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1 **How to measure chimpanzee party size? A methodological comparison**

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24

25 **Abstract**

26 Chimpanzees (*Pan troglodytes*) live in fission-fusion societies where community
27 members form temporary parties that frequently change in size and composition.
28 Chimpanzee party size and composition have been widely studied to identify proximate
29 causes of grouping patterns, and party size estimates are used to assess population sizes
30 and densities. Numerous socio-ecological factors influence chimpanzee party size, but
31 findings differ across studies. Various methods to measure party size exist, including
32 direct observations, motion-triggered camera (MTC) observations, and nest counts.
33 However, comparative analyses of these methods are lacking. Here, we assess relative
34 differences in four commonly used party size methods and we examine socio-ecological
35 factors influencing party size of unhabituated chimpanzees (*P. t. verus*) at Seringbara,
36 Nimba, Guinea. We also assess which method(s) best reflect the influence of socio-
37 ecological factors on party size. Using data collected over 69 months, we show that
38 night nest counts resulted in relatively larger party size estimates than the other
39 methods, and day nest counts resulted in relatively smaller party size estimates. Direct
40 and MTC observations did not differ in relative estimates of party size and composition.
41 Both fruit abundance and presence of estrous females positively influenced party size,
42 but this effect was only evident when measuring party size with MTCs. Methods thus
43 differ in relative party size estimates and their ability to assess the impact of socio-
44 ecological factors. We conclude that MTC observations best represent party size and the
45 effect of socio-ecological factors at Nimba. MTCs show promising potential for
46 studying grouping patterns in unhabituated chimpanzees.

47

48 **Keywords:** Chimpanzees; Party size; Fruit availability; Estrous females; Nest counts;
49 Camera traps.

50

51 **Introduction**

52 Animal group living has been studied extensively in terms of costs and benefits, and
53 group size is often interpreted as an adaptive trait that responds to social and ecological
54 factors (Chapman et al. 1995; Lehmann and Boesch 2004). Chimpanzees (*Pan*
55 *troglydites*) live in flexible fission-fusion societies, in which members of a stable
56 community form temporary subgroups, or parties, that frequently change in size and
57 composition (Itoh and Nishida 2007; Matsumoto-Oda et al. 1998; Newton-Fisher et al.
58 2000). Chimpanzee party size and composition have been widely studied to identify the
59 proximate causes of chimpanzee grouping patterns (Anderson et al. 2002; Basabose
60 2004; Doran 1997). Whereas early studies focused on identifying a single factor
61 responsible for grouping patterns, later studies have demonstrated that a complex
62 interplay of factors determines party size (Doran 1997; Hashimoto et al. 2001; Mitani et
63 al. 2002). The socio-ecological factors influencing chimpanzee party size include
64 predation pressure (Boesch 1991; Lehmann and Boesch 2004), food supply (Chapman
65 et al. 1995; Newton-Fisher et al. 2000), demographic factors (Lehmann and Boesch
66 2004; Mitani 2006), and presence of estrous females (Anderson et al. 2002; Wakefield
67 2008). Studies of chimpanzee party size have also been used to estimate community
68 sizes, population densities and/or distributions, especially for unhabituated chimpanzees
69 (Després-Einspenner et al. 2017; Furuichi et al. 2001a; Ndiaye et al. 2018).

70 Fruit availability, both in terms of abundance (i.e. amount) and distribution (i.e.
71 spatial arrangement), was found to be an important ecological factor influencing

72 chimpanzee party size across studies. Following the prediction that party size increases
73 with higher fruit abundance and larger (i.e. clumped) food sources due to decreased
74 costs of co-feeding, positive correlations have been found between party size and fruit
75 abundance (Tai, Ivory Coast: Anderson et al. 2002; Doran 1997; Kibale, Uganda:
76 Chapman et al. 1995; Mitani et al. 2002; Kalinzu, Uganda: Furuichi et al. 2001b;
77 Mahale, Tanzania: Itoh and Nishida 2007; Matsumoto-Oda et al. 1998), and between
78 party size and fruit distribution (Kahuzi-Biega, DRC: Basabose 2004; Kibale: Chapman
79 et al. 1995). Conversely, other studies found that party size was not influenced by fruit
80 abundance (Kalinzu: Hashimoto et al. 2001; Budongo, Uganda: Newton-Fisher et al.
81 2000; Kahuzi-Biega: Basabose 2004), or fruit distribution (Kalinzu: Hashimoto et al.
82 2001; Tai: Anderson et al. 2002; Budongo: Newton-Fisher et al. 2000).

