

Sex differences in the movement patterns of free-ranging chimpanzees (*Pan troglodytes schweinfurthii*): foraging and border checking

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6 **Sex differences in the movement patterns of free-ranging chimpanzees (*Pan***
7 ***troglodytes schweinfurthii*): foraging and border checking**

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17

18 Keywords: Chimpanzees (*Pan troglodytes*); Range use; Sex differences; Fission-fusion;
19 Individual movement patterns; Border checking.

20

21

22 **Abstract**

23 **Most social primates live in cohesive groups, so travel paths inevitably reflect**
24 **compromise: decision processes of individuals are obscured. The fission-fusion**
25 **social organisation of the chimpanzee, however, allows an individual's movements to**
26 **be investigated independently. We followed 15 chimpanzees (8 male and 7 female)**
27 **through the relatively flat forest of Budongo, Uganda, plotting the path of each**
28 **individual over periods of 1-3 days. Chimpanzee movement was parsed into phases**
29 **ending with halts of more than 20 minutes, during which individuals fed, rested or**
30 **engaged in social activities. Males, lactating or pregnant females, and sexually**
31 **receptive females all travelled similar average distances between halts, at similar**
32 **speeds, and along similarly direct beeline paths. Compared to lactating or pregnant**
33 **females, males did travel for a significantly longer time each day and halted more**
34 **often, but the most striking sex differences appeared in the organisation of**
35 **movement phases into a day's path. After a halt, males tended to continue in the**
36 **same direction as before. Lactating or pregnant females showed no such strategy**
37 **and often retraced the preceding phase, returning to previously visited food patches.**
38 **We suggest that female chimpanzee movements approximate an optimal solution to**
39 **feeding requirements, whereas the paths of males allow integration of foraging with**
40 **territorial defence. The 'continually moving forwards' strategy of males enables**
41 **them to monitor their territory boundaries – border checking – whilst foraging,**
42 **generally avoiding the explicit boundary patrols observed at other chimpanzee**
43 **study sites.**

44

45 Most studies of movement by primates have analysed ranging at a group level, because
46 most primate species range as cohesive groups. The ranging behaviour of individual
47 males and females living in a group inevitably represents compromise, as the optimal
48 strategy of an individual must be modified at different times in order to maintain the
49 benefits of grouping {Couzin, 2005 #3737; Kummer, 1968 #352; Moss, 1988 #3744;
50 Prins, 1996 #3751}. The decision process of any one animal of either sex is therefore
51 obscured. Here, we investigate the movement paths of individual chimpanzees.
52 Chimpanzees live in dispersed, ‘fission-fusion’ social groups called communities or unit
53 groups, in which individuals may travel alone or together with others of either sex within
54 the common home range {Goodall, 1986 #50; Nishida, 1990 #2691; Wrangham, 1979
55 #2411}. Temporary sub-groups or ‘parties’ vary in size and composition, and any one
56 party can persist for a few minutes to many hours. Thus, despite being social animals, the
57 ranging behaviour of an adult chimpanzee is more likely to reflect its personal decisions,
58 rather than a group compromise. We can therefore consider how a chimpanzee’s
59 navigational capabilities allow it to optimise the goals of daily movement paths, and how
60 that affects the overall socio-ecological strategy of males and females.

61 According to optimal foraging theory, movement strategy should maximise
62 fitness benefits relative to costs, for example by minimizing the time and energy spent
63 acquiring adequate nutrition. For mammals, female fitness - measured as reproductive
64 success - is linked directly to nutritional status, due to the high metabolic costs associated
65 with gestation and lactation {Lee, 1987 #1184}. Male fitness, in contrast, is limited by
66 number of potential mates {Krebs, 1997 #3740}. Thus, the life history of female
67 mammals should be primarily aimed at maximising feeding efficiency, whilst males are

68 expected to maximise their access to females {Sterck, 1997 #1932; van Schaik, 1989
69 #3758; Wrangham, 1979 #2411}. These divergent life histories necessitate differential
70 use of food and other resources, with many species therefore exhibiting sex-specific
71 ranging {Dunbar, 1988 #1177}.

72 The observed movement patterns of male and female chimpanzees vary across
73 study sites, presumably as a function of differing ecological constraints (see Lehmann
74 and Boesch, 2005){#3743}. In general, however, male chimpanzees move over a larger
75 area with longer daily range lengths than lactating females, whilst sexually receptive
76 females (those exhibiting ano-genital swellings) are known to move out of their normal
77 range areas in order to associate with males {Tutin, 1979 #115; Goodall, 1986 #50;
78 Nishida, 1987 #3749}. It is currently unclear how lactating females achieve the shorter
79 daily range lengths, and what impact this has on the resources they exploit. Compared
80 with males, they might visit fewer resources per day, travel shorter distances between
81 resources, move more slowly between resources, or spend less time travelling.

