1   **The effect of inter-group competition on intra-group affiliation in primates**

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15   Word count: 5,514

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Researchers from various disciplines have hypothesised that ecological conditions eliciting higher levels of inter-group contest competition (IGCC) should favour the evolution of behavioural traits, such as co-operation, altruism and friendship, which promote intra-group affiliation. Empirical support for this hypothesis is, however, scarce and mainly available from humans. We tested if the level of IGCC affects intra-group affiliation (i.e. intra-group grooming exchange) among male and female non-human primates. To quantify intra-group affiliation, we used social network measures and a grooming index. Our measure of IGCC combined frequency of inter-group encounters and proportion of aggressive encounters (N aggressive encounters / total encounters observed) and was calculated separately for males and females. We ran our analyses on 27 wild groups of primates belonging to 15 species (13 Cercopithecinae, 1Colobinae and 1 Cebinae). Our results show that females increased the density of their grooming networks and showed less variation in the number of same-sex grooming partners in response to increased IGCC, whereas we found no significant effect of IGCC on intra-group affiliation among males. Thus, our data provide partial support for an effect of IGCC on intra-group affiliation, but suggest that the exact nature of such an effect is sex-specific. These results may be explained by the differential costs and benefits males and females experience during aggressive inter-group confrontations and by sex-specific differences in intra-group affiliation.

Keywords: affiliation, collective action problem, competition, grooming, monkeys

Highlights

- We tested the hypothesis that inter-group competition affects intra-group affiliation

- We found the first partial support for this hypothesis in non-human primates

- Female primates increased intra-group affiliation when inter-group competition was high

- Intragroup affiliation in males was not affected by inter-group competition

- Inter-group competition may bear different cost/benefit for male and female primates

Inter-group contest competition (IGCC), where members of one group aggressively attempt to access and monopolise valuable resources (e.g. food or water) at the expense of another group, is a phenomenon observed in many group-living species (e.g. Rubenstein 1986; Kitchen and Beehner 2007; Radford 2008a; Crofoot and Wrangham 2010). The outcome of an aggressive inter-group encounter can affect individual fitness (e.g. Radford and Fawcett, 2014), especially when ecological conditions elicit frequent aggressive interactions between groups (e.g. due to habitat saturation or food scarcity) that bear high cost/benefits payoffs (e.g. Mitani et al. 2010). Aggressive inter-group encounters represent a typical example of collective action problems (Nunn and Lewis 2001; Willems et al. 2013; Willems and van Schaik, 2015): groups where all members take part in the aggressive confrontation are expected to have the best chances to win a fight (other things being equal; e.g. group size, sex ratio) and thus gain access to the resources at stake. However, because aggressive inter-group encounters also bear potential high costs for individuals (e.g. injuries or death; Mitani et al. 2010), the risk of free-riding is high: some individuals could gain the benefits of their group winning a fight with another group, without incurring any potential cost, by not taking an active role in the aggressive confrontation (Nunn and Lewis 2001; Crofoot and Gilby 2012; Willems et al. 2013; Willems and van Schaik, 2015).

Researchers have hypothesised that strong intra-group affiliation should reduce the probability that animals in a group free-ride during collective action problems (Alexander and Borgia 1978; Choi and Bowles 2007; Puurtinen and Mappes 2009). Thus, individuals from groups where intra-group affiliation is strong should out-perform groups with weak intra-group affiliation during inter-group confrontations, because everybody is taking part in the interaction. These groups should then gain overall fitness benefits. Under this scenario, individuals in populations that face a high level of IGCC should become progressively more affiliative towards their group members over evolutionary time, thereby increasing the overall intra-group affiliation of the group. Furthermore, individuals from groups where intra-group affiliation is strong should also be more likely to take part in collective actions (such as protecting a food source from other groups) than individuals from

groups with weak intra-group affiliation (Conradt and List 2009; Miller et al. 2013). Following this logic, researchers from a range of different disciplines, including evolutionary biology (Reeve and Hölldobler 2007), behavioural ecology (Wrangham 1980; Sterck et al. 1997), psychology (West et al. 2006; van Vugt and Park 2009) and anthropology (Haas 1990; Choi and Bowles 2007), have predicted that a high level of IGCC should favour the evolution of behavioural traits which promote intra-group affiliation, such as social bonding and parochialism (Alexander and Borgia 1978; Reeve and Hölldobler 2007).