83 The presence of estrous females was found to be an important social factor
84 influencing chimpanzee party size (Anderson et al. 2002; Wakefield 2008). For the
85 purpose of copulation, sexually receptive females are predicted to join parties and
86 attract males, leading to larger parties (Anderson et al. 2002; Wallis 2002). Following
87 this prediction, positive correlations between the presence of estrous females and party
88 size have been observed at a number of sites (Tai: Anderson et al. 2002; Kibale: Mitani
89 et al. 2002; Wakefield 2008; Mahale: Matsumoto-Oda et al. 1998; Kalinzu: Hashimoto
90 et al. 2001; Budongo: Wallis 2002; Gombe, Tanzania: Wallis 2002; Gashaka-Gumti,
91 Nigeria: Sommer et al. 2004).

92 Inconsistencies in the influence of socio-ecological factors on chimpanzee party
93 size may stem from temporal and/or spatial variability in chimpanzee grouping patterns
94 across sites and studies, but may also be a consequence of differences in field
95 methodologies to measure fruit abundance (e.g. Chapman et al. 1995; Doran 1997;

96 Hashimoto et al. 2001; Itoh and Nishida 2007), fruit distribution (e.g. Anderson et al.
97 2002; Basabose 2004; Newton-Fisher et al. 2000), estrous females (e.g. Anderson et al.
98 2002; Sommer et al. 2004), and/or party size (see below). As the causes of variation
99 between studies are unknown, comparisons of the socio-ecological factors influencing
100 chimpanzee party size are rendered problematic. Yet, based on the majority of studies
101 outlined above, fruit availability and presence of estrous females can be expected to
102 positively influence chimpanzee party size.

103 Across studies, methods of measuring chimpanzee party size differ. Four
104 methods are commonly used: direct observations, motion-triggered camera
105 observations, day nest counts and night nest counts (Basabose 2004; Brownlow et al.
106 2001; McCarthy et al. 2018). The properties of each of these methods differ, which
107 likely affects their ability to correctly represent chimpanzee party sizes (Basabose 2004;
108 Brownlow et al. 2001; Després-Einspenner et al. 2017). To date, these different
109 methods have not been assessed all together at the same study site. Hence, comparative
110 analyses to assess the relative differences in party size estimates across these methods
111 are long overdue. This is especially important when studying unhabituated chimpanzee
112 communities, where actual party sizes are unknown.

113 Measuring chimpanzee party size during direct observations is the most
114 commonly used method (Chapman et al. 1995; Matsumoto-Oda et al. 1998; Newton-
115 Fisher et al. 2000), and involves researchers collecting data on the number of
116 chimpanzees present (Anderson et al. 2002; Basabose 2004). If chimpanzees are
117 unhabituated, direct observations can be challenging as chimpanzees can be difficult to
118 find due to their large home range and fission-fusion dynamics (Bertolani and Boesch
119 2008). As a consequence of behavioral and methodological factors, large parties may be

120 found more easily and tolerate humans better than small parties; yet individuals,
121 especially females, may flee upon encountering humans and peripheral individuals may
122 be missed, which may affect relative party size estimates (Table 1, H1 – H4: Basabose
123 2004; Bertolani and Boesch 2008; Sommer et al. 2004).

124 Motion-triggered camera (MTC) observations provide an indirect measure of
125 party size that circumvents these difficulties when dealing with unhabituated
126 chimpanzees (Boyer-Ontl and Pruetz 2014; Després-Einspenner et al. 2017; McCarthy
127 et al. 2018). With minimal human interference and environmental disturbance, camera
128 traps can provide detailed data on chimpanzee behavior in the absence of human
129 observers (Boyer-Ontl and Pruetz 2014; McCarthy et al. 2018). However, MTCs do
130 have limitations. Methodological difficulties, for example, include camera placement
131 and the restricted film frame of the camera (Després-Einspenner et al. 2017; McCarthy
132 et al. 2018). With regards to behavior, chimpanzees may actively avoid MTCs
133 (Després-Einspenner et al. 2017; McCarthy et al. 2018). These limitations may allow
134 some individuals to pass unnoticed and may lead to relatively lower party size estimates
135 as compared to the other methods (Table 1, H5 and H6).

