and possessed transversely broad thoraces that are distinct from the  
102 dorsoventrally deep thoraces in other stem hominoids (e.g. the habitually quadrupedal  
103 proconsulid *Ekembo nyanzae*), and extant Old World monkeys (Ward, 1993; Moya-Sola  
104 and Kohler, 1996; Moya-Sola et al., 2004; Maclatchy, 2004). Limb lengths are not  
105 preserved for *Morotopithecus* or *Pierolopithecus*, but the intermembral index for  
106 *Hispanopithecus laietanus* is consistent with that of apes rather than Old World monkeys or  
107 proconsulids (Ward, 1993; Moya-Sola and Kohler, 1996). While mobile shoulders, long  
108 arms and short legs have generally been interpreted as providing postural stability and large  
109 feeding spheres for arboreal apes (Grand, 1972), they have also been predicted to increase  
110 the efficiency of patterned arboreal locomotor behaviours, such as arm swinging and  
111 climbing vertically up tree trunks (Cartmill, 1974; Preuschoft et al., 1992, 1996). Thus

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

114

115 New research has shown that many human populations remain adept at arboreal  
116 locomotion, despite being committed terrestrial bipeds (Venkataraman et al., 2013; Kraft et  
117 al., 2014). Modern humans still share with the other apes many of the adaptations for  
118 orthograde (upright-trunked) arboreality, such as the broad, shallow chest and shoulder  
119 blades positioned on the back that allow an extensive range of motion in the shoulders  
120 (Ward, 2007; Crompton et al., 2008). This allows many rainforest hunter-gatherer  
121 communities across Asia and Africa to routinely harvest arboreal resources such as honey,  
122 fruit, nuts, seeds, rattan and palm products (Venkataraman, et al., 2013, Kraft et al., 2014).  
123 Humans' natural climbing ability is also used in sports and gymnastics, particularly by  
124 parkour athletes ('traceurs'), who specialize in developing new techniques for moving  
125 through complex, three-dimensional urban environments whilst avoiding the ground. These  
126 involve the limbs in a wide range of joint positions, in suspension and compression, much  
127 like the locomotion of living non-human apes (Hunt et al., 1996; Thorpe and Crompton,  
128 2006; Kelly, 2011). In the present study, we investigate the energetics of parkour athletes as  
129 an elite and tractable hominoid model traversing an 'arboreal' assault course. Reilly et al.  
130 (2007) show that animals do not necessarily use the energetically cheapest available gaits  
131 for their primary locomotor sequences and argue that locomotor costs may be driven more  
132 by ecological relevance than by the need to optimize locomotor economy. We follow this  
133 framework by quantifying the morphological, behavioural and ecological variables that  
134 influence whether the metabolic cost of locomotion can be reduced if animals are able to

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

148

#### 149 **Material and methods**

150 The study was approved by the University of Birmingham Ethics Committee and all  
151 athletes provided written, informed consent for their participation. We measured the impact  
152 of variation in morphology and locomotor behaviour on the rate of oxygen consumption (  
153  $\dot{V}_{O_2}$ , ml O<sub>2</sub> min<sup>-1</sup>) of 19 elite male parkour athletes (aged 18–35 years) as they repeatedly  
154 traversed an arboreal-like assault course of 103 m horizontal length in a gymnasium at the  
155 University of Birmingham, U.K (from January to March 2012). The athletes traversed the  
156 course four times with a rest of at least 15 minutes between each trial. The course consisted



157 of a range of generic gymnasium apparatus such as vaulting horses, raised blocks, high  
158 bars, wall bars, and areas filled with loose foam blocks to emulate the range of mechanical  
159 conditions present in an arboreal pathway, rather than the exact structure of the forest  
160 canopy. Thus parts of the course incorporated support compliance, irregularity and  
161 discontinuity to reflect the conditions experienced during gap crossing between tree  
162 crowns, while others were rigid and predictable to reflect the phases between bouts of gap  
163 crossing when even large-bodied apes may walk into and out of the core of a tree along  
164 thick boughs (full details of the course route and types of challenge are presented in the  
165 Supplementary Online Material [SOM]). It was also designed to allow a range of locomotor  
166 solutions to each obstacle and the parkour athletes were instructed to complete the course  
167 ‘wasting as little energy as possible’. The course was co-designed by the researchers and  
168 the lead athlete from EMP Parkour, who did not subsequently take part in the experiment.  
169



