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1 Durability and flexibility of chimpanzee grooming patterns
2 during a period of dominance instability

3
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ABSTRACT

22
23 Growing evidence from studies on primates and other taxa has shown that the maintenance
24 of long-term affiliative patterns influences fitness. Thus, understanding how individuals
25 regulate social interactions in response to environmental and social factors contributes to
26 our understanding of the evolutionary basis of sociality. We investigated the durability of
27 affiliation patterns in chimpanzees across three 3-month periods of varying social
28 uncertainty depending on the degree of stability in the male hierarchy, with a 2-yr gap
29 between each period. Periods were unstable (no clear alpha male), recently stable (new
30 alpha male just established) and stable (alpha male in place for two years). We focused on
31 three features of social exchange shared by human and non-human primates: consistency of
32 exchanges across periods, durability of preferred partners, and degree of reciprocity in each
33 period. We compared male-to-male, female-to-female, male-to-female and female-to-male
34 grooming patterns. Overall, more grooming was exchanged in the stable period. Grooming
35 patterns were not consistent across the three periods, but were only consistent between the
36 recently stable and stable periods for female-to-female and male-to-female dyads. As
37 predicted from the opportunistic nature of male relationships, male-to-male grooming was
38 least likely to be correlated across all periods and males had relatively fewer durable (i.e.,
39 preferred partners in all periods) same-sex partners than females. Our predictions that
40 grooming reciprocity would be less likely during the unstable period and in male-male
41 dyads were only partially supported. We found grooming reciprocity in all periods for
42 female-female dyads but only in the stable period for male-male and female-male dyads.
43 Although long-term affiliative patterns are well studied in primates, this is the first study to
44 investigate the association between social uncertainty and durability of affiliative patterns.

45 Our findings suggest social uncertainty influences social exchange and highlight the
46 importance of considering group instability in studies of social relationships.

47 Key words: social uncertainty; exchange; long-term; primate

48

49

INTRODUCTION

50 Recently, empirical research demonstrating a direct link between social
51 relationships and fitness has been accumulating across a range of taxa, e.g. primates
52 (Lehmann et al., 2016; Schülke et al., 2010; Silk et al., 2003, 2009), horses (Cameron et al.,
53 2009), dolphins (Stanton & Mann 2012), rodents (Wey et al., 2013), and birds (Royle et al.,
54 2012). Therefore, investigating how individuals manage their social relationships in
55 response to environmental and social factors can shed light on the evolutionary basis of
56 sociality (e.g. Dunbar & Shultz, 2010; Kutsukake 2009). Long-term studies are recognized
57 as providing a wealth of data for a variety of analyses (Kappeler & Watts, 2012). For
58 example, long-term data have provided the opportunity to focus on affiliation patterns over
59 time. Among non-human primates the most frequently used measures of affiliation are
60 spatial proximity and grooming exchanges between group members (Cords, 1997; Dunbar,
61 1991). Using these measures, long-lasting affiliation patterns have been documented in
62 several non-human primate species, such as baboons (*Papio sp.*, e.g. Silk et al., 2006; 2010;
63 2012), rhesus macaques (*Macaca mulatta*, Weinstein & Capitanio, 2012; Massen & Sterck,
64 2013), Japanese macaques (*M. fuscata*, Nakamichi & Yamada, 2007) and bonobos (*Pan
65 paniscus*, Moscovice et al., 2017). Changes in group membership, and thus partner
66 availability, can create social instability (e.g. Beisner et al., 2015) which has been shown to

67 have negative health consequences e.g. in rodents (*Rattus norvegicus*, Herzog et al., 2009;
68 *Heterocephalus glaber*: Clarke & Faulkes 1997) and primates (*M. mulatta*, Capitanio &
69 Cole 2015; *M. fascicularis*, Manuck et al., 1983). Two earlier studies have explored the
70 effect of rank reversals in the male hierarchy on relationships within a primate group (de
71 Waal 1989; Perry 1998) but none so far have explicitly considered the impact of social
72 uncertainty on the durability of affiliation patterns in non-human primates, and the role of
73 social uncertainty on durability of human social relationships is poorly understood
74 (Bukowski et al., 1998). Chimpanzees (*Pan troglodytes*) are a suitable species to examine
75 the role of social uncertainty on the durability of affiliation patterns as enduring affiliation
76 patterns have been reported between males and between females (Gilby & Wrangham,
77 2008; Langergraber et al., 2009; Lehmann & Boesch, 2009; Koski et al., 2012; Mitani,
78 2009), and males are known to engage in flexible social interactions which may depend on
79 social uncertainty (e.g. Nishida, 1983).

