Kinship and intra-group social dynamics in two sympatric African colobus species

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Short title: Socio-genetics of colobus monkeys

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25 **ABSTRACT**

26   Kinship has been described as a major factor shaping primates' social dynamics,

27 with individuals biasing their affiliative interactions to their related counterparts.

28 However, it has also been demonstrated that, under certain circumstances, social

29 bonding can be established in the absence of kin. The fact that *Colobus polykomos*

30 (Western black-and-white colobus) and *Procolobus badius temminckii* (Temminck's red

31 colobus) often live in sympatry (subject to the same ecological/anthropogenic

32 pressures) but exhibit contrasting social systems, makes them good models to test which

33 factors shape their social systems. We investigated the influence of kinship on intra-

34 group social dynamics of one focal group of each species present in Cantanhez National

35 Park, Guinea-Bissau. Between October 2008 and June 2009 we used focal sampling to

36 collect information on the individuals' nearest neighbors and *Ad libitum* sampling to

37 collect data on intra-group social interactions. We estimated pairwise relatedness using

38 fecal DNA from nine *Colobus polykomos* individuals and 15 *Procolobus badius*

39 *temminckii* individuals genotyped at 15 microsatellite loci. We found that, in the

40 *Colobus polykomos* focal group, individuals showed no preference to interact or be

41 spatially closer to related partners. Moreover, mainly unrelated females and related

42 males composed the *Procolobus badius temminckii* focal group but grooming was most

43 frequent among female dyads and only rarely involved male dyads. We conclude that

44 kinship is not an important factor determining the social bonding in either study species

45 suggesting that other factors (e.g anthropogenic, ecological) may be at play shaping

46 these groups' social bonding.

47

behavior; West Africa

INTRODUCTION

Since cooperating with kin increases inclusive fitness, the assumption that individuals should preferentially address their affiliative and cooperative behavior to close kin constitutes a starting point for many of the models that attempt to explain the evolution of primate social systems (e.g. Chapais 2001; Gouzoules and Gouzoules 1987; Hamilton 1964a, b; Silk 1987, 2002;). Accurately testing this hypothesis has been facilitated by the development of molecular techniques for quantifying relatedness (Lynch and Ritland 1999; Pamilo and Crozier 1982; Queller and Goodnight 1989). By allowing the assessment of paternity, kinship and population structures, molecular data can provide insights into these features of social systems (Di Fiore 2003). For example, long-term observational studies of chimpanzee (*Pan troglodytes*) communities have demonstrated the existence of strong affiliative and cooperative bonds among philopatric males, suggesting that related males exhibit closer affiliation than non-related females (e.g. Watts and Mitani 2001; Wrangham and Peterson 1996). However, studies that evaluated intra-community relatedness of chimpanzees showed that the affiliative and cooperative behaviors observed among males did not arise as a direct result of kin selection and that other evolutionary mechanisms may be at play (e.g. mutualism, reciprocal altruism; Gagneux et al. 1999; Vigilant et al. 2001). The same was demonstrated for *Colobus vellerosus* for which all groups' social dynamics were female bonded regardless of their relatedness (Wikberg et al. 2012). Cooperation has also been demonstrated in the absence of kinship in other studies, reinforcing the notion that intra-group relatedness is not always enough to explain social dynamics (e.g. in

74 primates *Papio cynocephalus*: Bercovitch 1988; Noe 1990; and non-primates *Tursiops*

75 *aduncus*: Connor et al. 2001 and *Chiroxiphia linearis*: McDonald and Potts 1994). For

76 instance, an increase in intra-group competition can induce the establishment of social

77 bonds among non-related individuals in wild primates (e.g. Barton et al. 1996; Lehmann

78 & Boesch 2009). This clearly suggests that intra-group social dynamics can change as a

79 result of changes in the socio-ecological context.

80 The increasing changes in natural habitats that result from anthropogenic-related

81 pressures and climate change, are forcing wild animals to rapidly adapt to poorer

82 environmental conditions (Hockings et al. 2015; Mortelliti et al. 2010). The extent to

83 which a species is able to persist in more degraded habitats is highly dependent on its

84 socio-ecological plasticity (Di Fiore and Rodman 2001, Frankham 2006; Hockings et al.