136 A last indirect method of measuring party size is using nest counts (Brownlow et
137 al. 2001; Furuichi et al. 2001b; Ogawa et al. 2007). Nests built together in time and
138 space are referred to as nest groups (or parties), and nest counts are often used as an
139 indicator of party size (Brownlow et al. 2001; Furuichi et al. 2001b; Ogawa et al. 2007).
140 A distinction should be made between day and night nest counts, as day and night nests
141 differ in function and construction (Brownlow et al. 2001; Koops et al. 2012a).
142 Chimpanzees build simple day nests as a place to rest during the day, yet construct
143 complex nests each night to sleep in (Brownlow et al. 2001; Koops et al. 2012a). Day

144 and night nest counts may result in relatively lower party size estimates as compared to
145 the other methods, as 1) not all chimpanzees may build a nest at daytime (Table 1, H7:
146 Brownlow et al. 2001; Goodall 1962); and 2) some nests may be missed by human
147 observers when searching for nest groups (Table 1, H8 and H13: van Leeuwen *personal*
148 *experience*). Alternatively, day and night nest counts may result in relatively higher
149 party size estimates as compared to the other methods, as 1) some chimpanzees may
150 build more than one nest during the day (Table 1, H9: Plumptre and Reynolds 1997); 2)
151 chimpanzees may aggregate at night (Table 1, H11: Anderson et al. 2002; Ogawa et al.
152 2007); and 3) larger nest groups may be more easily located by human observers (Table
153 1, H10 and H12: van Leeuwen *personal experience*).

154 This study aims to explore party size methods and grouping patterns for the
155 unhabituated chimpanzees at the Seringbara study site in the Nimba Mountains
156 (Guinea). Specifically, we investigate 1) relative differences in estimating chimpanzee
157 party size between the four methods, 2) which socio-ecological factors influence
158 chimpanzee party size at Nimba, and 3) which party size method(s) best reflect the
159 influence of these factors. Relative differences between party size methods are expected
160 according to the hypotheses and predictions outlined in Table 1. We focus here on
161 relative differences in party size estimates, since actual party sizes are unknown for the
162 unhabituated chimpanzees. Moreover, we are thus unable to test the causal factors, i.e.
163 methodology or behavior, of the relative differences in party size estimates between
164 methods. Fruit abundance, fruit distribution, and presence of estrous females are all
165 predicted to have a positive influence on party size. As relative party size estimates are
166 expected to differ between the four methods, the methods are also expected to differ in
167 their ability to reflect the influence of these socio-ecological factors.

168

169 ** Insert Table 1 around here ***

170

171 **Methods**

172 **Study site and species**

173 We studied chimpanzees (*P. t. verus*) at the Seringbara study site (N 07.37°; W 08.28°)
174 in the Nimba Mountains, Guinea, West Africa. The Seringbara study area covers
175 approximately 25 km², and is situated ~6 km from Bossou, where a chimpanzee
176 community has been studied since 1976 (Matsuzawa et al. 2011). The Seringbara study
177 site is characterized by great topographical diversity with steep hills and deep valleys
178 ranging in altitude from 600 – 1752 m above sea level. Vegetation includes primary
179 tropical forest interspersed with secondary forest, riverine forest, terrestrial herbaceous
180 vegetation (THV) dominated forest, and savanna grassland (Koops et al. 2012a). The
181 climate is characterized by a 9-month rainy season between February and November,
182 and 3-month dry season (Koops 2011). The Nimba Mountains have been surveyed for
183 chimpanzees intermittently since 1992 (Humble and Matsuzawa 2001; Matsuzawa and
184 Yamakoshi 1996; Shimada 2000), and a near-constant research presence at the
185 Seringbara study site has been maintained since 2003 (Koops et al. 2007; Koops et al.
186 2012a; Koops et al. 2012b; Koops et al. 2013). The study area is inhabited by at least
187 two chimpanzee communities (Tongbongbon and Gahtoy communities), based on
188 repeated direct and MTC observations of known individuals (Koops *personal*
189 *observation*), as well as genetic evidence (Koops et al. 2012b). The chimpanzees remain
190 largely unhabituated to the presence of human observers (i.e. only some individuals
191 tolerate human presence), due to the difficulties of habituating chimpanzees in such

192 extremely mountainous terrain. As such, the exact demographic compositions of the
193 study communities are unknown.

194

195 **Data collection**

196 Data collection took place over 69 months of study between July 2003 and April 2014
197 (Jul 2003 – May 2004, Apr – Aug 2006, Dec 2006, Nov 2007 – Dec 2008, Mar 2011 –
198 Apr 2014). Data were collected by KK (2003 – 2014) and KL (2011) with the help of a
199 local field guides and an international team of research assistants.

200

201 **Party size methods**

202 We used four party size methods. For direct and MTC observations, party size was
203 measured as “the [total] number of individuals present [during a single encounter] that
204 feed and travel independently”, i.e. excluding infants and juveniles (Anderson et al.
205 2002, p. 92). For day and night nest counts, party size was measured as the total number
206 of nests of the same age present in a nest group, i.e. < 30 m from the nearest nest
207 (Furuichi et al. 2001a; Koops et al. 2012a).