82 The larger ranges of males are thought to function in allowing territorial defence.
83 At several sites, male chimpanzees cooperate to actively exclude non-community
84 members from their range. Parties of males make ‘boundary patrols’ in border zones,
85 attacking and sometimes killing males, non-sexually receptive females, and/or their
86 infants, from neighbouring communities {Boesch, 2000 #2965; Chapman, 1993 #3735;
87 Sherrow, 2007 #3755; Watts, 2001 #3759; Wrangham, 1980 #3765}. During these
88 patrols, which are quite distinct from foraging movements, males become silent, walk in
89 single file, and do not feed. Although the time and energy male primates expend in active
90 territorial defence undermines their nutritional intake {Strier, 2000 #2656}, the

91 reproductive success of male chimpanzees is at least partly dependent on their ability to
92 defend the community {Wrangham, 1980 #3765}. Male chimpanzees specifically defend
93 the feeding area rather than females per se: increasing the territory size increases the food
94 availability and therefore the reproductive success of the community females {Williams,
95 2004 #3763}. The territorial behaviour of males renders border areas unsafe, however,
96 and it is because of this danger that females tend to avoid the edges of the territory
97 {Chapman, 1993 #3735; Watts, 2002 #3760}.

98 In this study, we compare the movements of individual adult chimpanzees of the
99 Sonso community of the Budongo Forest Reserve, Uganda, a community where boundary
100 patrols have rarely been seen {Reynolds, 2005 #3753}. GPS was used to construct high-
101 resolution maps of individual chimpanzees' movement paths. We parsed each path into
102 'phases' of movement between potentially important resources, evaluating each
103 movement phase on a series of measurable parameters. We then separately examined the
104 geometry of male and female routes, assessing how phases were structured into each
105 complete movement path, with the aim of deducing the ranging strategies used by
106 individual males and females.

107

108 **Materials and Methods**

109 **Study Site and Subjects**

110 The Budongo Forest Reserve, Uganda, consists of moist, medium-altitude tropical forest
111 covering 793km² {Reynolds, 2005 #3753}. With an estimated 640 individuals, Budongo
112 holds the second largest population of chimpanzees in Uganda {Plumptre, 2003 #3750}.
113 The Sonso chimpanzee community, which has been studied continuously since 1990

114 through the work of the Budongo Conservation Field Station, ranges over an estimated
115 6.8km² (minimum convex polygon **method, MCP**; {Newton-Fisher, 2003 #3678}).

116 Our data were collected between September 2002 and September 2003. By
117 September 2003, the community consisted of 63 named individuals: 8 adult and 4 sub-
118 adult males, 19 adult and 3 sub-adult females, and 29 juveniles and infants. We followed
119 15 individual adult subjects, 8 male and 7 female, over the course of this study. Four of
120 the target females were lactating throughout the study period, and one was gestating at
121 the start of the study and subsequently lactating, having given birth six months into the
122 study; two were sexually receptive, but one of these became pregnant during the study (as
123 determined by subsequent birth records) so the sexually receptive female sample size fell
124 from two to one and the number of females in the lactating/gestating group rose from five
125 to six. The lactating/gestating is henceforth referred to simply as lactating females. Of the
126 male focal subjects, two were rated as low ranking, two as mid-rank and four as high
127 rank, including the alpha male. One of the high-ranking male subjects died from a spear
128 wound nine months into the study.

129

130 **Data Collection**

131 We collected data on only one of the 15 subjects at a time (focal animal **sampling**:
132 {Altmann, 1974 #237}). During each focal sample period, the target individual was
133 followed continuously through the forest for up to three consecutive days, from when it
134 left its night nest at sunrise to when it made another night nest around sunset. We
135 amassed 50 focal animal samples over the study period, with a range of 1 to 6 samples
136 per subject (median = 4). If the target animal was lost during a focal sample, every