80 Affiliation between male chimpanzees is high both in the wild and in captivity
81 (reviewed in Muller & Mitani, 2005). Males are the philopatric sex, are more gregarious
82 and spend more time grooming one another than females do (e.g. Boesch & Boesch-
83 Achermann, 2000; Goodall, 1986; Nishida, 1979). Previous research has emphasized the
84 opportunistic nature of male-male social interactions (e.g. Nishida, 1983; de Waal, 1989;
85 Newton-Fisher, 2002), however, affiliation patterns in some male-male dyads have been
86 found to be durable for up to 10 years in the wild (Mitani, 2009).

87 Chimpanzee females have been often described as having weak social relationships
88 with one another due to their dispersal from the natal group limiting opportunities to
89 interact with kin, and the lack of a need to form coalitions (Nishida, 1979; Goodall, 1986;

90 Wrangham, et al., 1992; Arnold & Whiten 2003). However, more recent findings reveal
91 that females can form long-term cooperative relationships and opportunistic female-female
92 coalitions (Boesch & Boesch-Achermann, 2000; Newton-Fisher, 2006; Lehmann and
93 Boesch, 2008, 2009; Langergraber et al., 2009; Wakefield, 2013; Foerster et al., 2015). The
94 potential for female chimpanzees to form strong relationships was first documented in
95 captivity (de Waal 1984, 1989; Baker & Smuts, 1994), and subsequent captive studies have
96 continued to provide evidence that females can form high-quality relationships with each
97 other (e.g. Fraser et al., 2008; Koski et al., 2012). Only one study so far has assessed
98 temporal durability in female grooming patterns (Lehmann & Boesch, 2009). While the
99 majority of females had at least one same preferred association partner (association being
100 defined as being in the same subgroup) for three of four consecutive years, only a fifth of
101 all adult females maintained a long-term female grooming partner and only 5% of dyads
102 were classified as long-term grooming partners.

103 Fewer studies have focused on affiliative exchanges between females and males in
104 chimpanzees. In the wild levels of proximity and grooming are lower in female-male dyads
105 than in male-male dyads but higher than in female-female dyads (Langergraber et al., 2013;
106 Machanda et al., 2013). In captivity, there appears to be less variation in affiliation between
107 dyads of different sex-combinations (Fraser et al 2008). Both wild and captive studies
108 report that females form coalitions with males (de Waal, 1994; Kahlenberg et al., 2008).
109 There is also some evidence that interaction patterns between females and males are
110 maintained across time as indices of female-male association in the same subgroup during
111 two periods three years apart were highly correlated (Langergraber et al., 2013).

112 Thus, there is growing evidence for the existence of durable affiliation patterns
113 between males, between females and between females and males, but no study so far has
114 examined the impact of social uncertainty on the durability of grooming patterns. Gilby &
115 Wrangham (2008) compared association preferences between periods with different alpha
116 males, but omitted the replacement period from their analyses. Two studies have examined
117 how affiliation patterns vary depending on social instability but they did not compare the
118 consistency of dyadic affiliation patterns across periods differing in social uncertainty (de
119 Waal, 1984; Hemelrijk & Ek, 1991).

120 The gradual change in alpha male that began at the start of our study provided a
121 unique opportunity to investigate how social uncertainty affected the durability of
122 affiliation patterns in chimpanzees. We identified three periods of varying social
123 uncertainty depending on the degree of stability in the male hierarchy (unstable, recently
124 stable and stable) spanning four years. We focused on three features of social exchange that
125 are shared by human and non-human primates (e.g. Krappman, 1998; Massen, et al., 2010;
126 Silk, 2002; Vigil, 2007): the consistency of exchanges across periods, the durability of
127 preferred partners and the degree of reciprocity in each period.

128 We examined these three features by investigating grooming exchanges in male-
129 male, female-female and female-male dyads. If social relationships were not affected by
130 social uncertainty, we expected grooming to be exchanged consistently over time and
131 therefore be correlated across the three periods (Prediction 1). If grooming exchanges were
132 disrupted by the lack of a clear alpha male, we expected consistency only between the
133 recently stable and stable periods (Prediction 2). Due to the opportunistic nature of male-
134 male relationships, especially during periods of uncertainty such as dominance instability,

135 we expected male-male grooming patterns to be the least likely to be correlated across all
136 periods (Prediction 3). We also expected differences in the durability of preferred grooming
137 partners, with a relatively smaller number of preferred partners maintained across all three
138 periods for male-male dyads than for female-female and female-male dyads (Prediction 4).
139 Similarly, we expected grooming reciprocity to be less likely during the unstable period
140 (Prediction 5). This pattern is expected especially for male-male dyads (Prediction 6), as
141 males are expected to shift their exchange of grooming for grooming to grooming for
142 potential support during unstable periods when alliances may be shifting.

