1   **Title: Practise makes perfect: performance optimisation in 'arboreal' parkour**

2   **athletes illuminates the evolutionary ecology of great ape anatomy**

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4   **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 it not being possible 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

46

Introduction

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

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

69   2016), but it comes at a price. Without tendon recoil to provide much of the work involved

70   in locomotion, arboreal travel needs to be powered almost entirely by muscular contraction,

71   which strongly influences the metabolic cost of locomotion (Reilly et al, 2007).

72

73   Ancestral apes must therefore have evolved morphological and behavioural mechanisms to

74   compensate for the mechanical and energetic demands associated with their large size.

75   Field observations of living apes and monkeys provide an insight into what those

76   mechanisms might have been. Whereas the arboreal pathways (habitual routes between

77   resources) of individual monkeys within a group tend to be wide, ranging 25 m from the

78   group's geographical centre (Di Fiore and Suarez, 2007, Hopkins 2011), individual apes

79   consistently use the same branches and locomotor behaviours to travel between

80   neighbouring major fruit trees and when travelling long distances between trees that fruit

81   infrequently (Mackinnon 1974; Fleagle, 1976; Thorpe and Crompton 2006). As well as

82   reducing the risk of falls, repeated use of uniform branch-to-branch routes allow apes to

83   learn about the affordances of familiar branches and lianas, which could enable them to

84   optimize performance by matching locomotor behaviours to the mechanical properties of

85   the arboreal supports. Unfortunately, very little is known about how large-bodied great apes

86   might optimize their energetic performance in arboreal locomotion, because recording

87   oxygen consumption in freely moving apes is currently impossible. However, mathematical

88   modelling of tree-sway in wild orangutans provides tantalizing evidence to support this

89   theory; orangutans, particularly large adult males, repeatedly sway compliant tree trunks

90   back and forth to cross gaps in the canopy (Thorpe and Crompton 2006). This tree-sway is

91   an order of magnitude less costly than descending to the ground and crossing terrestrially

92 (Thorpe et al, 2007), but the orangutans' repeated use of the same tree trunks for swaying

93 suggests they need to be familiar with the mechanical properties of the support. The greater

94 use of this behavior by adult males relative to females and adolescents also suggests that

95 increased size can be advantageous as compliance is greater underneath a larger body mass.

96

97 The origins of large ape size seem temporally linked to the emergence of other unique great

98 ape traits in crown hominoids, such as long arms relative to legs (high intermembral

99 indices) and broad but shallow chests. Thus early crown hominoids (e.g. *Morotopithecus*

100 *bishop,* 16-20 million years ago [MA], *Pierolapithecus catalaunicus* [11.9 MA] and

101 *Hispanopithecus laietanus [*9.6 MA]) were similar in weight to living female orangutans

102 (30-40 kg) and possessed transversely broad thoraces that are distinct from the

103 dorsoventrally deep thoraces in other stem hominoids (e.g. the habitually quadrupedal

104 *Proconsul* [*Ekembo* after McNulty et al, 2015)] *nyanzae)*, and extant old world monkeys

105 (Ward, 1993; Moya-Sola and Kohler, 1996; Moya-Sola et al 2004; Maclatchy 2004). Limb

106 lengths are not preserved for *Morotopithecus* or *Pierolopithecus*, but the intermembral

107 index for *Hispanopithecus laietanus* is also consistent with apes rather than old world

108 monkeys or proconsulids (Ward, 1993; Moya-Sola and Kohler, 1996). While mobile

109 shoulders, long arms and short legs have generally been interpreted as providing postural

110 stability and large feeding spheres for arboreal apes (Grand, 1972), they have also been

111 predicted to increase the efficiency of patterned arboreal locomotor behaviours, such as arm

112 swinging and climbing vertically up tree trunks (Cartmill, 1974; Preuschoft et al., 1992,

113 1996). Thus these morphological features might also allow arboreal apes to optimise their

114 locomotor performance over time.