Several mathematical models, that support the hypothesis that the level of IGCC has a positive effect on the evolution of intra-group affiliation, have been developed (e.g. Reeve and Hölldobler 2007; Bowles 2009). However, empirical tests of this hypothesis are sparse and have mostly focused on the proximate link between IGCC and intra-group affiliation. There is consistent experimental evidence in humans showing that co-operation increases when groups are competing with one another compared to situations without inter-group competition; this effect is independent from kin relationships amongst group members (Erev et al. 1993; West et al. 2006; Tan and Bolle 2007; Puurtinen and Mappes 2009). This evidence has led some authors to propose that the extensive period of warfare that our ancestors faced in the Pleistocene and Holocene has driven the evolution of group-beneficial behaviours, such as in-/out-group categorisation in humans (Choi and Bowles 2007; Bowles 2009).

For non-human species, data on the proximate effect of IGCC on intra-group affiliation are relatively scarce (for a review: Grueter 2013), although the same principles should apply to all taxonomic groups (see e.g. Wrangham 1980; Reeve and Hölldobler 2007). A few studies have focused on post inter-group encounter allo-preening and allo-grooming, as a measure of intra-group affiliation (Radford 2008a), as these two behaviours have important social functions in many mammals and birds (e.g. they promote agonistic support and food tolerance; Dunbar 1991; Ventura et al. 2006; Radford 2008a). In the co-operatively breeding green woodhoopoe (*Phoeniculus purpureus*) the frequency and duration of allo-preening between group members increases

following a conflict with another group (Radford 2008a, b, 2011). Conversely, in captive tufted

capuchin monkeys (*Cebus apella*) visual interactions between groups did not result in increased

grooming exchange within the group (Polizzi di Sorrentino et al. 2012). Another measure of

affiliation that has been used is spatial proximity between group members. In chimpanzees (*Pan*

troglodytes) and spider monkeys (*Ateles geoffroyi*) individuals were found to stay closer together

when feeding in the home range of a neighbouring group (i.e. an area where the risk of a conflict

with another group is high) than when feeding in their home range (Aureli et al. 2006; Mitani et al.

2010). However, all of these studies have tested the immediate effects of inter-group encounters on

intra-group affiliation. It remains unclear if such effects are only short-lived and thus temporary

(e.g. an emotional response to the stress of the encounter; Radford 2008a, 2011; Polizzi di

Sorrentino 2012), if such an increase in affiliative behaviour occurs primarily between already

closely bonded partners and/or those who have actively participated to the inter-group encounter

(i.e. affiliation is partner specific), or if such behavioural responses to inter-group encounters would

indeed lead to an overall more general increase in intra-group affiliation.

  To our knowledge, only two studies (Cheney 1992; Grueter 2013) have attempted to test the

generality of the hypothesised relationship between IGCC and intra-group affiliation across a

number of different species. Cheney (1992) used allo-grooming (hereafter grooming) distribution

(averaged across individuals of the same group) as a measure of group affiliation in non-human

primates. She predicted that animals would increase their effort to distribute their grooming more

evenly to their potential grooming partners, instead of mostly grooming with fewer individuals, the

higher the level of IGCC they faced. Grueter (2013) also investigated non-human primates and used

the average grooming time per species as a measure of intra-group affiliation. These two studies

hypothesised that the proximate effect of IGCC on intra-group affiliation would extend beyond the

first few minutes after an inter-group encounter. Groups facing higher IGCC would have overall

stronger intra-group affiliation than groups facing a lower level of IGCC, irrespective of the timing

and occurrence of each inter-group encounter (Wrangham 1980; Sterck et al. 1997). Contrary to

122 what was predicted, IGCC was not found to have a significant effect on either grooming

123 distribution among group members (Cheney 1992) or on total grooming time (Grueter 2013).