143

144 **METHODS**

145 **Subjects and housing**

146 The study group was well established and consisted of 20 adults (5 males and 13
147 females), two adolescent females and nine immature individuals. Females were considered
148 as adult after they were observed with sexual swellings and mating with males. Adult males
149 were between the ages of 25 and 34 years at the start of the study but we also include M1,
150 who was 13.5 years old in this age category due to his successful challenge for the alpha
151 male position. All five adult males and 12 adult females (one female aged 53 years that
152 never groomed was excluded) were selected as subjects. Using pedigrees, we considered as
153 kin those maternally related individuals with $0.125 \leq r \leq 0.5$. A total of seven kin adult
154 dyads (one male-male, one female-male and five female-female dyads) were present in the
155 group.

156 The group was housed at Chester Zoo, UK in an enclosure containing a 143-m², 12-
157 m high round indoor yard, and a 2000-m² outdoor area covered in grass (Caws et al., 2008).

158 The outdoor area contained a variety of bushes and shrubs and 50 vertical poles with
159 interconnecting ropes and nets for enrichment purposes whilst the indoor enclosure
160 contained a 9m high complex metal tower with platforms, ropes and nets and an artificial
161 termite-fishing area. The chimpanzees had access to these two areas during the day and an
162 off-show area during the night. Water was freely available indoors and outdoors, nesting
163 material was provided daily and the chimpanzees were fed 2-3 times a day on fruit,
164 vegetables and pellets.

165 In 2000 the incoming alpha male (M1) ceased to greet the outgoing alpha male
166 (M2) with pant-grunts, the typical submissive signal in chimpanzees (Noë et al., 1980).
167 This was the start of a gradual rank reversal (or inside takeover) process (Teichroeb & Jack,
168 2017) until M1 was established by the end of 2002 (Wehnelt et al., 2006). From September
169 2002, the remaining males consistently greeted with pant-grunts the new and not the former
170 alpha, and female pant-grunt greetings switched to be given at a higher rate to the new
171 rather than former alpha. Based on the consistency and rate of pant-grunts among adult
172 males, we labeled the 2000 period with an unclear alpha male as the unstable period; the
173 2002 period with the recent settlement of the alpha male dispute as the recently stable
174 period; and the 2004 period with a clear alpha male for at least two years as the stable
175 period. Of the remaining three males only one male could be clearly and consistently
176 positioned at the bottom of the hierarchy (M5) and the remaining two males were ranked
177 equally (M3 and 4) as no pant-grunt greeting was observed between them. It was not
178 possible to construct a dominance hierarchy for females due to the scarcity of dominance-
179 related interactions between females.

180

181 **Data collection**

182 Observations were collected by a trained research assistant and KR in three periods
183 from October to December in 2000, 2002 and 2004 on weekdays between 10.00 and 16.00.
184 The research assistant trained KR to ensure inter-observer reliability. Instantaneous scan
185 sampling with a minimum of 15-minute intervals was carried out on each subject to record
186 the identity of grooming partners and whether grooming was given or received. As in some
187 previous studies (e.g. Lehmann & Boesch, 2009) mutual grooming was recorded as two
188 separate grooming events (i.e. A grooms B and B grooms A).

189

190 **Statistical analyses**

191 As females' attractiveness can influence grooming interactions with males (e.g.
192 Anderson et al., 2006; Koyama et al., 2012; Mastumoto-Oda et al., 1998; Slater et al.,
193 2008) we analyzed data from females when they did not have the ano-genital area swollen,
194 i.e. not sexually attractive to males. There were days in which some individuals were not in
195 the group, resulting in an uneven number of scans across dyads. The range of scans per
196 dyad was 306-339 in the unstable period, 335-381 in the recently stable period, and 284-
197 315 scans in the stable period. First, we tested for differences in the percentage of scans
198 spent grooming between periods at the individual level with a repeated measures ANOVA,
199 with Dunn-Šidák-corrected pair-wise comparisons, for each dyad type (female-female,
200 male-male, male-female and female-male). Then, we constructed matrices of the
201 percentage of scans spent grooming given (and of grooming received) for each dyad type
202 for each period and carried out Kendall's (τ_{rw}) rowwise matrix correlation tests (de Vries,
203 1993, Hemelrijk et al., 1990), a variant of the Mantel test (Mantel, 1967), using MatmanTM

204 1.1 (de Vries et al., 1993). Matrix correlation methods avoid problems arising from the non-
205 independence of dyadic data as the same individuals are present in multiple dyads and have
206 been used widely in previous studies in chimpanzees (de Waal & Luttrell, 1988;
207 Langergraber et al, 2009; Newton-Fisher & Lee, 2011; Stumpf & Boesch, 2010; Wakefield,
208 2013). Kendall's (τ_{rw}) rowwise matrix correlation test accounts for the presence of
209 individuals in more than one dyad by running the correlations within rows.