115

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 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 utilized 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 their energetically cheapest gaits available 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

138 energetic performance as they become familiar with the affordances of the course.

139 Specifically we predict: 1) that improved energy economies will be achieved through

140 changing locomotor behaviour in response to learning about the mechanical characteristics

141 of the supports, and that the athletes' ability to optimise performance will be influenced by

142 their morphology such that 2) heavier individuals and 3) those with relatively longer arm

143 spans and shorter legs will be better able to work their environment to their advantage and

144 exploit support compliance as they become familiar with it, compared to those with the

145 converse morphologies.

146

147 Our experimental approach has made it possible to flesh out the scanty fossil record

148 through quantifying the energy economies of locomotion gained by a large-bodied ape from

149 repeatedly traversing an arboreal route, and how these gains are moderated by morphology

150 and locomotor behaviour.

151

152 **Material and methods**

153 All participants provided written, informed consent. We measured the impact of variation

154 in morphology and locomotor behaviour on the rate of oxygen consumption ($\dot{V}_{O_2}$, ml O_2

155 min^{-1}) of 19 elite male parkour athletes (age: 18-35 years) as they repeatedly traversed an

156 arboreal-like assault course of 103 m horizontal length in a gymnasium at the University of

157 Birmingham, U.K (from January to March of 2012). The athletes traversed the course four

158 times with a rest of at least 15 minutes between each trial. The course consisted of a range

159 of generic gymnasium apparatus such as vaulting horses, raised blocks, high bars, wall

160   bars, and areas filled with loose foam blocks to emulate the range of mechanical conditions

161   present in an arboreal pathway, rather than the exact structure of the forest canopy. Thus

162   parts of the course incorporated support compliance, irregularity and discontinuity to reflect

163   the conditions experienced during gap crossing between tree crowns, while others were

164   rigid and predictable to reflect the phases between bouts of gap crossing when even large-

165   bodied apes may walk into and out of the core of a tree along thick boughs (full details of

166   the course route and types of challenge are presented in the Supplementary material:

167   Methods). It was also designed to allow a range of locomotor solutions to each obstacle and

168   the parkour athletes were instructed to complete the course 'wasting as little energy as

169   possible'. The course was co-designed between the researchers and the lead athlete from

170   EMP parkour, who did not subsequently take part in the experiment.

171   INSERT FIGURE 1 HERE

172

173   Before their first trial, the athletes were shown around the course to familiarise them with

174   the general route to be taken, the obstacles to be traversed, and the few 'rules' to be

175   followed, such as not touching the ground and not using the edges of certain obstacles.

176   They were then allowed two minutes to further look around (but not touch) the course. This

177   ensured that athletes were relatively naïve concerning the mechanical properties of the

178   supports for their first trial, while being clear about the general route.

179

180    $\dot{V}_{O_2}$ of the athletes was measured via a mobile respiratory gas analyser (Oxycon mobile,

181   Viasys, Germany). Immediately prior to each course attempt the athletes were required to

182   undertake a low-intensity 5-minute graded warm up on a rowing machine where for the

183   first minute they performed a stroke once every 5 s, then once every 4 s, and once every 3 s

184   for the final three minutes. Within a minute of completion of the rowing they started the

185   course. This procedure ensured aerobic metabolism was primary throughout each trial. We

186   were able to confirm that while traversing the course the athletes were mainly metabolising

187   aerobically from respiratory exchange ratios almost always being below 1 and otherwise

188   below 1.1, and rating of perceived exertion (RPE) scores almost always below 16 and

189   otherwise below 17 (Scherr et al., 2012). Measures of $\dot{V}_{O_2}$ are considered to be an accurate

190   representation of rate of energy expenditure during mainly aerobic activity. The athletes

191   had at least 15 minutes of rest before undertaking the next iteration of the course and

192   reported being fully recovered each time. Mean RPE scores did not differ between

193   iterations 1 and 4 of the course.