208 Direct observations (Sep 2003 – Apr 2014; data collected for 48 months in total)
209 were defined as all visual chimpanzee encounters. Chimpanzees were encountered
210 following traces and/or vocalizations. Parties were scored as female(s) only, female(s)
211 and offspring, male(s) only, and mixed sex (following Koops et al. 2019). When
212 measured on the same day, parties were defined as separate parties when no overlap
213 between individuals was observed, and when subsequent party observations around the
214 same location were more than 1 hour apart. This 1 hour cut-off point was selected based
215 on the frequency distribution between subsequent party observations from MTC data

216 (Electronic Supplementary Material (ESM), *Online Resource 1*), and hence parties are
217 statistically independent. Due to the incomplete habituation of the chimpanzees, parties
218 of unknown type, i.e. parties where too few individuals could be reliably identified so
219 no assessment of party composition could be made, as well as individuals of unknown
220 age-/ sex class were excluded from analyses.

221 Motion-triggered cameras (Bushnell Trophy Cam XLT 8MP Trail Cameras,
222 PixController DVDREye™, and Trailmaster TM700v Passive IR Trail Monitors with
223 Sony DCR-HC9: Jan 2008 – Apr 2014; data collected for 42 months in total) were set
224 up at 39 randomly-selected locations of known chimpanzee activity (e.g. trails, feeding
225 sites) within the home range. We therefore used a targeted camera placement approach
226 (Boyer-Ontl and Pruetz 2014; Després-Einspinner et al. 2017; McCarthy et al. 2018),
227 which is expected to increase detection probability and is recommended for party size
228 data collection (Després-Einspinner et al. 2017). All MTCs recorded videos of one
229 minute in length for data collection, with one second re-trigger time between subsequent
230 videos. We included only traveling parties for analyses (N = 399, out of 587 parties in
231 total) in order to minimize the confounding influence of camera placement, i.e.
232 chimpanzee party size may vary systematically depending on the activity (Anderson et
233 al. 2002; Boesch 1996). Parties observed on the same day at the same location were
234 considered to be the same party when there was overlap between individuals or when
235 subsequent parties were filmed within 1 hour of each other. Due to incomplete
236 habituation of the chimpanzees, parties of unknown type and individuals of unknown
237 age- / sex class were excluded from analyses.

238 For day nest counts (Aug 2003 – Mar 2014; data collected for 49 months in
239 total) and night nest counts (Aug 2003 – Mar 2014; data collected for 62 months in

240 total), all nests that were less than one week old were included. Nest age was assessed
241 by the state of leaves and branches (*sensu* Koops et al. 2012a). For each nest group, nest
242 status was scored as either 1) day nests: nests that were simple in construction and were
243 judged structurally too weak to hold a chimpanzee's weight overnight; 2) night nests:
244 nests that were elaborately constructed, and often associated with feces or urine below
245 the nests; or 3) nests of unknown status (*sensu* Koops et al. 2012a). Day nests and night
246 nests were analyzed separately (Brownlow et al. 2001; Koops et al. 2012a), and based
247 on nest age and distance between nests, nests groups were statistically independent.
248 Nest groups of unknown status were excluded from the analyses.

249

250 **Party composition and estrous females**

251 For parties observed during direct encounters and filmed with MTCs, data were
252 recorded on party composition and presence of estrous females. Data were recorded on
253 the sex class, age class (i.e. adult: > 11 years, adolescent: 8 – 11 years, juvenile: 4 – 7
254 years, infant: 0 – 4 years; Sugiyama 1999), and sexual status (i.e. adult and adolescent
255 females: estrous or no estrous) of all individuals present. As results were similar, no
256 distinction was made between full and semi anogenital swellings, and all swollen
257 females were analyzed as 'estrous females'. Parties with estrous females were scored as
258 '1', and parties without estrous females were scored as '0'. Information on the age- and
259 sex class of the individuals in a party was used to calculate the adult sex ratio. Adult sex
260 ratio was calculated using the formula:

$$261 \quad \text{sex ratio} = \frac{(\# \text{ adult males})}{(\# \text{ adult males}) + (\# \text{ adult females})}$$

262 in which the sex ratio denotes the proportion of adult males in a given party. This
263 calculation differs from the standard sex ratio measure to include unisexual, i.e.
264 female(s) only or male(s) only, parties.

265

266 **Rainfall**

267 Rainfall data (Aug 2003 – Apr 2014; data collected for 65 months in total) were
268 recorded daily at 17.30h with a manual rain gauge at base camp (Madei camp), which is
269 located at an altitude of 670 m. Daily rainfall measures were used to calculate monthly
270 amounts of precipitation.