170  
171 Fig. 1. Typical locomotor behaviours exhibited by the athletes. A) forelimb swing, B)  
172 vertical climb, C and D) pronograde scramble, E) brachiation, F) forelimb swing  
173

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

180

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

196

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

206

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

215

### 216 *Statistical analysis*

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

219 the time taken to complete the course, rate of oxygen consumption ( $\dot{V}_{O_2}$ ) during the course,  
220 and total oxygen consumed ( $VO_2$ ) to complete the course. A general linear model (GLM)  
221 and a multiple linear regression (MLR) were then employed to explore the behavioural and  
222 morphological factors, respectively, that influenced the change in  $\dot{V}_{O_2}$  between the athletes'  
223 1<sup>st</sup> and 4<sup>th</sup> trials. The GLM included the change in time taken to complete the course and  
224 the two behavioural measures (change in the number of different locomotor behaviours  
225 [mode and submode – see SOM Figure S1] used between the 1<sup>st</sup> and 4<sup>th</sup> trials and whether  
226 the athletes profiled as leapers or as scramblers). The final MLR, obtained from both  
227 backwards and forwards stepwise methods, included the change in time taken to complete  
228 the course, along with two morphological variables (hip height and arm span). Analysis  
229 was performed using SPSS v19. Data figures were generated using R (R Development Core  
230 Team, 2011) and the 'beeswarm' package (Eklund, 2011). Multiple tests indicated that each  
231 model was robust. In each case the independent variable was approximately normally  
232 distributed, plots of the regression standardised residuals against the regression  
233 standardised predicted values offered little evidence of heteroscedasticity, and the partial  
234 plots also did not suggest heteroscedasticity. For the MLR there was no evidence of  
235 multicollinearity since variance inflation factors all suggested that the regressions were not  
236 biased, tolerance was always about 0.5 and each predictor variable had its variance loading  
237 on different eigenvalues. The Durbin-Watson value suggested strong independence of the  
238 residual terms, and there were no obvious patterns of over or under-dispersion, or non-  
239 homogeneity of variance. The Cook's distance values for all data points were well below 1,  
240 the Mahalanobis distances were all below 9 and the centred leverage values were

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

244

## 245 **Results**

246 To test the validity of our model and course design, we first compared the locomotor  
247 behaviour of the parkour athletes on the course to published data for the other great apes.  
248 Our aim in the study was to present a large bodied-ape with similar mechanical challenges  
249 to those experienced in wild arboreal habitats, and to quantify the morphological attributes  
250 and behaviours that facilitated performance optimisation. Thus, it was not our purpose to  
251 specifically replicate non-human great ape locomotion. Nevertheless, the range of  
252 locomotor behaviours employed by the parkour athletes incorporated many of the  
253 behaviours exhibited by non-human apes in response to similar mechanical challenges (Fig.  
254 1, Table 1), such as leaping, arm-swing, brachiation, and both pronograde (horizontal  
255 trunk) and orthograde (upright trunk) clambering (Hunt et al., 1996; Thorpe and Crompton,  
256 2006). Even though the course contained much less environmental variation than the  
257 habitats in which data were collected for the other species (because all our athletes followed  
258 the course whereas the data for the other great apes is based on animals ranging freely in  
259 broad geographical areas), the results show that all of the core locomotor modes (families  
260 of biomechanically-linked types of locomotion) typical of great apes were exhibited by the  
261 athletes. Torso-pronograde suspension, ride and bridge were not exhibited by the athletes,  
262 but current data suggest they may be specific to orangutans (Thorpe and Crompton, 2006,  
263 Thorpe et al., 2009). Frequencies did, of course, differ, with the athletes' locomotion

