

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 (\dot{V}_{O_2} , ml O₂ min⁻¹) of 19 elite male parkour athletes (aged 18–35 years) as they repeatedly
153 traversed an arboreal-like assault course of 103 m horizontal length in a gymnasium at the
154 University of Birmingham, U.K (from January to March 2012). The athletes traversed the
155 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 1st and 4th 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 ± 7.5
208 cm), mass (73.9 ± 8.1 kg), hip height (height of the anterior superior iliac spine (102.3 ± 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 ± 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 ± 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 1st and 4th 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 1st and 4th 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

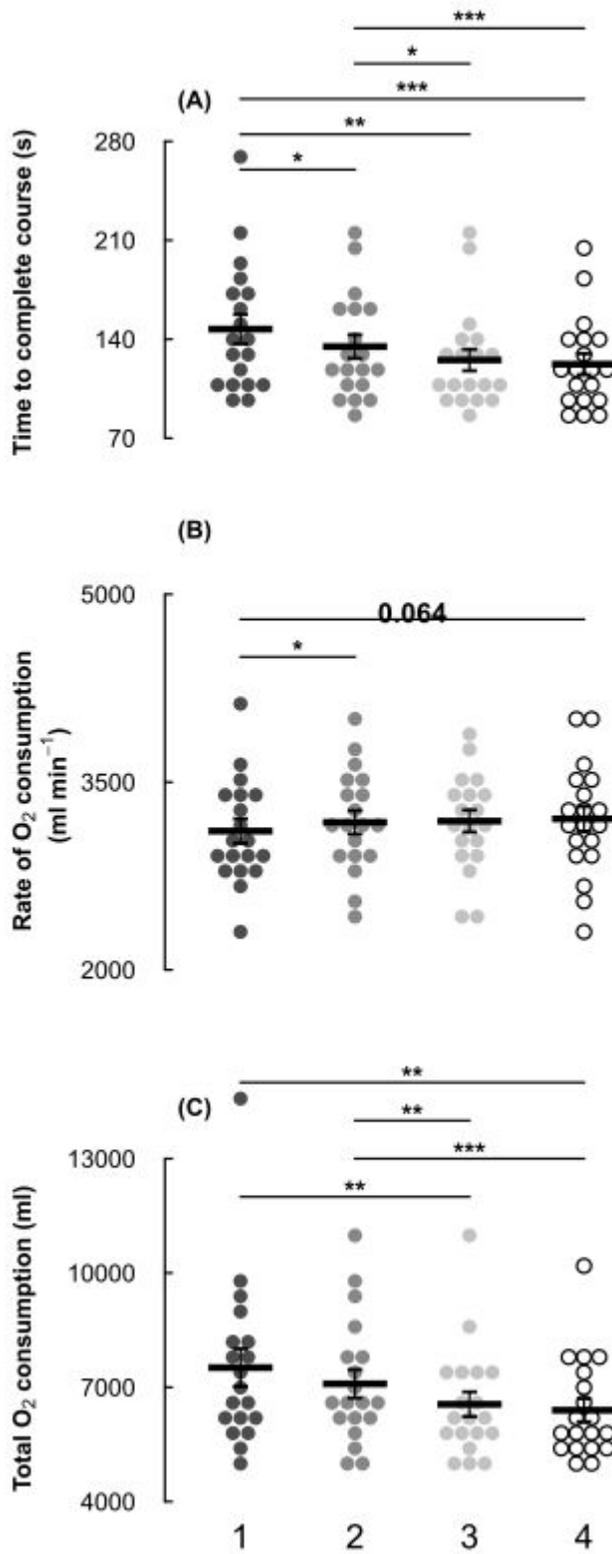
267 INSERT TABLE 1 HERE

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 1st 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

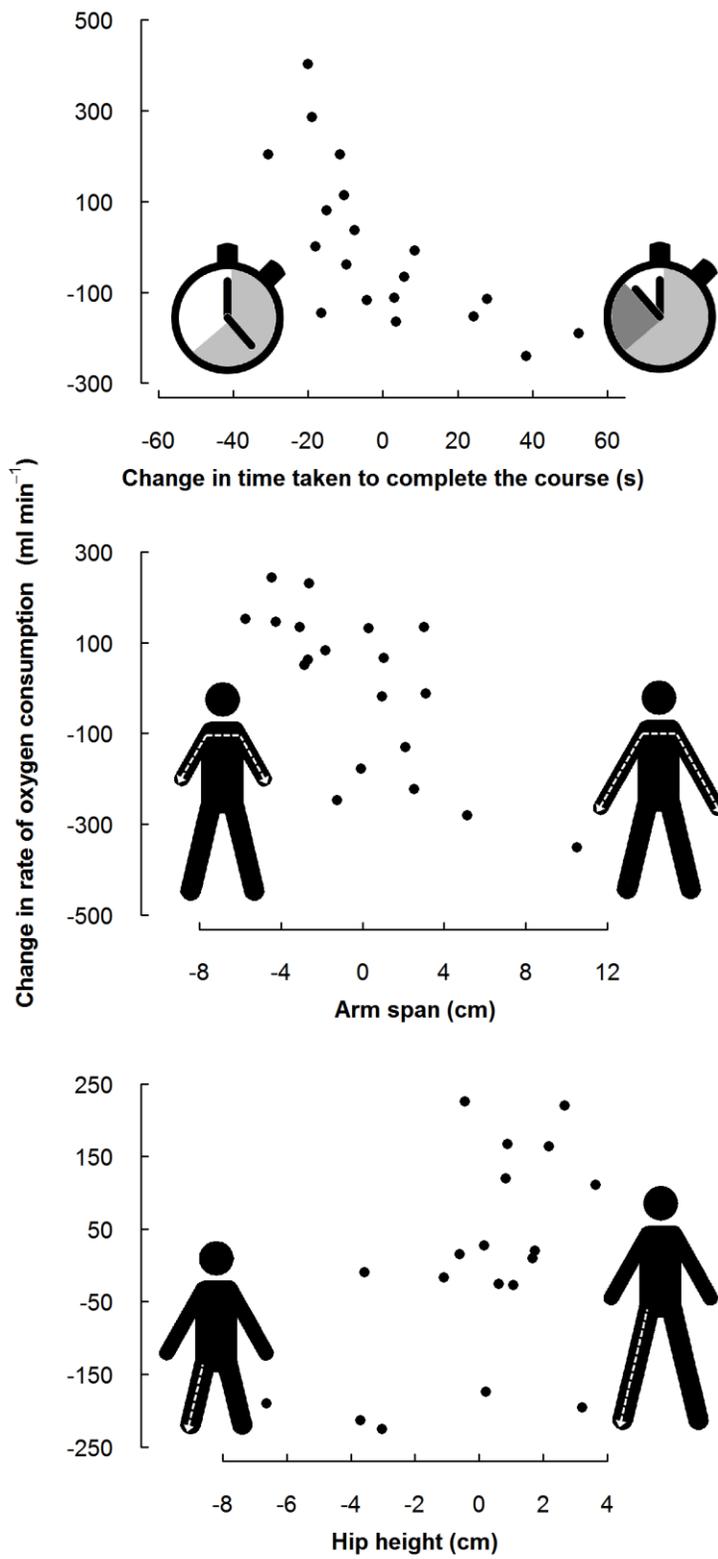
294

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 4th
321 iteration compared to the 1st 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 4th compared to the 1st 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.^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.

582

583