271

272 **Fruit availability**

273 To monitor the temporal and spatial availability of ripe fruit (Jul 2003 – Mar 2014; data
274 collected for 56 months in total), twenty-four 500m transects were set up on 12
275 hills/valleys throughout the study site. Transects were located according to a stratified
276 random design. Confirmed chimpanzee feeding tree and vine species with a DBH \geq 10
277 cm within 5 m of the transect line were monitored for the presence of ripe fruit on a
278 monthly basis (i.e. first half of each month). Ripe fruit was scored on a 0 – 4 scale, with:
279 0) ripe fruit absent; 1) 1 – 25% of canopy containing ripe fruit; 2) 26 – 50% of canopy
280 containing ripe fruit; 3) 51 – 75% of canopy containing ripe fruit; and 4) 76 – 100% of
281 canopy containing ripe fruit.

282 As a measure of fruit abundance, ripe fruit scores were used to calculate monthly
283 Fruit Availability Indices (FAI) using the following formula (*sensu* Hockings et al.
284 2010; Takemoto 2004):

285
$$FAI = \frac{\sum(P_i \times F_i)}{\sum(P_i \times 4)} \times 100$$

286 where FAI is the fruit availability index (%), P_i is the basal area of the tree (cm^2) and F_i
287 is the ripe fruit availability score of the tree or vine. Months with a FAI score of > 1
288 were considered as high fruit abundance months, and months with a FAI score of < 1
289 were considered as low fruit abundance months (Koops 2011).

290 As a measure of ripe fruit distribution, Coefficients of Dispersion (CD) were
291 calculated using the following formula (*sensu* Basabose 2004; Chapman et al. 1995):

292
$$CD = \frac{\sigma^2}{\mu}$$

293 in which μ is the mean and σ^2 is the variance of the mean of the cumulative DBHs of
294 trees and vines providing ripe fruit in a given month. CD values equal 1 when fruit
295 distribution is random, < 1 when fruit distribution is uniform, and > 1 when fruit
296 distribution is clumped. CD could not be calculated for months with $FAI = 0$.

297

298 **Data analysis**

299 Data were tested for normality using Kolmogorov-Smirnov tests (Field 2009). All
300 analyses were performed two-tailed, and the significance level alpha (α) was set at 0.05.
301 Statistical tests were performed using IBM SPSS Statistics (version 22). Data from the
302 Gahtoy and Tongbongbon communities were combined for analyses, as results were
303 similar for the two communities.

304 Individual party size measures obtained for each method per month were used to
305 calculate average ‘monthly’ party sizes. To compare monthly party sizes across the four
306 methods on a month-by-month basis, we used a Friedman’s ANOVA test. *Post-hoc*
307 Wilcoxon signed-rank tests were used to assess individual differences between methods

308 (Field 2009). To control for multiple comparisons, a Bonferroni procedure was used
309 (i.e. $\alpha = 0.05 / 6 = 0.008$). Sex ratios of parties recorded during direct and MTC
310 observations were compared with Mann-Whitney U tests.

311 To assess the influence of estrous females on party size (i.e. for parties measured
312 during direct encounters and with MTC observations), we compared the size of parties
313 with and without estrous females with Mann-Whitney U tests. To assess the influence
314 of estrous females on sex ratios, we compared sex ratios of parties with and without
315 estrous females with Mann-Whitney U tests.

316 Monthly FAI (fruit abundance) and CD (fruit distribution) values were
317 correlated using Spearman's correlation coefficient (Field 2009). To assess the effect of
318 fruit availability on party size, we used linear regression (Field 2009) for all four
319 methods. In case of a significant correlation between FAI and CD, monthly party sizes
320 were related to monthly FAI and CD values separately, as well as combined using a
321 multiple linear regression model (fruit availability). A Bonferroni correction was used
322 to control for multiple comparisons (i.e. $\alpha = 0.05 / 4 = 0.0125$). As residuals in the linear
323 regression models were not normally distributed, we used Spearman's correlation
324 coefficients for all methods to check for significant rank correlations between monthly
325 party size, FAI and CD (Field 2009). Monthly party sizes during high and low fruit
326 abundance months were compared using Mann-Whitney U tests; monthly party sizes for
327 all party size methods were analyzed separately, and a Bonferroni correction was used
328 to control for multiple comparisons (i.e. $\alpha = 0.05 / 4 = 0.0125$).

329

330 **Results**

331 **Party size methods compared**

332 Month-by-month party size estimates varied significantly across methods (Fig. 1 and
333 Table 2; Friedman's ANOVA: $\chi^2 = 23.91$, $df = 3$, $p < 0.001$). *Post-hoc* Wilcoxon
334 signed-rank tests showed that monthly party sizes measured with night nest counts were
335 significantly larger than those measured with direct observations ($T = 13$, $Z = -3.23$, $p =$
336 0.001 , Fig. 2), MTCs ($T = 11$, $Z = -2.70$, $p = 0.006$, Fig. 2) and day nest counts ($T = 4$,
337 $Z = -5.29$, $p < 0.001$, Fig. 2). Monthly party sizes measured with day nest counts were
338 significantly smaller than those measured with direct observations ($T_+ = 10$, $Z = -2.94$, $p =$
339 0.003 , Fig. 2), and tended to be smaller than monthly party sizes based on MTCs ($T =$
340 10 , $Z = -2.15$, $p = 0.031$, Fig. 2). Monthly party sizes measured with direct observations
341 and MTCs were not significantly different ($T = 13$, $Z = -0.07$, $p = 0.947$, Fig. 2).