137 attempt was made to regain contact, but if this was not possible after a maximum elapsed
138 time of 120 minutes, a new focal sample of a different target individual was initiated the
139 following day, that again lasted for up to three days. The focal samples ranged from 150
140 minutes to 1860 minutes (31 hours, recorded over three consecutive days) in duration,
141 with a mean duration of 700 minutes \pm 507 (11 hrs 40 min \pm 8 hrs 45) for males, 874
142 minutes \pm 451 (14 hrs 35 min \pm 7 hrs 30) for lactating females, and 1050 minutes \pm 343
143 (17 hrs 30 min \pm 5 hrs 45) for sexually receptive females. Males were observed at dawn
144 leaving their night nests 21 times, lactating females 12 times, and sexually receptive
145 females four times. We recorded continuous nest-to-nest follows on ten days for males,
146 and seven days for lactating females. Sexually receptive females were only followed
147 continuously from nest to nest on one occasion. We followed the target animal
148 continuously - for at least 8 hours without losing it - on 27 days for males, 13 days for
149 lactating females, and 3 days for sexually receptive females.

150 During a focal sample, we recorded the location of the subject every five minutes
151 when it was travelling, using a hand held Garmin XL GPS device, giving reasonably high
152 temporal and spatial resolution of daily movement paths (the GPS was measured to have
153 an error of up to 14m, when taking 5 consecutive readings of the same 4 locations over a
154 1-month period). In areas where the forest cover was too thick to maintain reliable GPS
155 coverage, we marked the location of the subject at the same five minute intervals on a
156 paper map of the forest that showed the numbered trail lines cut through the home range
157 of the community. Trail lines run from north to south and east to west at 100m intervals.
158 Scan samples recorded every 15 minutes registered the activities of all the other
159 independent individuals present in the target subject's party throughout the focal sample,

160 allowing us to keep track of the party size, composition and activity. In total, 4096 scan
161 samples were collected over the duration of the study. Any individual within a 35m
162 radius of the target individual was considered to be in the same party.

163 When the subject halted travel for 20 minutes or more we marked the time and
164 location of the halt, and continuously recorded the subject's behavioural activity (feeding,
165 socialising, drinking, nesting or inactive) on a dictaphone, noting the time of changes in
166 activity state (see Analysis: Phases of movement section, below). We recorded the food
167 species and plant part eaten at all feeding halts. 'Social activity' denoted any kind of
168 affiliative or aggressive behaviour involving two or more individuals, and we
169 documented which individuals were involved as well as their actions. Self-grooming
170 behaviour as well as resting was treated as 'inactivity'. Nesting was recorded when the
171 subject began construction of its night nest.

172 Movements of the target animal and its party within a 20+ minute halt were not
173 recorded. When the subject was engaged in social activity, nesting, inactive, or drinking,
174 we defined the area of the 20+ minute halt as within a 35m radius of the initial stopping
175 point of the target animal. When the subject was feeding, a 20+ minute halt area was
176 taken to be equivalent to a food patch, i.e. any discrete area where an individual can feed
177 continuously without having to interrupt its food gathering when moving around
178 {Chapman, 1994 #3736; White, 1988 #2788}. This translated as either a single food tree
179 isolated at its crown from any others, or adjacent food trees with inter-connecting crowns.

180

181 **Analysis**

182 Statistical tests were conducted using SPSS (version 12), and circular statistics were
183 conducted using Oriana (version 2). All the hypotheses considered were two-tailed and
184 tested at a significance level of $\alpha=0.05$. Data were tested for normality and homogeneity
185 of variance before applying parametric tests, and non-normally distributed data were log
186 transformed. The travel phases of all routes recorded were treated as independent; the
187 occurrence of each was separated by at least 20 minutes, and it is the structuring of each
188 of these individual phases one after the other throughout the day that is of interest here.
189 Therefore, all statistical tests were between subjects, and multivariate ANOVA
190 (MANOVA) was used where appropriate to avoid the problems of multiple testing.

191

192 *Daily Movement Behaviour*

193 We compared the distance travelled per day by males, lactating females, and sexually
194 receptive females using a between subjects ANOVA (sex class by mean daily range
195 length) with Tukey HSD post hoc tests. For this analysis we only used those focal
196 samples where the target individual was observed for at least 8-hours consecutively, to
197 avoid the pitfalls of using samples where the target animal had been temporarily lost and
198 subsequently found within 120 minutes. We examined several variables to assess whether
199 males and females maintain different activity budgets: (a) The time of day target
200 individuals left their night nests, using a between subjects ANOVA; (b) The total
201 duration of the day between night rests, using an independent samples t-test between
202 males and lactating females; (c) The number of 20+ minute halts per daily follow of at
203 least 8-hours, again using an independent samples t-test; (d) The time spent engaged in

204 each activity state per day, derived from the 4096 scan samples, using MANOVA of the
205 four activity types between the three sex classes. Because equal variances were not
206 assumed on this last test, a Dunnetts T3 post hoc test was used.