194

195   The athletes were also video-recorded at 25 frames per second (DCR-SR90, Sony, Japan)

196   to allow subsequent identification of locomotor behaviours. From this two measures were

197   calculated: a) the proportion of locomotor behaviours that were changed between each

198   athlete's 1st and 4th trials (see Supplementary Figure 1) and b) whether the athletes profiled

199   as 'leapers' whereby they employed predominantly patterned gaits such as leaping,

200   brachiation and vertical climbing, or as 'scramblers', whereby they exhibited

201   predominantly unpatterned clambering gaits. Separation of the athletes into patterned and

202   unpatterned locomotor profiles was based on the fact that they clearly employed one of

203 these locomotor strategies rather than combining the two types of locomotion (see

204 Supplementary Figure 2).

205

206 The following morphometric data were collected from each participant: height (178.7 ± 7.5

207 cm), mass (73.9 ± 8.1 kg), hip height (height of the anterior superior iliac spine; 102.3 ± 4.9

208 cm), right arm length (distance between the acromion process and the webbing between the

209 thumb and index finger; 60.2 ± 4.9 cm) and arm span (distance between the webbing

210 between the thumb and index finger on the left hand and the corresponding location on the

211 right hand: 156.9 ± 7.1 cm). The webbing between the fingers was used rather than finger

212 tips to reflect the distance from the shoulder at which an object may be grasped.

213

214 *Statistical Analysis*

215 General linear repeated measures models with least-squares difference (LSD) post hoc pair-

216 wise comparisons were conducted to test for differences between course trials one to four in

217 the time taken to complete the course, rate of oxygen consumption ($\dot{V}_{O_2}$) during the course,

218 and total oxygen consumed (VO_2) to complete the course. A general linear model (GLM)

219 and a multiple linear regression (MLR) were then employed to explore the behavioural and

220 morphological factors, respectively, that influenced the change in $\dot{V}_{O_2}$ between the athletes'

221 1st and 4th trials. The GLM included the change in time taken to complete the course and

222 the two behavioural measures (change in the number of different locomotor behaviours

223 [mode and submode – see Supplementary Figure 1]) used between the 1st and 4th trials and

224 whether the athletes profiled as leapers or as scramblers). The final MLR, obtained from

225   both backwards and forwards stepwise methods, included the change in time taken to

226   complete the course along with two morphological variables: hip height and arm span).

227   Analysis was performed using SPSS v19. Data figures were generated using R (R

228   Development Core Team, 2011) and the 'beeswarm' package (Eklund, 2011). Multiple

229   tests indicated that each model was robust. In each case the independent variable was

230   approximately normally distributed, plots of the regression standardised residuals against

231   the regression standardised predicted values offered little evidence of heteroscedasticity,

232   and the partial plots also did not suggest heteroscedasticity. For the MLR there was no

233   evidence of multicollinearity since variance inflation factors all suggested that the

234   regressions were not biased, tolerance was always about 0.5 and each predictor variable had

235   its variance loading on different eigenvalues. The Durbin-Watson value suggested strong

236   independence of the residual terms, and there were no obvious patterns of over or under-

237   dispersion, or non-homogeneity of variance. The Cook's distance values for all data points

238   were well below 1, the Mahalanobis distances were all below 9 and the centred leverage

239   values were acceptable, indicating that that no data points were excessively influential. The

240   collinearity statistics reported variance inflation factors below 4 suggesting no cause for

241   concern. Case-wise diagnostics indicated no values with standardized residuals greater than

242   2.

243

244   **Results**

245   We first compared the locomotor behaviour of the parkour athletes on the course to

246   published data for the other great apes, to test the validity of our model and course design.

247   Our aim in the study was to present a large bodied-ape with similar mechanical challenges

248   to those experienced in wild arboreal habitats, and to quantify the morphological attributes

249   and behaviours that facilitated performance optimisation, thus it was not our purpose to

250   specifically replicate non-human great ape locomotion. Nevertheless, the range of

251   locomotor behaviours employed by the parkour athletes incorporated many of the

252   behaviours exhibited by non-human apes in response to similar mechanical challenges (Fig.