85 2015; Villard 2002). Some primate populations have shown the ability to adapt their

86 dispersal system, group size, home range size, diet composition and/or behavioral

87 patterns when faced with changing environments (e.g. *Colobus polykomos*: Minhós et

88 al. 2013a; *Colobus guereza*: Onderdonk and Chapman 2000; *Cercopithecus cephus:*

89 Tutin 1999; *Procolobus rufomitratus*: Decker 1994; *Macaca sylvanus*: Ménard et al.

90 2013, *Colobus galeritus*: Wieczkowski 2005; *Pan troglodytes verus*: Carvalho et al.

91 2013; Hockings et al. 2012; Sousa et al. 2011).

92 *Colobus polykomos* (Western black-and-white colobus) and *Procolobus badius*

93 *temminckii* (Temminck's red colobus) exhibit very different social systems despite

94 being phylogenetically related and often living sympatrically (and thus subject to

95 similar ecological/anthropogenic pressures), making them excellent models to evaluate

96 the factors shaping their social dynamics. *Colobus polykomos* live in relatively small

97 groups, comprising 1-3 adult males and 4-6 adult females (Dasilva 1989; Galat and

98   Galat-Luong 1985). As in all other *Colobus* species, dispersal is thought to be male-

99   biased with episodes of female migration (e.g. *Colobus polykomos*: Minhós et al. 2013a;

100 *Colobus satanas*: Fleury and Gautier-Hion 1999; *Colobus guereza*: Harris et al. 2009;

101 *Colobus vellerosus*: Teichroeb et al. 2009; Wikberg et al. 2012). It has been suggested

102 that *Colobus polykomos* females only disperse when the cost of staying in their natal

103 group is high (e.g. inbreeding avoidance: Isbell and van Vuren 1996, Isbell 2004,

104 Korstjens et al. 2005). Within social units, *C. polykomos* females either maintain closer

105 relationships with one another than they do with males or exhibit loose social bonds

106 with no preference to interact affiliatively with other females (Korstjens et al. 2002;

107 Oates 1977; Struhsaker and Leland 1979). This provides evidence that different

108 strategies can be adopted by females in response to different ecological and/or social

109 constraints. Affiliative interactions among males are almost non-existent and they

110 display a clear dominance hierarchy (Dasilva 1989).

111 *Procolobus badius temminckii* live in large multi-male, multi-female groups that

112 range from 12 to 65 individuals (Galat and Galat-Luong 1985; Korstjens 2001;

113 Struhsaker 1975; Struhsaker and Oates 1975;). As in all other red colobus, *P. b.*

114 *temminckii* dispersal is female-biased, with a patrilineal society (Minhós et al. 2013a;

115 Starin 1991, Struhsaker 2010,). Social interactions among females are rare and allo-

116 grooming is more frequent among males (Struhsaker and Leland 1979, Struhsaker

117 2010). In the highly fragmented Abuko Nature Reserve, The Gambia, Starin (1991,

118 1994) found lower rates of inter-male grooming and proximity for *P. b. temminckii* than

119 described for other red colobus populations. Males only cooperated when either an alien

120 male or a neighboring troop was in proximity. The differences exhibited by the

121 population from Abuko Nature Reserve compared to other red colobus highlight the

122 importance of understanding the factors shaping these primates' social dynamics.

123 Here we present a socio-genetic study of two sympatric social groups of the

124 Endangered *Procolobus badius temminckii* and the Vulnerable *Colobus polykomos*

125 (Oates et al. 2008a,b). We conducted the study in Cantanhez National Park, Guinea-

126 Bissau, where previous population genetic analysis has shown that dispersal is mainly

127 mediated by females in *P. b. temminckii* and by both sexes in *C. polykomos* (Minhós et

128 al. 2013a). Our aim is to understand if kinship is the main factor shaping the social

129 dynamics of these species. To achieve this goal we examine the relationship between

130 intra-group relatedness and social bonding. According to the hypothesis that kinship

131 plays a major role shaping these primates' social systems, we expected individuals to

132 direct their affiliative behaviors (e.g. grooming) mostly to their related counterparts and

133 their aggression towards non-related partners. Alternatively, in the case that other

134 factors (e.g. ecological/anthropogenic) determine intra-group social bonding, we

135 predicted no correspondence between affiliative or aggressive behaviors and kinship (Di

136 Fiore 2003; Hamilton 1964a;).

137

138 **METHODS**

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140 *Study site and social groups*