210 To find out if grooming exchanges were consistent across the three periods
211 (Prediction 1-2) depending on the dyadic sex combination (Prediction 3), we ran Kendall's
212 (τ_{rw}) rowwise matrix correlation tests of grooming given between the unstable and the
213 recently stable period, between the recently stable and the stable period and between the
214 unstable and the stable period, for male to male grooming, male to female grooming and
215 female to male grooming. As five of the total 66 female-female dyads (8 females) included
216 close kin we used partial matrix correlation tests ($\tau_{rw;XYZ}$) that controlled for the effect of
217 kinship while the correlation between grooming in the two years was calculated. We did
218 not control for proximity across dyads as in captivity group members are always relatively
219 close to one another, in contrast to the fluid party membership seen in the wild (Goodall,
220 1986; Nishida, 1979).

221 We ran 10,000 iterations for each rowwise matrix correlation test and report exact
222 two-tailed p values, adjusting our level of significance using the sequential Bonferroni
223 technique (Holm, 1979) to reduce the likelihood of Type 1 errors. As there were separate
224 matrices for each dyadic sex combination (female-female, male-male, female-male and
225 male-female) we treated each combination as a subset of k tests for the Bonferroni
226 correction.

227 We evaluated the durability of preferred grooming partners depending on the dyadic
 228 sex combination (Prediction 4) by identifying the preferred grooming partners as those that
 229 were groomed above an individual's dyadic mean in each of the three periods: unstable,
 230 recently stable and stable. Durable preferred grooming partners were those individuals that
 231 were preferred grooming partners in all periods.

232 To assess patterns of reciprocity (Prediction 5-6) based on partner choice (Schino &
 233 Aureli, 2017) across dyads within each period, we correlated grooming given matrices with
 234 grooming received matrices for each sex combination of dyads, partialling out kinship for
 235 the female-female dyads. In addition, to examine whether subjects exchanged grooming
 236 bouts more reciprocally with durable preferred grooming partners than with other grooming
 237 partners, we calculated a reciprocity index (Mitani, 2009 rescaled from Nishida, 1988) for
 238 each dyad:

$$239 \quad 1 - [g_{AB}/(g_{AB} + g_{BA}) - g_{BA}/(g_{AB} + g_{BA})]$$

240 where g_{AB} is the percentage of scans A spent grooming B, g_{BA} is the percentage of scans B
 241 spent grooming A. We calculated a mean reciprocity index for each individual with its
 242 durable preferred grooming partners and the remaining grooming partners for each period.
 243 We used a paired t-test to investigate differences between these mean reciprocity indexes at
 244 the individual level for females only, due to sample size constraints. We used SPSS 20.0
 245 (SPSS Inc., Chicago, IL, U.S.A.) to analyze differences between periods.

246 At the time of the study, observational, noninvasive animal research did not require
 247 approval of the university ethics committee. The study adhered to U.K. legislation and to
 248 the American Society of Primatologists' Principles for the Ethical Treatment of

249 Primates. Chester Zoo approved the research protocols used in this study and gave
250 permission to conduct the study.

251

252

253

RESULTS

254

255

Female-female grooming patterns

256

257 Grooming was observed in around two-thirds of all dyads in each period (Table 1). Females
258 groomed other females differently across the three periods ($F_{2,22}=47.4$, $P<0.001$, with a
259 higher percentage of scans spent grooming in the stable period (mean \pm SD: 7.3 ± 2.7) than in
260 the unstable (2.1 ± 1.2 ; $P<0.001$) and recently stable period (1.9 ± 1.1 ; $P<0.001$). There was
261 no difference between the unstable and recently stable period ($P=0.9$).

262

263 *Table 1 here*

264

265

Consistency across periods. Female-female grooming patterns showed some
266 consistency over the four years (Table 2) with positive correlations between the unstable
267 and recently stable periods and between the recently stable and stable periods. However,
268 there was no correlation between the unstable period and the stable period (Table 2),
269 indicating an overall shift in grooming patterns over time.