253   1, Table 1), such as leaping, arm-swing, brachiation, and both pronograde (horizontal

254   trunk) and orthograde (upright trunk) clambering (Hunt et al, 1996: Thorpe and Crompton

255   2006). Even though the course contained much less environmental variation than the

256   habitats in which data were collected for the other species (because all our athletes followed

257   the course whereas the data for the other great apes is based on animals ranging freely in

258   broad geographical areas), the results show that all of the core locomotor modes (families

259   of biomechanically-linked types of locomotion) typical of great apes were exhibited by the

260   athletes. Torso-pronograde suspension, ride and bridge were not exhibited by the athletes,

261   but current data suggest they may be specific to orangutans (Thorpe and Crompton 2006,

262   Thorpe et al, 2009). Frequencies did of course differ, with the athletes' locomotion

263   dominated overall by bipedalism, and leaping and jumping; the latter was often used in

264   situations where wild great apes would use vertical climbing and descent.

265

266   INSERT TABLE 1 HERE

267

268   Raw data are provided in Table 2. We found that, with greater familiarity of the course, the

269   athletes tended to complete it more quickly; Figure 2A shows that time taken to complete

270   the course decreased significantly with each trial (for example, a mean of 8% between trials

271   1 and 2, P = 0.023; 7% between trials 2 and 3, P = 0.011; and 17% overall i.e. between the

272   1st and 4th trials, P < 0.001). Conversely, while $\dot{V}_{O_2}$ consequently increased with each trial

273   (Fig. 2B), these increases were very small (2% between trials 1 and 2, P = 0.035; 0%

274   between trials 2 and 3, P = 0.761; and overall by a mean of 3%, P = 0.064). As a result,

275   VO$_2$ (a function of $\dot{V}_{O_2}$ and time) decreased with each trial (by 6% between 1 and 2, P =

276   0.123; then 8% between 2 and 3, P = 0.003; and overall by 15%, P = 0.001). In summary,

277   the increases in $\dot{V}_{O_2}$ were small despite large reductions in the time taken, indicating that

278   the athletes were improving their energetic economy to traverse the course as they became

279   more experienced at it.

280

281   INSERT TABLE 2 HERE

282   INSERT FIGURE 2 HERE

283

284   To identify how the athletes were able to optimise their performance we explored the

285   factors that influenced the change in $\dot{V}_{O_2}$ (mean: 97.6 ml O$_2$ min^{-1}; standard deviation: 215)

286   between the athletes' 1st and 4th trials. We found that the change in time taken to complete

287   the course, and athlete arm span and hip height combined to explain the change in $\dot{V}_{O_2}$

288   between the athletes' first and final trials (Table 3). There was no evidence that body mass

289   was a predictor variable. In most instances the athletes completed the 4th trial faster than the

290   1st. Since (as described earlier) this was on average associated with only a very small

291   increase in $\dot{V}_{O_2}$ (Fig. 3A), our results indicate that the increased $\dot{V}_{O_2}$ was attenuated

292   through energetic savings. Athletes with longer arm spans and, to a lesser extent, shorter

293   legs were particularly able to attenuate the increase in $\dot{V}_{O_2}$ (Fig. 3B and C). This indicates

294   that long arm spans and short legs improved the athletes' capacity to find energy savings

295   around the course and thus minimise the increase in rate of energy expenditure associated

296   with completing the course in a shorter time. There was no evidence to suggest that the

297   locomotor behaviour profile of each athlete (leaper or scrambler) or the proportion of

298   locomotor behaviours that they changed between the 1st and 4th trials influenced their

299   ability to attenuate the increase in $\dot{V}_{O_2}$.