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142 Cantanhez National Park (CNP) comprises a mosaic of savannah, forest and

143 mangrove habitat and covers an area of 1.067 km^2 (105 767 ha) in the southwest of

144 Guinea-Bissau (NE limit: 11°22'58''N, 14°46'12''E; SW limit: 11°2'18''S.

145 15°15'58''W (WGS 84); Fig 1). The park has a high human population density (22,505

146 people distributed through 110 villages) with extensive agriculture (Hockings and Sousa

147 2013). As a consequence, the forests are severely fragmented comprising several

148 patches of various sizes (ranging from 47.5 to 250 ha; Simão 1997). The annual

149 temperature ranges from 28ºC to 31ºC and the annual rainfall is 2000 to 2500mm

150 (Simão 1997).

151 We observed one group of *Colobus polykomos* and one group of *Procolobus*

152 *badius temminckii*. Both groups' home ranges overlapped with a village that is also a

153 tourist site, though the primates were not provisioned. As a result, the groups were

154 already partially habituated, allowing observations to commence at the beginning of the

155 study. Proximity to the tourist site may provide these groups some protection from local

156 hunters. Even though CNP is a protected area, both colobus species are hunted within

157 the park. The hunting pressure seems more intense for *P. b. temminckii* than for *C.*

158 *polykomos* (T. Minhós pers obs; Hockings and Sousa 2013). For *P. b. temminckii,* we

159 counted a minimum of 27 animals in the group, including three adult males, 10 adult

160 females, six juveniles and eight infants. However, it was not possible to see all group

161 members at the same time and accurately determine the size of the group. For *C.*

162 *polykomos,* we were able to individually recognize all group members. The group

163 comprised 10 individuals: one adult male, one sub-adult male, four adult females, two

164 juvenile males, one juvenile female and one infant. By the end of March 2009, the adult

165 male, sub-adult male, a juvenile male and an adult female with the infant left the group

166 and did not return so the group was reduced to half of its initial size.

167 *Ethical note*

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169 We carried out all sampling with the approval and under the legal requirements of

170   the National Institute for Biodiversity and Protected Areas (IBAP) and the Forestry and

171   Fauna Department (DGFC) from Guinea Bissau.

172

173   *Intra-group relatedness*

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175   We collected fecal samples for all known individuals of the *Colobus polykomos*

176   focal group and several *Procolobus badius temminckii* individuals for which we

177   identified the sex and age class. We extracted fecal DNA using the QIAampDNA Stool

178   Kit following the manufacturer's instructions and stored at -20 ºC (Qiagen, Valencia,

179   CA). We genotyped all samples for 15 human-derived microsatellite *loci.* The

180   genotyping procedures and the information on the microsatellite *loci* used are described

181   in detail in Minhós et al. (2013a). In the *C. polykomos* focal group, we were able to

182   genotype most of the original group: one adult male, one sub-adult male, three adult

183   females, two juvenile males and one juvenile female. For the *P. b. temminckii* focal

184   group we were able to genotype 11 adult females and four adult males. We estimated

185   the relatedness coefficient of Queller and Goodnight (1989) for all intra-group dyads

186   using Kingroup v2_101202 (Konovalov et al. 2004). We applied a maximum-likelihood

187   relatedness estimator, where we only considered the significantly related dyads ($p <$

188   0.05) to be truly related. We based these estimates on the allelic frequencies from a

189   bigger sample of the population (52 *C. polykomos* and 72 *P. b. temminckii* individuals;

190   for detailed description see Minhós et al. 2013a) and not only from the individuals in

191   the focal groups. The *C. polykomos* relatedness analyses correspond to the full genetic

192   characterization of the social group. For *P. b. temminckii,* our data represents minimum

193   estimates, since there were more adult individuals in the group from which we did not

194 obtain genotypes. We calculated the mean pairwise relatedness for all possible dyads of

195 individuals and assessed the number of pairs of closely related females and pairs of

196 closely related males in the group. We do not use our microsatellite panel to make

197 inferences on the level of relatedness (e.g. parent-offspring, full-or half-siblings), but

198 only to access whether a pair of individuals is related or not, regardless of their degree

199 of relatedness.