270

271 *Table 2 here*

272

273 ***Durable preferred grooming partners.*** In each period the majority of females
274 groomed a selected number of preferred partners but they groomed an even smaller number
275 of preferred partners in all three periods (Table 3). Nine of 12 females had at least one
276 durable preferred grooming partner, i.e. the same preferred partner in each of the three
277 periods. Of the three females without durable preferred partners, one did not groom any
278 other females in two of the three periods and two groomed preferred partners consistently
279 in only two of the three periods. Six of the nine females with durable preferred partners had
280 kin in the group, but two females with kin in the group did not have durable preferred
281 partners. When we excluded kin, six of the 12 females had at least one durable non-kin
282 preferred grooming partner.

283

284 ***Reciprocity.*** Grooming given and received within each period was positively
285 correlated indicating grooming reciprocity (Table 2). The mean (\pm SD) reciprocity index
286 with durable preferred partners was not significantly higher than that with other grooming
287 partners in the unstable (durable= 0.36 ± 0.2 , other= 0.17 ± 0.2 ; $T_5=1.37$, $P=0.23$) and recently
288 stable (durable= 0.57 ± 0.29 , other= 0.33 ± 0.23 , $T_8=1.7$, $P=0.14$) periods, and not
289 significantly different in the stable period, although close to the alpha level (durable=
290 0.84 ± 0.16 , other= 0.70 ± 0.18 , $T_8=2.3$, $P=0.054$).

291

292 *Table 3 here*

293

Male-male grooming patterns

294

295 Males groomed other males differently across periods ($F_{2,8}=7.6$, $P=0.014$), with a higher
296 percentage of scans spent grooming in the stable period (3.4 ± 2.1) than in the recently stable
297 period (1.2 ± 0.9 ; $P=0.048$). There was no difference between the unstable period (1.4 ± 0.9)
298 and the recently stable ($p=0.9$) or stable ($P=0.2$) periods.

299

300 ***Consistency across periods.*** Grooming given by males to other males was not
301 overall consistent across the three periods, although there was a correlation in grooming
302 given between the unstable period and the recently stable period (Table 4).

303

304 ***Durable preferred grooming partners.*** Three of the five males had at least one
305 durable preferred grooming partner (Table 3); the durable preferred grooming partners were
306 all non-kin. These three males were the new alpha male M1, M4 and M5.

307

308 ***Reciprocity.*** Reciprocity of grooming given and received was only found in the
309 stable period (Table4).

310

311 *Table 4 here*

312

313

314 **Grooming patterns between the sexes**

315

316 Females groomed males differently across the three periods ($F_{1,3,14,3}=15.0$, $P<0.001$), with a
317 higher percentage of scans spent grooming in the stable period (4.4 ± 2.9) than in the

318 unstable (1.5 ± 1.4 ; $P=0.008$) and recently stable period (1.1 ± 0.7 ; $P=0.004$). There was no
319 difference between the unstable and recently stable period ($P=0.6$). There was no difference
320 in the percentage of scans spent by males grooming females among the three periods
321 (unstable: 5.0 ± 4.4 ; recently stable: 3.7 ± 1.8 ; stable: 7.7 ± 2.7 ; $F_{1,4}=2.1$, $P=0.2$).

322

323 ***Consistency across periods.*** There was some consistency in male grooming given
324 to females across the three periods (Table 5). Males who groomed females in one period
325 were more likely to groom them in the next period although these relationships shifted over
326 the course of the study from the unstable to the stable period. There was a correlation in
327 female grooming given to males only between the unstable period and the recently stable
328 period (Table 5).

329

330 *Table 5 here*

331

332 ***Durable preferred grooming partners.*** Four of the five males had at least one
333 durable preferred female partner across the three periods (Table 3). The new alpha male,
334 M1, preferentially groomed three female (non-kin) partners across all periods. The
335 outgoing alpha male, M2, and M4 had two females as durable preferred partners, whereas
336 M3 had only one durable preferred female partner. The lowest ranking male, M5, did not
337 have any durable preferred female partner.

338

339 In contrast, only five of the 12 females had durable preferred non-kin male
340 grooming partners (Table 3): two females had one durable preferred male partner (the
outgoing alpha M2) and three females had two durable preferred male partners (M2 and M3

341 for one female and M3 and M4 for two females). None of the females had the new alpha
342 male M1 or the lowest ranking male M5 as a long-term preferred male grooming partner.

343

344 ***Reciprocity.*** Similar to the male-male dyads, reciprocity of grooming given and
345 received in male-female dyads only occurred in the stable period (Table 3).