300

301   INSERT TABLE 3 HERE

302   INSERT FIGURE 3 HERE

303

304

305   **Discussion**

306   Energy is a fundamental currency of life, required for all physiological and behavioural

307   processes including growth and reproduction, and larger animals typically require more

308   energy on a daily basis than do smaller animals (Nagy, 2005). Arboreal great apes are both

309   large and live in an energetically challenging environment. A number of studies have

310   indicated they display energy-saving adaptations in their locomotion (Pontzer et al., 2010;

311   Thorpe et al., 2007). Yet to date there have not been any studies into how their morphology

312   and locomotor strategies provide economic efficiencies when moving around their forest

313   habitat.

314

315   Our hypothesis that the athletes would be able to optimise their performance as they

316   became familiar with the course was supported. However, this was not achieved entirely as

317   we predicted. Our results offer tantalising experimental evidence that re-using the same

318   branch-to-branch arboreal pathway just once can make a difference to energy expenditure

319   for large bodied apes and re-using it several times may facilitate substantial energy savings.

320   However, contrary to our prediction, the energetic benefit of route familiarity did not lie in

321   changing locomotor behaviour at a gross level (Supplementary Figure 1) in response to

322   learning about the mechanical characteristics of the supports. Nevertheless, it is likely that

323   the athletes may have refined their behaviour at the more subtle level of hand and foot

324   placements, stride lengths, and push off and landing forces to increase the smoothness of

325   motion, reduce unnecessary movement and attenuate energy loss to compliant supports.

326   Similarly, humans walking on complex terrain are able to modify foot placement to

327   maximally harness the passive mechanical forces inherent in steady-state bipedal gait,

328   despite the irregular stride lengths and velocity changes associated with uneven terrain

329   (Matthis and Fajen, 2013). It is also possible that the athletes would further improve their

330   energetic economy with continued exposure to the course both through further refinement

331   of their locomotor behaviour (the fact that some athletes took longer in the 4th trial than the

332   first may suggest they were still testing ways to reduce their energetic cost) and as their

333   muscles became habituated to the specific types of locomotion required.

334

335   Our other prediction, that performance optimisation would be linked to morphological

336   variation between the athletes, was supported. Athletes with longer arm-spans and shorter

337   legs were particularly able to find energetic economies to attenuate the increase in $\dot{V}_{O_2}$

338   associated with completing the course more quickly (Figs. 3B and C). Long arms and short

339   legs allow living apes to harness passive mechanical forces to save energy in patterned

340   gaits. Longer arms, for example, enhance pendulum-length in steady-state brachiation and

341   magnify impulse in leaping, while shorter legs reduce the body's moment of inertia during

342   arm swinging behaviours (Cartmill, 1974; Preuschoft et al., 1992, 1996) (although long

343   legs might be more beneficial during landing to allow impact forces to be absorbed over a

344   longer period) (Preuschoft et al, 1996). However, in the present study it was arm span

345   rather than arm length that facilitated the largest energy savings. The mechanics of

346   unpatterned gaits are little understood because mechanical modelling is restricted to

347   locomotor modes that can be viewed as static systems or are broadly cyclic. However, they

348   are generally perceived to be less beneficial for obtaining energy savings than patterned

349   gaits. We suggest that the benefit of an elongated arm span (more so than only long arms) is

350   that it greatly enhances reach in bridging and reaching manoeuvres, which will enhance the

351   efficacy of both patterned and unpatterned gaits. This explains why the athletes' locomotor

352   profiles as leapers or as scramblers (Supplementary Figure 2) were eliminated in the

353   modelling process.

354

355   From an evolutionary perspective, our results imply that natural selection for increased arm

356   span and decreased leg length in ancestral arboreal apes travelling and feeding in the forest

357   canopy along consistent routes could have been significantly enhanced because of its

358   impact on the animal's energy costs. To find such strong associations within a single

359 species with limited morphological range - the level at which selection would occur -

360 indicates the energetic benefits that can be accrued from minor morphological variation and

361 is fundamental to understanding the processes through which morphology changed in

362 hominoid evolution. To our knowledge the present study provides the first experimental

363 evidence that directly tests the energetic benefits accrued by the evolution of key great ape

364 morphological adaptations.