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201

202 *Social interactions*

203

204 We collected *Ad libitum* data between October 2008 and March 2009 on a daily

205 basis (Altmann 1974). We observed each social group on 19 separate days, from 7:00 to

206 19:00. We alternated observations of the two groups on a weekly basis and recorded

207 date, time, habitat, location, individual, activity and their partner. We attempted to

208 record the individual identities or age-sex classes of the interactants, whenever possible.

209 We collected data continually during the day, every time we observed a social

210 interaction. For the *Colobus polykomos,* we only used the data prior to the

211 disappearance of the males from the focal group. Since it was not possible to observe

212 all group members of *Procolobus badius temminckii* simultaneously, we observed the

213 largest subset of temporarily adjacent individuals to record the maximum number of

214 interactions possible. We recorded the following activities: agonism (aggressive and

215 submissive interactions involving two individuals such as threat, fight, chase, displace,

216 flea, present), grooming, social fight (aggression involving three or more individuals),

217 copulation, play and vocalizations. For allo-grooming we considered only one event for

218   each individual even if the grooming direction changed several times. For all behavioral

219   categories, if the interaction was interrupted for less than 3 minutes, we considered it as

220   the same event (Korstjens et al. 2002).

221

222   *Spatial proximity*

223

224   We only inferred the relationship between spatial proximity and relatedness

225   among pairs of individuals for the *Colobus polykomos* group, as we did not individually

226   recognize all *Procolobus badius temminckii* group members. We carried out focal

227   sampling between March and June 2009. Each focal observation was four hours long,

228   and three sessions were carried out *per* day. We recorded the identity of the nearest

229   neighbor (within 3m) of each focal individual every half-hour. When the individual

230   under the focal observation was out of sight, we paused the sample and continued after

231   finding the individual again. If the focal individual was out of sight for more than 30

232   minutes straight, we terminated the focal sampling. We only included focal samples in

233   the final dataset that contained more than 1h of observation. We sampled all group

234   members and whenever possible, resampled them following the same order. We never

235   sampled the same individual twice in the same day and each individual was sampled

236   during three periods throughout the day (7am-11am, 11am-3pm, 3pm-7pm). We carried

237   out 276 hours of focal observations on one adult male, one sub-adult male, four adult

238   females, two juvenile males and one juvenile female.

239

240   *Within-species comparisons*

241   We used generalized linear mixed effects models (GLMM) with Poisson error

242 distribution to test for the effects of the sex combination (i.e. male dyads, female dyads

243 and male-female dyads) on the daily rates of intra-group agonistic and grooming

244 interactions (Bolker et al., 2009). Here, we considered each observation day as the

245 sampling unit in both social groups and calculated the mean rate of each social

246 interaction (i.e. number of times a given social interaction was observed for each sex

247 combination/total number of observations for that social interaction) across the total

248 number of observation days. We included the observation days as random factors in the

249 model and analyzed each variable using a separate univariate model. We carried out

250 GLMM using the lme4 package in R 2.14.1 (Bates et al.2011; R Development Core

251 Team, 2012). We tested the statistical significance of the full model (with the sex

252 combination as the fixed factor) by comparing it to a null model (excluding the sex

253 combination variable) using a likelihood ratio test (R function "anova") (Dobson &

254 Barnett, 2002). We ran analyses for each species separately and only included adult and

255 sub-adult individuals in this analysis.

256   As we could individually recognize all group members of the *Colobus*

257 *polykomos* focal group, we were able to test whether grooming, agonistic interactions or

258 proximity more frequently involved related or non-related individuals. For each animal

259 we estimated the percentage of times that each social interaction happened with a

260 related or with a non-related partner. We then calculated the mean of those percentages

261 for the social group. Each individual had a different number of related and non-related

262 partners within the group. Therefore, we corrected for this potential bias in partner

263 availability by dividing the percentage of each social behavior with related and non-

264 related partners by the total number of available related and non-related partners in the

265 group. We tested differences using Wilcoxon signed-rank tests implemented in R v.

266 2.12.0 (R Development Core Team 2009). In this analysis, we used all genotyped

267 individuals except for one juvenile male, as we had very limited data on social

268 interactions for this individual.

269

270 *Between-species comparisons*

271

272 We used GLMMs with Poisson error distribution to test for a species effect on

273 the daily rates of each intra-group social interaction (i.e. number of observations of a

274 given social interaction/total number of social interactions observed), as described for

275 the within-species comparisons. We included observation days as random factors and

276 species as the fixed factor in the model.