207

208 *Phases of Movement*

209 We generated digital maps of each subject animal's movement paths using ArcView GIS
210 (version 3.2), with movement between consecutive 5-minute location points
211 approximated by a straight line. We parsed each complete movement path of a focal
212 subject into phases, each phase defined as continuous movement ending at a 20+ minute
213 halt. The criterion of a 20+ minute halt was intended to capture the majority of travel
214 halts for feeding or social purposes, but to exclude as many inactive pauses as possible, as
215 the latter are unlikely to contribute materially to decisions about travel direction. We
216 reasoned that simply basing our criterion on activity was unlikely to be useful, as
217 chimpanzees may pause briefly yet frequently to eat a fallen fruit or leaf; such pauses
218 would not be an important determinant of their travel routes. We therefore chose to use a
219 time criterion to demarcate movement phases. The specific choice of 20+ minutes was
220 arbitrary, but halts of less than 20 minutes constituted less than 20% of all halts recorded
221 and inactivity was observed in 84% of these; moreover, no social or nesting activity was
222 recorded at halts of less than 20 minutes.

223 We identified 344 phases of movement between 20+ minute halts: 224 from
224 males, 87 from lactating females and 33 from sexually receptive females. The
225 predominant activity-state of the subject at the end of each movement phase was noted,
226 and the distributions were compared using a Chi square test of association. Nesting was

227 only recorded if it was the sole activity observed at the site: if any feeding occurred at the
228 same 20+ minute halt, it was recorded as a food stop.

229 For each of the 344 movement phases, we calculated three variables: (1) The
230 distance travelled, by summing the distances between all locations recorded at 5-minute
231 intervals within one phase; (2) The mean travel speed, by dividing the distance travelled
232 by travel time; time measurements were accurate to 1 minute; (3) The linearity, derived
233 by dividing the direct, 'beeline' distance between the start and end locations of the phase
234 by the actual distance travelled along that phase. These variables were skewed so we
235 applied log transformations to better approximate normal distributions.

236

237 *Movement Between Resources*

238 We used ArcView GIS to determine the angle turned through between the successive
239 phases of one focal sample, generating 288 inter-phase angles in total. The Rayleigh test
240 was used to determine if the distribution of angles was clumped or uniform, and V-tests
241 compared the distribution to a test value, where significant values indicate a distribution
242 clumped around the test value {Batschelet, 1981 #3642}. The distribution of angles
243 turned through by males, lactating females and sexually receptive females were compared
244 to the test angle of 0°, which represents a continuation in the same direction as that prior
245 to reaching the 20+ minute halt. The angles turned between successive phases were
246 compared between the three sex classes using the non-parametric Mardia-Watson-
247 Wheeler test, which tests for differences between two independent samples. A non-
248 parametric test was necessary as the data violated the assumptions relating to the
249 concentration of angles in each sample that are required for use of the parametric

250 Watson-Williams test {Batschelet, 1981 #3642}. Inter-phase angles that fell between the
251 ranges of 0-45° and 315-0° were considered as continuing on the same line as the
252 previous movement phase. In analysing the travel distance and activity state of the
253 subject at the end of these co-linear movement phases, only those where the end-point of
254 the co-linear movement was known were included.

255

256 *Range Use*

257 It is known that chimpanzees spend the majority of their time in a relatively small
258 proportion of their range {Boesch, 2000 #2965}, with estimates of peripheral areas
259 varying from 40-65% of the total range {Newton-Fisher, 2000 #3746; Wrangham, 1980
260 #3765}. To delineate a boundary between ‘central’ and ‘peripheral’ areas, we took a
261 distance of 1km from the edge of the known-range boundary of the Sonso chimpanzee
262 community (as calculated with the **MCP method** {Newton-Fisher, 2003 #3678}). This
263 then separated the central 45% of the community range from the peripheral 55% of the
264 range.