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

266

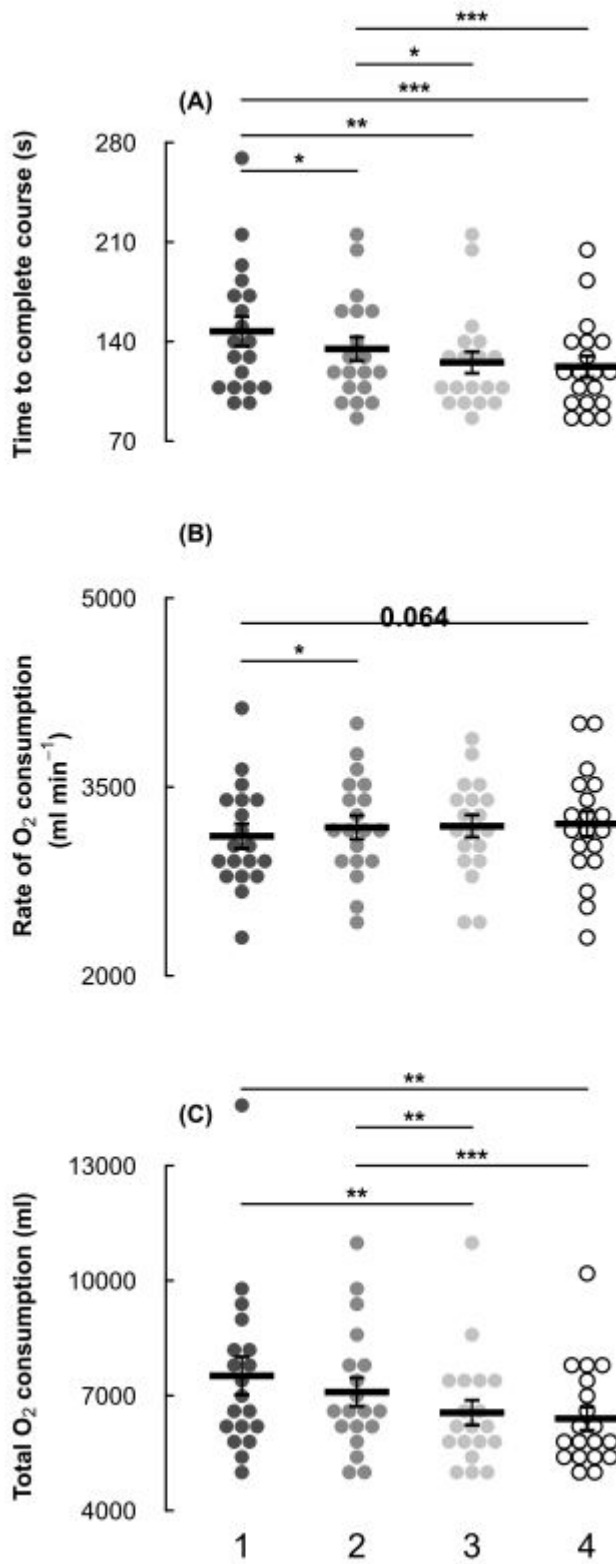
267 INSERT TABLE 1 HERE

268

269 Raw data are provided in Table 2. We found that, with greater familiarity of the course, the  
270 athletes tended to complete it more quickly; Figure 2A shows that time taken to complete  
271 the course decreased significantly with each trial (for example, a mean of 8% between trials  
272 1 and 2,  $p = 0.023$ ; 7% between trials 2 and 3,  $p = 0.011$ ; and 17% overall i.e. between the  
273 1<sup>st</sup> and 4th trials,  $p < 0.001$ ). Conversely, while  $\dot{V}_{O_2}$  consequently increased with each trial  
274 (Fig. 2B), these increases were very small (2% between trials 1 and 2,  $p = 0.035$ ; 0%  
275 between trials 2 and 3,  $p = 0.761$ ; and overall by a mean of 3%,  $p = 0.064$ ). As a result,  
276  $VO_2$  (a function of  $\dot{V}_{O_2}$  and time) decreased with each trial (by 6% between 1 and 2,  $p =$   
277  $0.123$ ; then 8% between 2 and 3,  $p = 0.003$ ; and overall by 15%,  $p = 0.001$ ). In summary,  
278 the increases in  $\dot{V}_{O_2}$  were small despite large reductions in the time taken, indicating that  
279 the athletes were improving their energetic economy to traverse the course as they became  
280 more experienced at it.