365

366 Despite large variation in the body masses of the parkour athletes (58-89 kg), their weight

367 was not a predictor of gains in energy economy, indicating that heavy and light athletes did

368 not differ in their ability to find energetic savings with course familiarity. This counters our

369 hypothesis that heavier individuals would be better able than lighter individuals to work

370 their environment to their energetic advantage, and may indicate that a threshold exists

371 above which greater body mass does not facilitate an increased ability to utilise support

372 compliance. While it also confirms that the statistically significant effect of arm span in this

373 study is not simply a proxy for body size, the two are likely to be coupled. In all mammals

374 the thorax and the rest of the axial system provides the foundation for the production of

375 mechanical work by the limbs (Schilling, 2011). The demands on the axial system in

376 arboreal apes are particularly high because they require high mobility and high grip forces

377 to manoeuvre the body in complex three-dimensional forest habitats (Myatt et al, 2011),

378 which results in forearm flexor muscles that are nearly four times as large as in cursorial

379 species (Alexander et al, 1981). This suggests that, as well as being under direct selective

380 pressure for contest competitions with monkeys, large ape body size was to some extent

381 also an evolutionary trade-off in the selection for the broad thorax and long powerful

382   forelimbs. Maintaining short hindlimbs would have helped minimize the increases in body

383   mass associated with elongating the arm span.

384

385   Finally, we speculate that the implications of our study may extend beyond hominoid body

386   mass and postcranial morphology. The energetic savings accrued by the athletes were

387   reliant on repeated use of the same supports along their route and such behaviour could

388   have had significant repercussions for the evolution of ape intelligence. The small size of

389   monkeys results in minimal branch deflection under their weight, which increases the range

390   of route choices available and results in a low risk of falls (Cartmill, 1974). In addition,

391   they often follow geographical features such as rivers and ridges (Di Fiore and Suarez,

392   2007, Hopkins 2011) and some species cover 50% of their home range every 5 days or less

393   (Milton, 2000). The requirement to remember detailed route information is therefore low.

394   In contrast, most supports deflect under an ape's large mass and may break; the dangers

395   from falls are greater for larger animals (Cartmill, 1974) and even non-fatal falls incur a

396   high cost through injury or time spent recovering. Nevertheless, observations of wild adult

397   apes suggest they rarely fall or retrace their steps (Thorpe and Crompton, 2006). Thus, we

398   suggest that to ensure that selected supports will take their weight and that they do not

399   reach dead ends forcing detours, apes must have evolved the ability to plan suitable, indeed

400   optimal, routes either in real time or in advance (Chappell and Thorpe, 2010; Tecwyn et al,

401   2013). Either option is cognitively demanding. However, we suggest that developing tree-

402   to-tree, branch-to-branch routes in advance that are remembered, refined, passed down the

403   generations and only slightly modified in real time in response to forest dynamics such as

404   tree falls or growth is less cognitively demanding than each individual independently

405 innovating new routes every time those routes are travelled. Moreover, it is less risky

406 because supports are familiar; it incurs a lower time cost than looking ahead to plan and, as

407 we have shown, it is more energetically efficient since route familiarity facilitates energy

408 savings. Thus, while enhanced intelligence must have been functionally coupled to large

409 size over evolutionary timescales, the use of arboreal pathways would have mitigated the

410 cognitive load of such demands on individuals. Whilst there is limited fossil evidence

411 available for brain size in ancestral apes, the cranial capacity is measureable for the mid-

412 Miocene *Hispanopithecus hungaricus* (Alba, 2010). The encephalisation residual (an

413 indicator of general intelligence) of *H. hungaricus* falls within the great ape range, and

414 contrasts with old world monkeys and Proconsul, indicating that increases in ape

415 intelligence did co-occur with large size and long arm spans.