265 We calculated an estimate of patch size based on the number of individuals that
266 were seen feeding in a patch multiplied by the number of minutes that each was feeding
267 for {White, 1988 #2788}. We used these estimates to compare the size of food patches in
268 central and peripheral areas as used by males at the end of extended periods of straight-
269 line movement. The average party size of males feeding in central and peripheral areas
270 was compared with an independent samples t-test. The number of vocalisations made by
271 male parties travelling in either central or core areas was compared with a 2*2 Fisher’s
272 exact chi-square test, counting the number of silent travel phases and the number of travel

273 phases that included a vocalisation, when in the central or peripheral areas. To determine
274 whether lactating females turn around in order to avoid the peripheral areas of the
275 community range, we measured the shortest distance from the end of their travel phases
276 to the boundary between the central and peripheral areas. We compared these distances
277 between travel phases where the lactating female subsequently continued to move
278 forwards (inter-phase angle of 315-45°), and those where she turned back on herself
279 (inter-phase angle of 135-225°), using an independent samples t-test.

280

281 **Results**

282 **Daily Movement Behaviour**

283 There were significant differences in the total distances travelled per day by males,
284 lactating females, and sexually receptive females (mean daily movement distance \pm sd:
285 males=2.7 km \pm 1.5; lactating females=1.2 km \pm 0.8; sexually receptive females=2.2 km
286 \pm 0.8; $F_{2,42}=5.89$; $p=0.006$). Post hoc tests showed lactating females travelled
287 significantly shorter distances per day than males ($p=0.004$) but not sexually receptive
288 females ($p=0.43$, ns). There was no significant difference between the daily range lengths
289 of males and sexually receptive females ($p=0.83$, ns).

290 There was no difference in the time of leaving the night nest between males,
291 lactating females, and sexually receptive females (mean time leaving night nest \pm sd:
292 males=6.56am \pm 32min; lactating females=6.46am \pm 13min; sexually receptive
293 females=6.37am \pm 12min; $F_{2,36}=1.31$, $p=0.28$, ns). The sexes did differ in the duration of
294 the active day, however. When followed continuously from nest to nest, males had
295 significantly longer days than lactating females (mean day duration \pm sd: males=11 hours

296 34 minute \pm 35min; lactating females=10 hours 57 minutes \pm 34 min; $t=2.139$, $df=15$,
297 $p=0.049$). Males made significantly more stops of 20+ minutes per day than lactating
298 females (mean number of stops \pm sd: males= 6.5 ± 1.8 ; lactating females mean= 4.5 ± 1.0 ;
299 $t=3.92$, $df=38$, $p<0.001$). On average, each of the stops made by males were shorter in
300 duration than those of lactating females (mean stop time \pm sd: males= 60 ± 50 minutes;
301 lactating females= 95 ± 83 minutes; receptive females= 56 ± 41 minutes; $F_{2,315}=9.341$,
302 $p<0.001$; Tukey's post hoc, male: lactating female $p=<0.001$; receptive female: lactating
303 female $p=0.005$). Figure 1 shows the mean percentage time that chimpanzees spent
304 engaged in each activity type. Overall, time budgets did not vary significantly with sex
305 class ($F_{6,56}=1.97$, $p=0.085$, Wilks $\lambda=0.681$, ns), although post-hoc tests show lactating
306 females spent significantly less time travelling than males ($p=0.028$) and receptive
307 females ($p=0.044$). Time spent engaged in any other activity did not vary significantly
308 with sex.

309

310 **Phases of Movement**

311 Halts of 20+ minutes were used to define phases of movement. Table 1 shows the mean
312 phase lengths, travel speeds, and linearity values for males, lactating females, and
313 sexually receptive females. Males, lactating females, and sexually receptive females all
314 travelled similar distances in a movement phase, at similar speeds, and in similarly
315 straight lines. There were no significant differences between any of the dependent
316 variables across the three sex classes ($F_{6,670}=0.88$; $p=0.513$, Wilks $\lambda=0.99$, ns).

317 Male movement phases ended with the subject feeding 68% and socialising 13%
318 of the time, whilst the movement phases of lactating females ended with feeding 84% of

319 the time, and socialising only 5%, as shown in figure 2. Thus, movement phases are more
320 food-directed in lactating females than in males. This difference in the distribution of
321 activity types at the end of each movement phase was significantly different to that
322 expected by chance ($\chi^2=10.1$, $df=3$, $p=0.018$). Male movement ended with feeding less
323 often, and socialising and inactivity more often than expected, whilst lactating female
324 movement phases end with feeding more often and socialising and inactivity less often
325 than expected.