346

347

348 **DISCUSSION**

349

350 We examined six predictions about how social uncertainty may affect the durability
351 of affiliation patterns in chimpanzees by focusing on three features of social exchange: the
352 consistency of exchanges across time, the durability of preferred partners and the degree of
353 reciprocity. We did so by comparing grooming exchanges in male-male, female-female and
354 female-male dyads across three periods differing in social uncertainty based on the degree
355 of stability in the male dominance hierarchy. Prediction 1, that grooming was exchanged
356 consistently over time, was not supported as no dyad type showed a correlation between the
357 unstable and the stable period which were 4 years apart. Prediction 2, that consistency in
358 grooming patterns occurred only between the recently stable and stable periods, was
359 partially supported. A correlation between these two periods was found only for females
360 grooming other females and males grooming females, but not for males grooming other
361 males and females grooming males. Prediction 3, that male-to-male grooming was the least
362 likely to be correlated across all periods, was overall supported, although female-to-male
363 grooming was correlated only between two periods. Prediction 4 was supported as the

364 number of preferred partners maintained across all three periods was relatively smaller for
365 male-male dyads than for female-female and female-male dyads. Interestingly, within the
366 female-male dyads the number of such preferred partners was relatively higher for males
367 grooming females than for females grooming males. Prediction 5, that grooming reciprocity
368 was less likely during the unstable period, was partially supported because there was
369 reciprocity in female-female dyads during this period, whereas there was no reciprocity in
370 the other dyad types during the unstable and the recently stable periods. Prediction 6, that
371 grooming reciprocity was less likely during unstable periods in male-male dyads than in the
372 other dyad types, was not fully supported as reciprocity was demonstrated in all periods in
373 female-female dyads, but reciprocity could be shown only in the stable period in female-
374 male dyads, like in male-male dyads. Overall, our findings support previous studies, as the
375 majority of individuals appeared to maintain at least one durable partner, and add to a
376 growing body of research on the durability of affiliation patterns in primates (e.g. Massen
377 & Sterck, 2013; Mitani, 2009; Moscovice et al., 2017; Silk et al., 2010, 2012).

378 Similar to recent studies from the wild (e.g. Lehmann & Boesch, 2009; Foerster et
379 al., 2015) and captivity (e.g. Fraser et al., 2008; Koski et al., 2012) we found evidence for
380 durability of grooming patterns between chimpanzee females. They showed consistency
381 between adjacent periods, but females shifted partner preferences between the unstable and
382 stable periods, which were 4 years apart. This shift provides evidence for flexibility in
383 female-female grooming patterns depending on changes in male dominance hierarchy. As
384 chimpanzee females may be less sociable when they have a young infant (e.g. Otali &
385 Gilchrist, 2006), one could argue that our findings may be due to differences in the number of
386 females with a young infant across periods. In our study, there was only one female with an

387 infant in the unstable period and two females with an infant in the stable period. Contrary to
388 what expected based on infant presence, we found more female grooming in the stable
389 period than in the other two periods. All but one of the females maintained at least one
390 preferred partner across all three periods, indicating resilience of some relationships
391 through periods of dominance instability and social uncertainty. These durable preferred
392 partners were kin and non-kin, and some females with female kin in the group had non-kin
393 as durable preferred grooming partners.

394 There was overall little evidence for durability in females grooming males. We
395 found only a correlation between the unstable and the recently unstable period. Only five of
396 the 12 females had durable preferred male grooming partners. Interestingly, these partners
397 were the outgoing alpha male and the middle ranking males, and no female preferentially
398 groomed the new alpha male across periods. Female support for the outgoing alpha male
399 has been previously reported; however, such support was later transferred to the new alpha
400 male, highlighting the flexibility in females' relationships with males (de Waal, 1986). In
401 our study, the durability of female preferences for male partners across periods of male
402 dominance instability may be related to the gradual process of changing the alpha male.
403 Similarly, the lack of a correlation between the unstable and stable period supports the
404 flexibility in females grooming males.

405 Few studies have examined males' affiliation patterns with females with somewhat
406 contrasting results (Langergraber et al., 2013; Machanda et al., 2013). Similar to the
407 grooming patterns between females, we found males showing consistency in grooming
408 females between adjacent periods. All males, except the lowest ranking male, had durable
409 preferred female grooming partners, highlighting the importance of females as long-term

410 partners for males. These findings support the observations of females playing an important
411 role in mediating male-male interactions in captive chimpanzees (de Waal 1982). Males
412 changed their partner preferences between the more distant periods (i.e., the unstable and
413 stable periods), supporting the importance of flexibility in affiliation patterns depending on
414 the social context.