416

417 Hunt's (2016) synthesis of the evolutionary ecology of extant apes and monkeys suggested

418 that large ape mass was selected for because it provided a size-related advantage in contest

419 competitions for food with monkeys. Our results expand this hypothesis to suggest that

420 large mass evolved as part of a multifactorial functional trait complex (Cheverud, 1982) in

421 which selection for long, strong forelimbs, broad chests and a strong axial system,

422 enhanced intelligence and the frequent use of uniform branch-to-branch arboreal pathways

423 were critical to off-setting the mechanical and energetic demands of large mass. Increased

424 stability, decreased rates of fatigue, and enhanced safety are other factors of likely

425 importance during arboreal locomotion. Whilst all of these will inherently influence the

426 metabolic cost of locomotion, these relationships are not yet fully understood (Reilly et al,

427 2007). Our study thus provides novel empirical evidence to aid reconstruction of the

428   mechanisms through which ancestral apes began to distinguish their most distinctive and

429   unique anatomical features from monkeys and stem hominoids.

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439

440   **Statement of Authorship:** LGH and SKST designed the study. LGH and SRLC collected

441   the data. LGH and SKST analysed the data. LGH prepared the figures. SKST wrote the

442   manuscript with input from LGH. All authors contributed to the paper and gave final

443   approval for publication.

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448   The authors declare they have no conflicting interests associated with this manuscript. On

449   acceptance the data will be Archived in Researchgate.

450

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561 Table legends

562 **Table 1. Arboreal locomotion in the parkour athletes' final trial compared to other**

563 **hominoids** (modified after Thorpe and Crompton, 2006)

564

565 **Table 2. Locomotor behaviour, athlete morphometric, and time-energy data from the**

566 **present study.** Each row is for an individual athlete (N = 19).

567

568 **Table 3. Final model generated from a stepwise multivariate regression analysis to**

569 **explore the factors that influence change in the rate of oxygen consumption ($\dot{V}_{O_2}$) of**

570 **parkour athletes traversing the course between the 1st and 4th iterations (N = 19).**

571

572 Figure legends

573 **Fig. 1. Typical locomotor behaviours exhibited by the athletes.** A) forelimb swing, B)

574 vertical climb, C and D) pronograde scramble, E) brachation, F) forelimb swing

575

576 **Fig. 2. Time taken and oxygen consumed to complete the course on each of four**

577 **attempts.** Each data point is for an individual parkour athlete (N = 19). The thick

578 horizontal bars amongst the data points are means, and the whiskers represent 95%

579 confidence intervals. % values of change and *p* values are presented for pairwise

580 comparisons between course attempts as indicated. A) time taken; B) rate of oxygen

581 consumption; C) total oxygen consumption. The presence of horizontal lines above the

582   graphs indicate where significant differences exist in the performance measures between

583   different trials (*: P < 0.05; **: P < 0.01, ***: P < 0.001). Note that the y axis for each

584   panel does not reach 0.

585

586   **Fig. 3. Partial regression plots showing the relationships between the change in** $\dot{V}_{O_2}$

587   **between course iterations 1 and 4 and the significant explanatory variables**. A: change

588   in time taken to complete the course between iterations 1 and 4; B: arm span; C: hip height,

589   in each case while controlling for the other significant factors. N = 19; **e**ach data point is for

590   a unique athlete. For changes in rate of oxygen consumption ($\dot{V}_{O_2}$), higher values indicate

591   that the increase in $\dot{V}_{O_2}$ between course iterations 1 and 4 was greater. For changes in time

592   (panel A), lower values indicate that the athlete reduced their time taken to complete the 4th

593   iteration compared to the 1st iteration by a greater amount. Thus for example in panel A,

594   high y values, indicating that an athlete exhibited a large increase in $\dot{V}_{O_2}$ between course

595   iterations 1 and 4, tend to be associated with low x values, which indicate that the athlete

596   went much quicker on the 4th compared to the 1st iteration. Because partial regression plots

597   show the effect of adding another variable to a model already populated with predictor

598   variables, the panels herein should be interpreted qualitatively rather than quantitatively.

599
600