326

327 **Movement Between Resources**

328 How do male and female chimpanzees continue along their day's path, when they resume
329 moving after a 20+ minute halt? Does movement resume in the same direction as before,
330 begin anew in any direction at random, or follow some other principle? To answer these
331 questions, we examined the 288 angles turned between successive movement phases. For
332 males, the mean angle between consecutive phases was 13.2° (circular $sd \pm 82.3^\circ$). Male
333 inter-phase angles were clumped (Rayleigh test: $z=24.4$, $p<0.001$) and clustered around a
334 value of 0° (V-test: $u=6.80$; $n=192$; $p<0.001$). The same pattern was found for sexually
335 receptive females, with a mean inter-phase angle of $10.7^\circ \pm 71.4^\circ$, clumped (Rayleigh
336 test: $z=6.1$, $p=0.002$) and clustered in the forward direction of 0° (V test: $u=3.44$; $n=29$;
337 $p<0.001$). There were no significant differences between the angles of males and sexually
338 receptive females (Mardia Watson-Wheeler test: $W=1.67$; $n=192, 29$; $p=0.43$, ns). In
339 contrast, for lactating females the inter-phase angles were not significantly clumped
340 (Rayleigh test: $z=0.69$, $p=0.50$, ns) and therefore were not clustered around 0° (V-test: $u=-$
341 1.16 ; $n=67$, $p=0.88$, ns). Lactating females displayed significantly different distributions

342 of inter-phase angles to males (Mardia Watson-Wheeler test: $W=16.22$; $n=192$, 67;
343 $p<0.001$) and sexually receptive females (Mardia Watson-Wheeler test: $W=10.72$; $n=29$,
344 67; $p=0.005$; see Figure 3). Rather than continuing in the same direction, lactating
345 females tended to retrace their steps. Eleven of the lactating female angles were close to
346 0° , but ten were close to 180° , producing a mean inter-phase angle of $171.1^\circ \pm 122.6^\circ$:
347 lactating females were just as likely to turn back on their path after a halt as they were to
348 continue in the original direction.

349 Consistent with an increased tendency to retrace their steps and not to continue in
350 a forwards direction, lactating females showed a different pattern of usage of feeding
351 sites than males or sexually receptive females. Males only returned to a feeding patch on
352 average 0.14 (sd ± 0.46) times per 8-hour day of observation (sexually receptive females,
353 with fewer observations, were never seen to return to the same feeding patch at all).
354 Lactating females, however, returned to a previously used feeding patch on average 0.46
355 times per day (± 0.71). Consequently, lactating females made significantly more revisits
356 to previously used feeding sites per day than males (independent samples t-test: $t=2.08$,
357 $df=73$, $p=0.04$, homogeneity of variance not assumed; the sample size for sexually
358 receptive females was not large enough to include them in this analysis).

359 This means that males often continued moving in the same direction for two or
360 more phases of movement, although they obviously did always turn round at some point.
361 In a search for clues as to the function of linear ranging by male chimpanzees, we
362 examined the activities performed at the points where these extended co-linear phases
363 ended. The distribution of activities at termination of the 95 extended co-linear phases
364 was very similar to the distribution for individual movement phases for males ($\chi^2=4.19$,

365 df=3, p=0.24, ns). There seemed, therefore, to be no special activity that males performed
366 at these end-points.

367

368 **Range Use**

369 If there is no special activity at the points where male movement finally changes
370 direction, do these points occur in particular geographical regions? In particular, do males
371 at Budongo use peripheral areas more than females, as is known to be the case for other
372 communities of the *schweinfurthii* sub-species {Chapman, 1993 #3735; Williams, 2002
373 #3762}. We treated the outer 55% of the known range area as peripheral, consistent with
374 range use estimates used in other studies {Boesch, 2000 #2965; Newton-Fisher, 2000
375 #3746; Wrangham, 1980 #3765}. Of the 37 phases of movement that ended in the
376 peripheral areas, only five were made by lactating females, four by sexually receptive
377 females, and 27 by males. Lactating females use peripheral areas less than is expected by
378 chance, and males more so ($\chi^2=6.13$, df=2, p=0.047). Even in peripheral areas, however,
379 the activities in which males engaged before returning to central areas were not clearly
380 different to those at any other 20+ minute halts ($\chi^2=2.45$, df=3, p=0.48, ns). Where
381 extended co-linear phases of movement ended in peripheral areas, males fed at 17
382 locations but at 10 they did not: in three cases they showed some social activity, and in
383 seven they apparently did nothing at all.