124 However, these two studies could not effectively tackle some important issues. Cheney's (1992)

125 study was restricted to female primates and did not control for the phylogenetic relationship

126 between species. Grueter (2013) used a proxy of IGCC (i.e. home range overlap) that could equally

127 measure inter-group scramble competition (Wrangham 1980; Sterck et al. 1997). These factors

128 could potentially explain the discrepancy between the human and the non-human primate data.

129   The mixed results available on this topic so far make it difficult to determine if IGCC

130 played a key role in the evolution of group-beneficial behaviours (Choi and Bowles 2007; Bowles

131 2009) in non-human animals. Our aim was to analyse the effect of IGCC on intra-group affiliation

132 across primate social groups, using a phylogenetically controlled analysis and a variety of different

133 measures of intra-group affiliation. We measured the level of IGCC by combining the frequency of

134 inter-group encounters and the proportion of aggressive encounters (independently calculated for

135 males and females). Intra-group affiliation, using grooming distribution, was measured by three

136 different variables: (a) the evenness of grooming, assessing the distribution of grooming effort

137 across potential grooming partners (following Cheney 1992), (b) the inter-individual variation in the

138 number of grooming partners, and (c) grooming network density. If IGCC elicits intra-group

139 affiliation in primates, we predicted that, in groups with high IGCC, animals would increase their

140 effort to distribute their grooming more evenly to their group companions, inter-individual variation

141 in grooming partner numbers would be low, and more individuals would be involved in grooming

142 interactions (high network density). Due to the scarcity of data available on a wide range of primate

143 taxa our dataset is mostly composed of Cercopithecinae (See supplementary table 1), i.e. of species

144 where grooming is the main affiliative behaviour and where females are the phylopatric sex.

145 Although not ideal, this allowed us to some extent to control for species-specific differences in

146 affiliative behaviours. In addition, we ran the analyses separately for male and female primates,

147 because intra-group same-sex affiliation can differ strongly between non-human primate species

148 (Wrangham 1980; Sterck et al. 1997; Crofoot and Wrangham 2010). Moreover, the two sexes differ

149 in their aggressive participation in inter-group encounters (Majolo et al. 2005; Kitchen and Beehner

150 2007; Crofooot and Wrangham 2010) and might have markedly different cost-benefit ratios of

151 IGCC. We did not consider grooming interactions between males and females, as a different set of

152 hypotheses (e.g. hired-gun hypothesis; Rubenstein 1986) than the ones tested here focus on hetero-

153 sexual grooming.

154

155 **METHODS**

156 *Data collection*

157 We used the ISI Web of Knowledge (© Thomson Reuters) to review the primatological literature

158 published between 1st January 1950 and 1st June 2011. We selected papers that contained detailed

159 data on grooming interactions between adult and sub-adult group members (e.g. a matrix of

160 grooming exchange) and on IGCC on one or more social groups. Data on juveniles and/or infants

161 were not included in the analyses. When these data were not available in a single paper, we

162 combined different published studies containing the relevant data collected on the same social

163 group within the same overall time period (see Supplementary material for further details).

164 Our literature review showed that published studies providing detailed data on grooming

165 and IGCC on a single social group are scarce. Therefore, we contacted colleagues working on

166 primates in the field, asking if they were willing to share with us the following data for each of their

167 study groups: study species, dates when data were collected, duration of the study (in months) and

168 location, group size (i.e. number of adults, sub-adults, juveniles and infants in the group), whether

169 the group was provisioned (i.e. the group relied extensively on human-provisioned food) or not, and

170 frequency of intra-group contest food competition (i.e. number of aggressive interactions over food

171 / hour). We also requested a matrix containing the proportion or frequency of grooming interactions

172 among the adult and sub-adult males and/or females of the study group. Finally, we requested the

173 following data on IGCC: frequency of inter-group encounters (i.e. number of inter-group encounters

174 / day) for the study group and proportion of inter-group encounters in which at least one adult male

175 and/or female from the study group was aggressive towards the other group (i.e. N aggressive

176 encounters for males/females divided by total encounters observed). We asked colleagues to give us

177 data for this latter variable separately for males and females. Moreover, we asked colleagues to

178 provide us with their definition of inter-group encounter (or we extracted this information from the

179 selected literature). The minimum distance between two groups, for an inter-group encounter to

180 occur, ranged between 15 and 100 meters across the studies included in our dataset, with an average

181 distance of approximately 50 metres. Aggression towards another group was defined as an animal

182 displaying threatening facial expressions or giving a threat call towards, chasing or biting one or

183 more animals from the other group.