281

282 INSERT TABLE 2 HERE



284

285 Fig. 2. Time taken and oxygen consumed to complete the course on each of four attempts.  
286 Each data point is for an individual parkour athlete ( $n = 19$ ). The thick horizontal bars  
287 amongst the data points are means, and the whiskers represent 95% confidence intervals.  
288 Percent values of change and  $p$  values are presented for pairwise comparisons between  
289 course attempts as indicated. A) time taken; B) rate of oxygen consumption; C) total  
290 oxygen consumption. The presence of horizontal lines above the graphs indicate where  
291 significant differences exist in the performance measures between different trials (\*  $p <$   
292  $0.05$ ; \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ ). Note that the y axis for each panel does not reach 0.

293

294

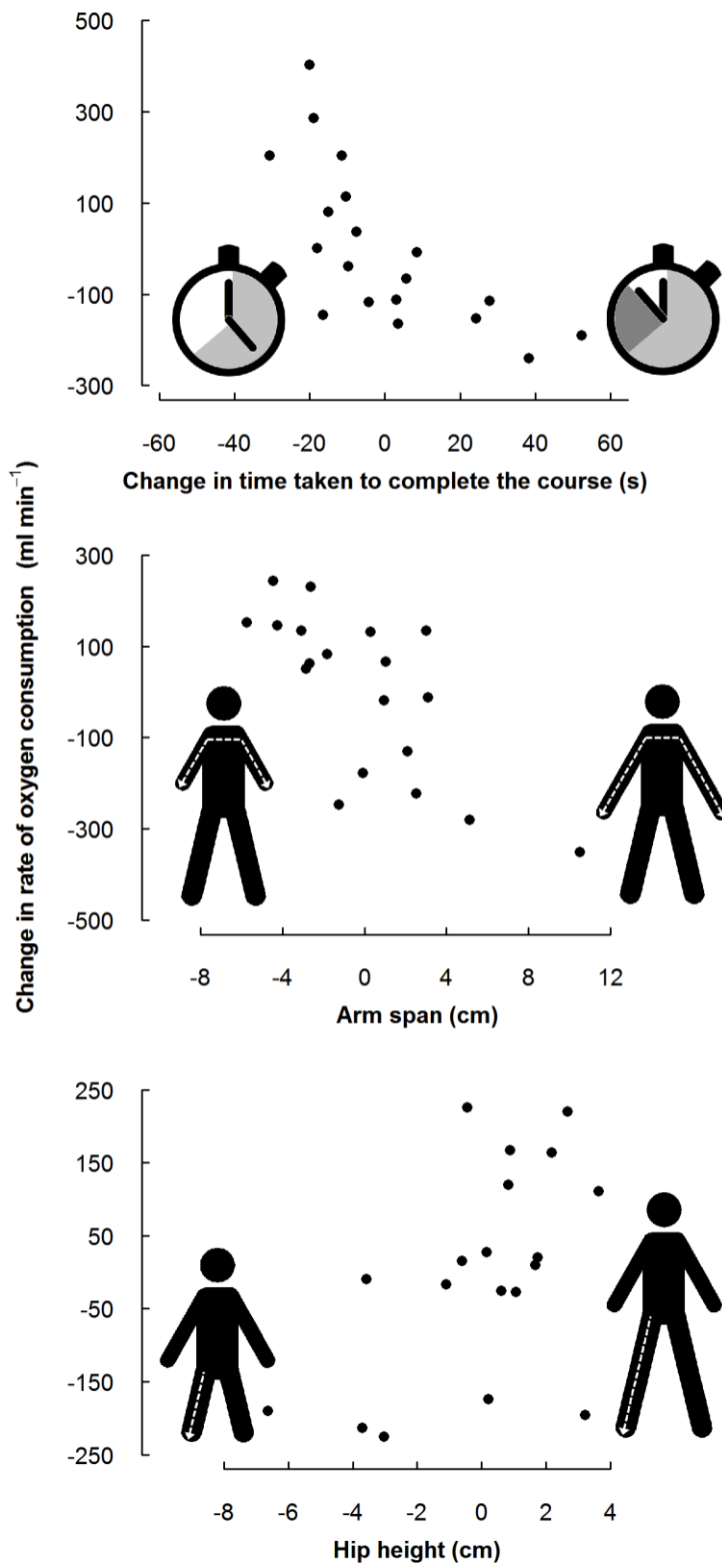
295 To identify how the athletes were able to optimise their performance, we explored the  
296 factors that influenced the change in  $\dot{V}_{O_2}$  (mean:  $97.6 \text{ ml O}_2 \text{ min}^{-1}$ ; standard deviation: 215)  
297 between the athletes' first and fourth trials. We found that the change in time taken to  
298 complete the course, and athlete arm span and hip height combined to explain the change in  
299  $\dot{V}_{O_2}$  between the athletes' first and final trials (Table 3). There was no evidence that body  
300 mass was a predictor variable. In most instances, the athletes completed the fourth trial  
301 faster than the first. Since (as described earlier) this was on average associated with only a  
302 very small increase in  $\dot{V}_{O_2}$  (Fig. 3A), our results indicate that the increased  $\dot{V}_{O_2}$  was  
303 attenuated through energetic savings. Athletes with longer arm spans and, to a lesser extent,  
304 shorter legs were particularly able to attenuate the increase in  $\dot{V}_{O_2}$  (Fig. 3B and C). This  
305 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