277 As group size in *Procolobus badius temminckii* was much larger than in *Colobus*

278 *polykomos*, the number of social interactions was much higher in *P. b. temminckii*. To

279 correct for this bias, we expressed social interaction results as the proportion of each

280 social activity relative to the total of intra-group observed social interactions for each

281 observation day. We only included adult and sub-adult individuals in this analysis.

282

283

284 **RESULTS**

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286 *Intra-group relatedness*

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288 In the *Colobus polykomos* focal group, of all 28 possible dyads only 9 (32%)

289 were significantly related (Table 1). Of those, there was only one dyad of related adult

290   females (Adult female 2 and 3) out of three possible dyads, meaning that one of the

291   three adult females (Adult female 1) was not related to any other adult female in the

292   group. Additionally, the adult male was significantly related to two of the adult females

293   (Adult female 2 and 3) and the juvenile female. The sub-adult male was only related to

294   the Adult female 1.

295   In the *Procolobus badius temminckii* focal group, of all 55 possible dyads of

296   adult females only seven pairs were significantly related (12.7%). However, for the

297   adult males, four of six possible dyads (66.7%) were significantly related.

298

299   *Social bonding*

300

301   *Within-species comparisons*

302

303   When we compared the sexes, there were species differences in agonistic and

304   grooming events between adults (Fig 2 and 3). In *Colobus polykomos*, we found an

305   effect of the sex combination on grooming, which occurred at a lower frequency among

306   male dyads compared to female and mixed dyads (Table 2, χ^2= 9.42, *P*= 0.009).

307   However, the sex combination did not have an effect on the observed levels of intra-

308   group agonism, since we found no differences between the model containing the sex

309   combination factor and the null model (χ^2= 4.25, *P*= 0.119).   In *Procolobus badius*

310   *temminckii*, we found an effect of the sex combination in both types of interactions.

311   Agonism was lower in female dyads compared to male and mixed-sex dyads (Table 2,

312   χ^2= 7.70, P= 0.021). The opposite pattern was true for allo-grooming, which occurred

313   at higher levels among dyads of females and less among males or individuals of

314   different sexes (Table 2, $\chi 2$= 14.90, P= 0.001).

315   *Colobus polykomos* individuals had more non-related than related partners in the

316   group (mean values, Table 3). We found no kin-biases in either grooming (Table 3,

317   Wilcoxon signed-rank test, N= 7, Z=-0.51, *P* = 0.61; corrected: Z=-0.51, *P* = 0.61) or

318   agonistic interactions (Table 3, Wilcoxon signed-rank test, N= 7, Z=-0.84, *P* = 0.40;

319   corrected: Z=-0.21, *P* = 0.83). Additionally, there was no difference in the time

320   individuals were spatially closer to related vs. non-related individuals (Table 3,

321   Wilcoxon signed-rank test, N= 7, Z=-1.15, *P* = 0.25; corrected: Z=-0.31, *P* = 0.75). We

322   could not apply the same approach to *Procolobus badius temminckii* because we could

323   not individually recognize the members of this group.

324

325   *Between-species comparisons*

326

327   For *Colobus polykomos,* we recorded 321 interactions (mean: 16.89

328   interactions/day ± SD 12.08). For *Procolobus badius temminckii,* we recorded a total of

329   828 interactions (mean: 43.63 interactions/day ± SD 16.68). Grooming was the most

330   frequent social behavior displayed by both species, followed by agonistic interactions

331   (Fig. 4, Table 4). Both groups also showed low levels of social fights and copulations

332   (Fig 4, Table 4). Social interactions were not significantly different between the

333   species, as demonstrated through the comparison of the model that included the factor

334   species with the null model (Table 4, Aggression: $\chi 2$ = 0.28, d.f. = 1, P = 0.597;

335   Grooming: $\chi 2$ = 0.31, d.f. = 1, P = 0.578; Social Fight: $\chi 2$ = 0.19, d.f. = 1, P = 0.6575;

336   Copulation: $\chi 2$ = 1.99, d.f. = 1, P = 0.158; Play: $\chi 2$ = 0.66, d.f. = 1, P= 0.418;

337   Vocalization: $\chi 2$ = 0.09, d.f. = 1, P = 0.769).

338

339

340 **DISCUSSION**

341   The combination of behavioral and genetic data in this study enabled us to

342 exclude kinship as a determinant factor shaping the intra-group social dynamics of two

343 sympatric African colobus monkeys.