415 As expected based on previous studies (Nishida, 1983; Goodall, 1986; Mitani et al.,
416 2000; Newton-Fisher, 2002), we found little evidence for durability in patterns of grooming
417 between males, and only two of the five males had durable preferred male grooming
418 partners. Male-male grooming patterns were correlated only between the unstable and
419 recently stable periods, suggesting that after the male dominance hierarchy had stabilized
420 grooming patterns shifted. These differences across periods could reflect flexible
421 adjustments to patterns of support among males given that interactions between males are
422 often opportunistic and related to shifting temporary alliances (Nishida, 1983; de Waal,
423 1989).

424 In line with previous reports (e.g. de Waal, 1984; Hemelrijk & Ek, 1991; Boesch &
425 Boesch-Achermann, 2000; Watts, 2000; 2002) grooming reciprocity based on partner
426 choice was detected but there was a striking contrast between females and males. Female-
427 female grooming reciprocity was found within all three periods, consistent with Hemelrijk
428 & Ek (1991). However, in all dyads involving males, grooming was reciprocated only
429 during the stable period when the male hierarchy had been stable for two years. Previous
430 studies have reported grooming reciprocity based on partner choice between males (e.g.
431 Hemelrijk & Ek ,1991; Watts, 2002) including during periods without a clear alpha male.
432 Whether our findings regarding male reciprocity reflect differences in social uncertainty,

433 the lack of extensive kinship between males (Mitani, 2009), or the small number of males
434 in the study group, requires further research, although it should be noted that we found the
435 same pattern in female-male dyads.

436 The gradual alpha male replacement that occurred over two and a half years in our
437 study is unusual. Data from the wild suggest that most replacements occur more rapidly
438 lasting from one day (Kaburu et al., 2013) to several months (Riss & Goodall, 1977,
439 Nishida, 1983, Newton-Fisher 2002, Muller 2002), although there may be variability within
440 the same species depending on group composition (Teichroeb & Jack 2017). Alpha male
441 replacements in captivity occur over a similar time frame to the wild, from two (Seres et al.,
442 2001) to several months (de Waal, 1986). Thus, the longer replacement period in this study
443 is not necessarily an artefact of captive conditions and may have been due to group
444 dynamics. The formation of effective alliances with other adult males has been considered
445 crucial in determining the outcome of the dominance challenge and the fate of defeated
446 alpha males (Uehara et al., 1994; Hasegawa & Kutsukake, 2015). In our study, the
447 incoming alpha male maintained durable preferred grooming partnerships with one male
448 and two females, whereas the outgoing alpha male maintained such partnerships with four
449 females. These differences may reflect the strategies adopted by each male (e.g. de Waal,
450 1989; Foster et al., 2009).

451 Our findings shed light on an understudied aspect of primate sociality, that is
452 durability of affiliation patterns throughout social uncertainty, and contribute to our
453 understanding of durability and flexibility of human and non-human social relationships.
454 Social uncertainty in humans is associated with an increased probability of supporting a
455 friend contrary to local rules, given the strong correlation between a composite index of

456 economic, social and political instability and individuals' willingness to lie to help a friend
457 (Hruschka, 2010). This finding highlights the importance of considering social uncertainty
458 when investigating individuals' investment in social relationships. It is tempting to exclude
459 periods of social uncertainty from analyses of the durability of interaction patterns (e.g.
460 Gilby & Wrangham, 2008), but including them can draw attention to the relative patterns of
461 flexibility and durability of social relationships and contribute to our understanding about
462 their relative importance in the social arena. In this respect, our study contributes to the
463 understanding of sex differences in chimpanzee behavior by examining the role social
464 uncertainty in them. Overall, we found greater consistency in female-female than male-
465 male grooming patterns, which is in agreement with previous research on sex differences.
466 Our study also emphasizes the importance of maintaining long-term partners through
467 periods of instability with more consistent grooming patterns for females and more flexible
468 grooming patterns for males. Further research is needed to investigate the maintenance of
469 durable relationships by means of social interactions other than grooming and across
470 different types of social uncertainty. Our findings also illustrate that captive studies can
471 provide ideal settings to examine the details for potential flexibility of social interactions in
472 response to factors external to the interacting individuals, such as the gradual replacement
473 of the alpha male.