342 The sex ratio of parties measured through direct observations and MTC
343 observations did not differ between methods (Table 3; Mann-Whitney U test: $U =$
344 19549.50 , $Z = -1.07$, $p = 0.284$).

345

346 *** Insert Figure 1 around here ***

347

348 *** Insert Table 2 around here ***

349

350 *** Insert Figure 2 around here ***

351

352 *** Insert Table 3 around here ***

353

354 **Party size, party composition and estrous females**

355 The presence of estrous females had a significant effect on party size measured with
356 MTC observations: Parties with estrous females had significantly more individuals than
357 parties without estrous females (Table 4; Mann-Whitney U test: $U = 3599.5$, $Z = -6.29$,
358 $p < 0.001$). No significant difference was observed when party sizes were measured
359 with direct observations (Table 4; Mann-Whitney U test: $U = 573.50$, $Z = -0.95$, $p =$
360 0.348).

361

362 *** Insert Table 4 around here ***

363

364 For MTC observations, sex ratios of parties with estrous females were
365 significantly higher than sex ratios of parties without estrous females (Table 5; Mann-
366 Whitney U test: $U = 4771.50$, $Z = -3.91$, $p < 0.001$). No significant differences in sex
367 ratios between parties with and without estrous females were observed for direct
368 observations (Table 5; Mann-Whitney U test: $U = 434.50$, $Z = -1.15$, $p = 0.251$).

369

370 *** Insert Table 5 around here ***

371

372 **Party size and fruit availability**

373 Measures of FAI, CD and rainfall varied over the 69 months of study (Fig. 3), and
374 month-by-month comparisons of FAI and CD showed a significant positive correlation
375 ($N_{\text{months}} = 54$, $\rho = 0.529$, $p < 0.001$). No significant linear relationships were observed
376 across the four methods between party size and 1) fruit abundance (FAI), 2) fruit
377 distribution (CD), and 3) fruit availability (FAI and CD combined; ESM, *Online*

378 *Resource 2*). Correlations of monthly party size, FAI and CD resulted in one significant
379 correlation (ESM, *Online Resource 3*). Monthly party size measured with MTCs
380 showed a significant positive correlation with FAI (Spearman's rank correlation: N_{months}
381 = 39, $r_s = 0.502$, $p < 0.001$).

382

383 *** Insert Figure 3 around here ***

384

385 Monthly party size estimates measured with MTCs were significantly larger
386 during high as compared to low fruit abundance months (Fig. 4 and Table 6; Mann-
387 Whitney U test: $U = 62.50$, $Z = -3.47$, $p < 0.001$). No significant differences in party
388 size estimates between high and low fruit abundance months were found with direct
389 observations (Fig. 4 and Table 6; Mann-Whitney U test: $U = 109.50$, $Z = -1.91$, $p =$
390 0.056), day nest counts (Fig. 4 and Table 6; Mann-Whitney U test: $U = 160.50$, $Z = -$
391 1.12 , $p = 0.268$), and night nest counts (Fig. 4 and Table 6; Mann-Whitney U test: $U =$
392 190.00 , $Z = -2.18$, $p = 0.029$).

393

394 *** Insert Table 6 around here ***

395

396 *** Insert Figure 4 around here ***

397

398 **Discussion**

399 This study compared four commonly used methods to estimate chimpanzee party size,
400 and examined the socio-ecological factors influencing party size in unhabituated
401 chimpanzees at the Seringbara study site in the Nimba Mountains, Guinea. The four

402 methods differed in their party size estimates, with night nest counts resulting in
403 relatively larger estimates, and day nest counts resulting in relatively smaller estimates
404 as compared to the other methods. Direct encounters and MTC observations did not
405 differ in their relative estimates of party size and composition. Parties with estrous
406 females were relatively larger and had more adult males present. This effect was evident
407 when party size and composition were measured with MTCs, but not through direct
408 observations. Fruit abundance also had a significant effect on party size, with relatively
409 larger parties occurring when fruit was abundant. Again, this finding was only apparent
410 when measuring party size using MTCs and not through direct observations or nest
411 counts. Party size was not influenced by fruit distribution.