344   Pairs of related and unrelated females composed the *Colobus polykomos* focal

345 group with no kin bias in grooming, showing an absence of female-based kin-structure

346 and social bonding. At the individual level, *C. polykomos* individuals showed no

347 preference for directing any type of social interaction or maintaining proximity to

348 related versus non-related partners. Such results clearly demonstrate that, at least in this

349 particular *C. polykomos* social group, kinship is not the major factor shaping the social

350 dynamics for either sex. A similar pattern has also been described for a *Colobus*

351 *vellerosus* population from Ghana (Wikberg et al. 2012). This population was

352 characterized by great variation in its social system, with some social groups showing

353 female dispersal, absence of female kin-based structure and social bonding.

354   The *Procolobus badius temminckii* group is characterized by female-biased

355 dispersal, a male-based kin-structure and female-based social bonding, strongly

356 suggesting that kinship is not the main determinant for the observed social dynamics.

357 Although there were some related adult females, their numbers in the group are too few

358 to explain the extremely high frequency of grooming exchanged between females.

359 Additionally, if kinship is the main factor shaping this group's social dynamics we

360 would expect grooming between males to be more frequent, as it is in other studied red

361 colobus groups (Struhsaker and Leland 1979, Struhsaker 2010). A paucity of male-male

362 grooming was also described for red colobus males in both Abuko (*P. b. temminckii,*)

363 and Jozani, Zanzibar (*Procolobus kirkii,*) but it was only in Abuko that females also

364 groomed other females more than they groomed males (Siex 2003; Starin 1991). One

365 explanation is that females may have transferred into the Abuko group along with other

366 females from the same natal group (parallel dispersal, van Hooff 2000) (Starin, 1991). If

367 so, this could mean that females in a group are closely-related and, therefore, strongly

368 bonded. It is possible that parallel dispersal occurs in *P. b. temminckii* from CNP and

369 such related females prefer to groom each other instead of grooming non-related

370 females. However, we suggest that due to the low percentage of related females, parallel

371 dispersal and kinship among females cannot fully explain the strong social bonding

372 among these females, similar to what we found for the sympatric *Colobus polykomos*

373 group. Factors besides kinship, such as high resource competition, may be strong

374 enough for it to be advantageous for these females to establish strong social bonds with

375 non-related females.

376   The existence of strong social bonding in the absence of relatedness has already

377 been shown for *Colobus spp.* elsewhere (Wikberg et al. 2012, 2014). The forest of CNP

378 is highly fragmented and colobus monkeys are the target of human hunting (Costa et al.

379 2013; Minhós et al. 2013b; Sá et al. 2013) The fact that these particular groups have

380 their home range overlapping with the tourist village indirectly protects them from both

381 humans and others predators (e.g. chimpanzees). Poaching has never been reported in

382 these groups unlike several other groups in the surroundings (T. Minhós pers obs;

383 Hockings and Sousa 2013). The hunting pressure combined with the increased forest

384 loss and fragmentation elsewhere in CNP has caused increased colobus density in this

385 area, which is likely to increase the intra-group competition for resources, as suggested

386 for *Procolobus rufomitratus* at Tana River (Decker 1994). Under such a scenario, it may

387 be that colobus gain immediate benefits (e.g. coalitionary support in resource defense)

388 by forming social bonds with non-related individuals, which functions as an adaptive

389 survival strategy in response to anthropogenic changes in the habitat (Chapais 2001;

390 Seyfarth 1977). Research has described how primate females direct affiliative behaviors

391 to non-related group members if they provide them with coalitionary support or increase

392 their opportunities to access limited resources (Seyfarth 1977). For example, female

393 baboons (Papio spp.) showed higher levels of affiliation and coalitions under a scenario

394 of high intra-group contest competition for food (Barton et al. 1996). Lehmann &

395 Boesch (2009) also described an increase in social bonding among non-related female

396 chimpanzees during periods of high intra-group competition.

397   By combining data on social interactions and patterns of intra-group relatedness

398 we provide evidence that intense ecological and/or anthropogenic-related pressures may

399 act as major factors shaping intra-group social dynamics in two West African colobus

400 groups.

401

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