384 Males might be attracted to the peripheral areas to feed on better quality or larger
385 resources, so we compared the patch quality at points where males change direction after
386 feeding in central areas versus the periphery. There was no difference in the mean patch
387 quality whether these turn-around points occurred in the central or peripheral areas. Mean

388 patch quality was estimated as 159 ± 156 'chimp minutes' where males turn in central
389 areas, compared to 207 ± 208 chimp minutes when in peripheral areas ($t=0.88$, $df=23$,
390 $p=0.20$, ns, equal variances not assumed). Patch quality estimates were not affected by
391 party size as the mean party size of males feeding in central and peripheral areas was
392 similar (mean party size: central= 6.2 ± 4.2 ; peripheral= 7.9 ± 3.2 ; $t=-1.53$, $df=150$,
393 $p=0.13$, ns). Males were therefore not obviously attracted to the peripheral areas by larger
394 food patches.

395 Extended co-linear movements by male chimpanzees that terminate in peripheral
396 zones of their territory, but not at feeding sites, might represent 'border checking'. Male
397 chimpanzees of the Sonso community of Budongo only rarely engage in boundary patrols
398 described at other sites (Reynolds 2005). Nevertheless, we examined the detailed
399 behavioural logs of the 10 co-linear phases that ended in peripheral areas without feeding,
400 for signs of patrolling. One of these logs was indeed suggestive of a boundary patrol. In
401 this case, the males travelled silently and in single file to the outer peripheral area and,
402 upon returning to the central area of the range, successfully hunted a black and white
403 colobus monkey (*Colobus guereza*). On the other occasions, the travelling party made
404 vocalisations at the same rate as when in the central areas (Fisher's exact, $p=0.52$, ns),
405 and no indication was observed that a boundary patrol was in progress.

406 Did lactating females only turn back on themselves when they were approaching
407 the edge of the central area, in an attempt to avoid the potentially unsafe peripheral areas?
408 We compared the shortest distance to the central area boundary, for travel phases where
409 lactating females subsequently continued to move in the same direction and those where
410 they turned back on themselves. There was no difference in the distance to the periphery

411 when they turned around or when they continued to move straight ahead (mean distance
412 from the central: peripheral boundary: when continue straight ahead = $348 \text{ m} \pm 218$;
413 when turn back = $365 \text{ m} \pm 201$; $t=-0.39$, $df=84$, $p=0.70$, ns). Lactating females do not turn
414 back on themselves simply to avoid entering the peripheral areas.

415

416 **Discussion**

417 At several chimpanzee study sites, including Budongo, males (and sexually receptive
418 females) travel further than lactating females each day. Here, we aimed to go beyond this
419 summary statistic to discover how males and females structure their movement paths, and
420 how those structures influence their socio-ecological strategies.

421 All individuals spent approximately the same amount of time feeding each day
422 and all started their day at about the same time, but males had longer days than lactating
423 females, spending a significantly longer time travelling. We operationally defined
424 potentially important resources by the criterion that the chimpanzee should halt for at
425 least 20+ minutes. The distances that lactating females travelled between such resources
426 were not different from those of males and sexually receptive females. Lactating females
427 travelled to fewer potentially important resources per day, however, hence their shorter
428 overall travel lengths, and spent longer at each resource than males and sexually receptive
429 females. Males, sexually receptive and lactating females moved at approximately the
430 same speed between resources, and these movement phases were consistently linear in all
431 adult sex classes.

432 Our analysis of the angles turned between movement phases revealed that
433 lactating females differed from males and sexually receptive females in how their phases

434 were arranged to construct the overall path. Males and sexually receptive females
435 retained a ‘forwards’ heading significantly more than did lactating females, i.e. they
436 continued with the same trajectory after leaving a resource site. Lactating females
437 departed from resources with a wide spread of headings, and were specifically much
438 more likely to ‘turn back on themselves’, i.e. retrace the route by which they reached the
439 site. Lactating females therefore tended to move over a smaller area of the community
440 range, usually remaining in the central areas, and revisited food resources previously used
441 in the same day significantly more frequently than did males or sexually receptive
442 females. The movement phases of lactating females almost always ended in feeding, so
443 lactating female movement can be considered to be food directed. We therefore conclude
444 that lactating female chimpanzees behave as expected from optimal foraging theories.

445 Lactating females did not turn back on themselves just to avoid the potentially
446 unsafe peripheral areas of the community range. Repetitive use of small areas allows
447 females to maintain detailed knowledge of an area {Williams, 2002 #3762}. As shown
448 experimentally in domestic pigs {Laughlin, 2004 #3742}, individuals are more likely to
449 remember and use information about foraging patches when the cost of forgetting the
450 information is higher. Given that lactating females are under high nutritional stress, it is
451 likely that their need to remember the locations of food resources is high, and this favours
452 a strategy of ranging over smaller areas and revisiting resources of known yield.