412 The finding that night nest counts resulted in relatively larger party size
413 estimates than the other methods supports the hypothesis that chimpanzees aggregate at
414 night and/or that larger nighttime nest groups may be more easily located (Table 1, H11
415 and H12). We cannot currently distinguish between these methodological and
416 behavioral causal factors of chimpanzee party size estimates. Nonetheless, the relatively
417 larger party size estimates found with night nest counts indicate that this method may
418 not be the most suitable method in detecting diurnal party size variation. However, as
419 actual party sizes remain unknown for the unhabituated Seringbara chimpanzee
420 community, the conclusion that night nest counts may lead to overestimations of
421 chimpanzee party size remains preliminary and needs to be further explored. Day nest
422 counts resulted in relatively smaller party size estimates than direct observations, and
423 tended to be relatively smaller than MTC observations, which supports the hypothesis
424 that not all chimpanzees build a nest during the day and/or that some chimpanzee day
425 nests may be missed by human observers when locating daytime nest groups (Table 1,

426 H7 and H8). Although it is currently impossible to separate these hypotheses, the latter
427 hypothesis seems unlikely due to the experience of the field assistants and researchers in
428 tracing nest groups. The finding that day nest counts result in relatively smaller party
429 size estimates indicates that this may not be the most appropriate method for estimating
430 chimpanzee party sizes. Additionally, the smaller nest group sizes resulting from day
431 nests counts as not all individuals build daytime nests may affect estimates of
432 chimpanzee population sizes, densities and distributions, for which nest counts are often
433 used (e.g. Furuichi et al. 2001a). Again, however, this conclusion towards potential
434 underestimations of chimpanzee party sizes from day nest counts is preliminary as
435 actual chimpanzee party sizes remain unknown for our study. No support was found in
436 our study for the following hypotheses that: 1) direct observations result in relatively
437 larger party size estimates as a consequence of increased tolerance to humans in larger
438 parties or because larger parties may be more easily located (Table 1, H1 and H2); 2)
439 direct observations result in relatively smaller party size estimates due to chimpanzees
440 fleeing or human observers failing to detect all individuals (Table 1, H3 and H4); 3)
441 MTC observations lead to relatively smaller party size estimates because chimpanzees
442 pass outside of the film frame of the camera either due to active avoidance or the
443 restricted frame (Table 1, H5 and H6)); 4) day nest counts result in relatively larger
444 party size estimates as a consequence of chimpanzees building more than one nest
445 during the day or human observers more easily locating larger daytime nest groups
446 (Table 1, H9 and H10); and 5) night nest counts result in relatively smaller party size
447 estimates as some nests may be missed by human observers when locating nighttime
448 nest groups (Table 1, H13).

449 Direct and MTC observations did not differ in their relative estimates of party
450 size and composition. Boyer-Ontl and Pruetz (2014) also found that camera trap
451 observations of unhabituated chimpanzees in Senegal generally corroborated
452 observational data from habituated chimpanzees at Fongoli (Senegal), but no specific
453 data on party size or composition were presented. Similarly, McCarthy et al. (2018)
454 studied the accuracy of camera trap observations in comparison to observational data for
455 a habituated chimpanzee community at Tai and found that direct and MTC observations
456 resulted in similar demographic compositions. However, they also showed that MTCs
457 underestimated party size as compared to observational data (McCarthy et al. 2018).
458 This finding differs from ours, possibly due to a difference in habituation status between
459 the two sites. With actual party sizes known for the habituated Tai chimpanzees
460 (McCarthy et al. 2018), this suggests that both direct and MTC observations of
461 unhabituated chimpanzees may underestimate party size. Future research at Nimba will
462 assess party size estimates as habituation levels increase. In sum, our findings show that
463 different methods to measure party size result in different relative party size estimates
464 for chimpanzees. These results are important to take into consideration when comparing
465 chimpanzee party size measures across studies, and when using these methods to
466 estimate community sizes, population densities and distributions.

467 In line with other studies, we found that fruit abundance had a positive effect on
468 party size at Nimba, which supports the prediction that more individuals are able to join
469 a party when fruit is abundant, and costs of co-feeding are low. This effect was,
470 however, only observed when measuring party size with MTCs. Additionally, we found
471 no influence of fruit distribution on party size. At Kahuzi-Biega, chimpanzee party size
472 was positively influenced by the distribution of fruit from preferred tree species

473 (Basabose 2004), whereas our study focused on all identified chimpanzee food tree
474 species. Investigating the effect of fruit distribution of preferred tree species only at
475 Nimba is recommended for future studies. Our study adds to a growing body of
476 evidence that the presence of estrous females has a positive influence on party size. Sex
477 ratios were higher in parties with estrous females, indicating that more males were
478 present (Matsumoto-Oda 1999). Again, the effect of estrous females on party size and
479 composition was only evident when parties were measured using MTCs. Additional
480 factors may further influence party size at Nimba, such as predation pressure,
481 demography, time of day, location in home range, behavior, and presence of non-fruit
482 food items (e.g. Anderson et al. 2002; Boesch 1991; Lehmann and Boesch 2004;
483 Wrangham et al. 1996). Future research is needed to address the effects of these factors
484 on party size. In sum, differences in the factors influencing party size may stem from
485 temporal and spatial variability in chimpanzee grouping patterns, but our findings
486 highlight that the use of different party size methods may also affect research outcomes.