474

475

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774 Table 1. Summary data showing distribution of grooming across the three periods

775

		Period		
		unstable	recently stable	stable
% of dyads in which grooming was observed	all dyads	60.3	66.2	69.1
	female-female dyads	43.9	60.6	69.7
	male-male dyads	80.0	90.0	70.0
	male-female dyads	75.0	88.3	66.7

776

777 Table 2. Correlations between periods for female-to-female grooming dyads.

778

Grooming given between years			Reciprocity in grooming		
Periods	$\tau_{rw;XYZ}$	P	Periods	$\tau_{rw;XYZ}$	P
unstable & recently stable	0.23	0.006*	unstable	0.23	0.004*
recently stable & stable	0.21	0.008*	recently stable	0.28	0.001*
unstable & stable	0.13	0.1	stable	0.67	0.0002*

779 Partial Kendall rowwise correlations ($\tau_{rw;XYZ}$) for female-to-female grooming dyads (with kinship
 780 held constant) between periods with varying stability in the male hierarchy (unstable, recently
 781 stable, and stable period) and reciprocity within each period. * Significant p values after sequential
 782 Bonferroni correction.

783 Table 3. Number of same-sex and different-sex durable preferred grooming partners for
 784 females and males.
 785

subject s	Same-sex			Different-sex		
	no. durable preferred partners	no. related long-term preferred partners / no. close kin in group	mean (\pm SD) no. preferred grooming partners per period	no. durable preferred partners	no. related long-term preferred partners / no. close kin in group	mean (\pm SD) no. preferred grooming partners per period
F1	3	-	5.6 \pm 1.5	0	-	4.0 \pm 1.0
F2	0	-	2.3 \pm 4.0	0	-/1	3.3 \pm 0.6
F3	2	1/2	3.3 \pm 1.5	1	-	4.7 \pm 0.6
F4	2	1/2	3.7 \pm 0.6	0	-	2.3 \pm 0.6
F5	1	1/1	4.0 \pm 1.0	0	-	1.3 \pm 0.6
F6	2	1/1	4.7 \pm 1.5	2	-	4.3 \pm 0.6
F7	0	-/1	3.3 \pm 0.6	2	-	4.7 \pm 0.6
F8	2	-	5.3 \pm 1.2	0	-	4.3 \pm 1.2
F9	0	-	3.3 \pm 0.6	2	-	4.3 \pm 1.2
F10	1	0/1	5.3 \pm 1.2	0	-	5.0 \pm 0
F11	1	1/1	2.7 \pm 1.5	1	-	4.0 \pm 1.0
F12	1	1/1	2.3 \pm 1.2	0	-	3.7 \pm 0.6
M1-D	1	-	3.0 \pm 0	3	0/1	5.7 \pm 2.1
M2-B	0	-	2.7 \pm 0.6	2	-	3.0 \pm 1.0
M3-N	0	-/1	0.3 \pm 0.6	1	-	4.3 \pm 0.6
M4-F	1	0/1	3.3 \pm 0.6	2	-	4.7 \pm 0.6
M5-W	1	-	3.3 \pm 0.6	0	-	3.7 \pm 0.6

786 F=females; M=males; numbers following F and M serve to identify the 12 female and 5
 787 male subjects.
 788
 789

790 Table 4. Correlations between periods for male-to-male grooming dyads.

791

Grooming given between years			Reciprocity in grooming		
Periods	τ_{rw}	P	Periods	τ_{rw}	P
unstable & recently stable	0.47	0.003*	unstable	0.37	0.03
recently stable & stable	0.22	0.15	recently stable	0.28	0.12
unstable & stable	0.11	0.33	stable	0.81	0.0007*

792 Kendall rowwise correlations (τ_{rw}) for male-to-male grooming dyads across periods with varying
 793 stability in the male hierarchy (unstable, recently stable, stable) and reciprocity within each period.

794 * Significant p values after sequential Bonferroni correction.

795 Table 5. Correlations between periods for male-to-female and female-to-male grooming
 796 dyads.
 797

Grooming given between years			Reciprocity in grooming		
Periods	τ_{rw}	P	Periods	τ_{rw}	P
<i>Male grooming females:</i>					
unstable & recently stable	0.31	0.007*	unstable	-0.05	0.4
recently stable & stable	0.38	0.001*	recently stable	0.02	0.4
unstable & stable	-0.01	0.5	stable	0.71	0.0005*
<i>Female grooming males:</i>					
unstable & recently stable	0.30	0.011*	unstable	0.11	0.2
recently stable & stable	0.16	0.09	recently stable	-0.17	0.09
unstable & stable	0.14	0.1	stable	0.56	0.0005*

798 Kendall rowwise correlations (τ_{rw}) for male-to-female and female-to-male grooming dyads across
 799 periods with varying stability in the male hierarchy (unstable, recently stable, stable) and reciprocity
 800 within each period.* Significant p values after sequential Bonferroni correction.