453 Lactating females may also be restricted to using smaller areas of the territory due to
454 feeding competition from other females. However, the females of the Sonso community
455 are thought to be more gregarious than females at other study sites of the *schweinfurthii*

456 sub-species {Reynolds, 2005 #3753}, so the impact of female-female competition may be
457 reduced here.

458 In contrast to lactating females, sexually receptive females exhibit patterns more
459 like males. This suggests females change their ranging strategy depending on their stage
460 in the sexual cycle, either due to male coercion or to simply allow the females to find and
461 associate more freely with males {Tutin, 1979 #115}. When females are sexually
462 receptive, the need to remain with suitable males presumably outweighs the nutritional
463 costs of forgetting location information and expending energy on travelling further. The
464 movement of sexually receptive females therefore makes sense in terms of male
465 movement; the question is, what determines male movement patterns?

466 The extended co-linear paths of males are not explained by reaching larger
467 feeding patches. Long, linear movement paths have been noted in males of several
468 territorial species {Janson, 2007 #3739; Ramos-Fernandez, 2004 #3752}. That male
469 chimpanzees tend to travel in this way is therefore consistent with the idea that they have
470 to accommodate defence of territory as well as efficient food acquisition into their
471 movement patterns. Male chimpanzee reproductive success is at least partly dependent on
472 how successfully they defend the community area, with large, well-defended territories
473 attracting and retaining more females {Williams, 2004 #3763}. Cooperative boundary
474 patrols have therefore been argued to be very significant for chimpanzee reproductive
475 success, and are seen frequently at some study sites {Watts, 2001 #3759; Wrangham,
476 1980 #3765}, but they are rarely exhibited by members of the Sonso community. We
477 therefore interpret the Sonso males' extended co-linear movement phases into peripheral
478 areas as a novel form of territorial defence, an alternative sexual strategy to the boundary

479 patrols observed elsewhere. Instead of showing two different kinds of movement on
480 different occasions, i.e. food-directed movement and boundary patrols, males in the
481 Sonso community often appear to move according to a strategy that serves a dual role; to
482 reach food resources whilst at the same time monitoring the peripheral areas of the
483 community range¹. This ‘border checking’ hypothesis needs further testing, and in
484 particular the ecological factors that determine which strategy chimpanzees adopt at a
485 particular site need to be determined.

486

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495

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497

498 **References**

499

¹ Searching for sexually receptive females is an alternative, although not mutually exclusive, explanation for why males might travel more widely and spend more time in peripheral areas. In this study, however, males were never observed to join with sexually receptive females when in the peripheral areas of the range, so this possibility could not be investigated further.

500 Table 1: Mean travel distances, travel speeds, and linearity of movement phases for the
 501 three sex classes. Linearity is calculated as bee-line distance between successive 20+
 502 minute halts divided by the actual distance travelled along the phase.

Variable		Male (n=244)	Lactating female (n=87)	Receptive female (n=33)
Distance travelled (m)	Mean	357	277	319
	Sd	368	266	361
	Min	30	32	32
	Max	2206	1429	1403
Speed of travel (km/hr)	Mean	1.94	1.91	2.206
	Sd	1.67	1.20	1.907
	Min	0.27	0.32	0.43
	Max	14.27	6.20	10.21
Linearity of phase	Mean	0.939	0.948	0.960
	Sd	0.123	0.107	0.006
	Min	0.058	0.437	0.720
	Max	1.000	1.000	1.000

503

504

505

506 **Figure Captions**

507

508 **Fig. 1. Daily time budgets.** Histogram shows the percentage of the day engaged in each
509 activity, as recorded from 4096 party scans collected during all focal animal samples, for
510 males, sexually receptive females, and lactating females. Feeding time is shown as dark
511 grey; inactive periods, white; social activity, black; travel, pale grey.

512

513 **Fig. 2. Activity at the end of movement phases.** Data for male, sexually receptive
514 female and lactating female subjects are shown separately. Feeding is shown as dark
515 grey; inactive, white; social activity, black; nesting, pale grey. (Note that movement
516 phases were only deemed to end in nesting behaviour if nesting was the sole activity
517 undertaken; if any feeding was noted at the same site, it was recorded as a feeding site.)

518

519 **Fig. 3. Angles turned between successive phases of movement.** Inter-phase angles are
520 shown for males, sexually receptive females, and lactating females. The length of the
521 thick bars indicates the number of observations at each angle. For data that are
522 significantly clumped, the central tendency and 95% confidence interval are shown in
523 black.

524

525