487 This study highlights the potential for the use of MTCs to investigate
488 chimpanzee grouping patterns. Our findings show that at Nimba, MTC observations did
489 not result in relatively larger or smaller party size estimates as compared to the other
490 methods when measuring party size in unhabituated chimpanzees. Additionally, MTCs
491 were the only method to reflect the influence of fruit abundance and estrous females on
492 party size and composition. These findings suggest that the MTC method is suitable for
493 capturing the patterns and proximate causes of chimpanzee grouping patterns. In their
494 study of habituated chimpanzees at Taï, McCarthy et al. (2018) also highlighted the
495 usefulness of camera traps in investigating chimpanzee grouping patterns and
496 demographic variations. Even though their camera trap observations showed smaller

497 party size estimates than observational data, their results showed similar seasonal
498 fluctuations and demographic compositions as direct observations (McCarthy et al.
499 2018). Recent behavioral studies of unhabituated chimpanzee communities also showed
500 potential for MTC observations (Boesch et al. 2016; Köhl et al. 2016; Tagg et al. 2018).
501 MTCs have furthermore proven useful for investigating presence and densities of other
502 species (Rovero and Marshall 2009; Rowcliffe et al. 2008; Widness and Aronsen 2017).
503 MTCs enable the collection of relatively accurate, fine-scaled data non-invasively with
504 minimal human interference and ecological disturbance (McCarthy et al. 2018;
505 Rowcliffe et al. 2008), and thus provide an important conservation tool. As with all
506 methods, camera traps have limitations. For example, species' shyness to MTCs,
507 heterogeneity in camera detection probability, and restricted filming angles may affect
508 data collection (Després-Einspinner et al. 2017; McCarthy et al. 2018). Furthermore,
509 technological issues and weather conditions may pose challenges (Boyer-Ontl and
510 Pruett 2014; van Leeuwen *personal observation*). Although caution is warranted,
511 MTCs provide an efficient and promising method.

512 In conclusion, this study showed that the four commonly used methods to assess
513 chimpanzee party size differed in their relative party size estimates. Party size at Nimba
514 was influenced by fruit abundance and estrous females, but the effect of these factors
515 was only reflected by the MTC method. Our findings should be taken into account when
516 selecting a 'best' method of party size for a particular study focus. At Nimba, our results
517 showed that MTC observations best reflected chimpanzee party size and its influencing
518 socio-ecological factors. MTC observations thus show promising potential in the study
519 of unhabituated chimpanzees.

520

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535

536 **Compliance with ethical standards**

537 **Conflict of interest**

538 The authors declare that they have no conflicts of interest.

539

540 **Ethical approval**

541 This research was non-invasive, complied with the laws of Guinea, and was approved
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544 Division of Biological Anthropology, University of Cambridge, the host institute of the
545 lead researcher (K. Koops) during the study.

546

547 **Electronic supplementary material**

548 Supporting information on the frequency distribution of time intervals between
549 subsequent party observations (*Online Resource 1*), as well as the linear relationships
550 (*Online Resource 2*) and Spearman rank correlations (*Online Resource 3*) between
551 chimpanzee party size, fruit abundance, fruit distribution and fruit availability are
552 available online.

553

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724

725 **FIGURE LEGENDS**

726 **Fig. 1** Monthly party sizes measured with direct observations, MTC observations, day
727 nest counts, and night nest counts over 69 months. The monthly party sizes of the four
728 methods are presented in a stacked way that shows all values

729

730 **Fig. 2** Mean monthly party sizes for direct observations, MTC observations, day nest
731 counts, and night nest counts over 69 months. Significant differences between methods
732 are indicated with p values; 'n.s.' stands for 'not significant'

733

734 **Fig. 3** Fruit availability index (FAI), coefficient of dispersion (CD) and rainfall over 69
735 months

736

737 **Fig. 4** Mean monthly party sizes over 69 months for direct observations ('Direct'),
738 MTC observations ('MTC'), day nest counts ('Day'), and night nest counts ('Night') in
739 high *versus* low fruit abundance months. Significant differences are indicated with p
740 values; 'n.s.' stands for 'not significant'