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

327

328

### 329 **Discussion**

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

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

338

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

358

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

378

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

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

389

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

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

408

409 Finally, we speculate that the implications of our study may extend beyond hominoid body  
410 mass and postcranial morphology. The energetic savings accrued by the athletes were  
411 reliant on repeated use of the same supports along their route and such behaviour could  
412 have had significant repercussions for the evolution of ape intelligence. The small size of  
413 monkeys results in minimal branch deflection under their weight, which increases the range  
414 of route choices available and results in a low risk of falls (Cartmill, 1974). In addition,  
415 they often follow geographical features such as rivers and ridges (Di Fiore and Suarez,  
416 2007, Hopkins, 2011) and some species cover 50% of their home range every five days or  
417 less (Milton, 2000). The requirement to remember detailed route information is therefore  
418 low. In contrast, most supports deflect under an ape's large mass and may break; the  
419 dangers from falls are greater for larger animals (Cartmill, 1974) and even non-fatal falls  
420 incur a high cost through injury or time spent recovering. Nevertheless, observations of  
421 wild adult apes suggest they rarely fall or retrace their steps (Thorpe and Crompton, 2006).  
422 Thus, we suggest that to ensure that selected supports will take their weight and that they  
423 do not reach dead ends forcing detours, apes must have evolved the ability to plan suitable,  
424 indeed optimal, routes either in real time or in advance (Chappell and Thorpe, 2010;  
425 Tecwyn et al., 2013). Either option is cognitively demanding. However, we suggest that  
426 developing tree-to-tree, branch-to-branch routes in advance that are remembered, refined,

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

440

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



450 metabolic cost of locomotion, these relationships are not yet fully understood (Reilly et al.,  
451 2007). Our study thus provides novel empirical evidence to aid reconstruction of the  
452 mechanisms through which the most distinctive and unique anatomical features of ancestral  
453 apes were distinguished from those of monkeys and stem hominoids.

454

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465

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

469

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571

572

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.<sup>a</sup>

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 1<sup>st</sup> and 4<sup>th</sup> iteration of the course (  
581  $n = 19$ )<sup>a</sup>.

582

583