184

185 *Data analysis*

186 The analyses presented here were based on 27 study groups from 15 species, 13 Cercopithecinae,

187 1Colobinae and 1 Cebinae (males: 11 species, 19 study groups; females: 15 species, 25 study

188 groups; electronic supplementary table S1). We excluded from the analyses studies on 8 additional

189 species and 12 study groups because of missing data or because the study animals were not fully

190 habituated to researchers at time of data collection. The level of IGCC, our independent variable,

191 was quantified by multiplying the frequency of inter-group encounters (N of encounters/day) by the

192 proportion of these encounters that were aggressive. The level of IGCC had different values for

193 analyses done on males and females, as we calculated the proportion of aggressive encounters

194 separately for males and females (based on their involvement in them). We chose to combine these

195 two variables as each on its own does not accurately capture the level of IGCC. The frequency of

196 inter-group encounters does not imply anything about the nature of these encounters (i.e. aggressive

197 versus peaceful) while the proportion of aggressive encounters does not indicate anything about the

198 frequency in which these take place (e.g. 0.80 proportion of aggressive encounters twice a year or

199 twice per day would imply very different IGCC). Thus, by combining these two variables we

200   obtained a more informative measure of IGCC.

201   Matrices of grooming exchanges between group members were used to obtain three

202   measures of intra-group affiliation (our dependent variables). First, following Cheney (1992), we

203   used the Shannon-Wiener index (SWI; Wilson and Bossert 1971) to measure how an individual

204   distributes grooming to all the potential grooming partners (Supplementary material for further

205   details). The higher the value of SWI the more animals have evenly distributed grooming

206   relationships (i.e. they attempt to groom all of the available partners about equally). In addition to

207   the SWI, we calculated two commonly used social network metrics to quantify intra-group

208   affiliation (Borgatti et al. 2006; Wey et al. 2008). Because of the differences between studies in the

209   measures of grooming (e.g. percentage of grooming duration or simply frequency) we only

210   calculated network measures for binary networks (i.e. the presence/absence of a grooming

211   relationship) and not on bond strength. Our two network measures of intra-group affiliation were

212   standard deviation of the out degree and density (Borgatti et al. 2006). Standard deviation of the out

213   degree (SDOD) measures the inter-individual variation in the number of partners groomed. A low

214   SDOD value indicates that all group members groom a similar number of partners while a high

215   SDOD indicates that the number of grooming partners is skewed between group members. Density

216   measures the number of existing grooming relationships in relation to all possible grooming

217   relationships. All network metrics were calculated using UCInet 6 (Borgatti et al. 2006). The three

218   dependent variables were not significantly correlated to one another (Spearman pair-wise

219   correlations; all $P > 0.28$), suggesting that our indices of intra-group affiliation measured different

220   aspects of grooming distribution.

221   We controlled for four biologically relevant variables, which may affect the level of IGCC

222   and/or overall intra-group affiliation (electronic supplementary methods for further details): study

223   period length (measured in months), group size (number of animals in the social group, including

224   juveniles and infants), intra-group contest competition (aggressive events/hour) and provisioning

225   (binary variable: yes/no). We also controlled for additional variables that could bias our results,

226 including a 'data quality' variable (see electronic supplementary methods for details).

227

228 *Statistical analyses*

229 All the analyses were run considering data on each social group as a single data point, as IGCC and

230 intra-group affiliation are not likely to solely be species-specific traits and can vary significantly

231 across populations/groups (for a similar approach see Majolo et al. 2012). We ran phylogenetically

232 controlled generalized least square regression models (PGLS) in R 2.14.0 (R Development Core

233 Team 2011), using the CAPER 0.4 package (Orme et al. 2012). The phylogenetic tree for the

234 analyses was obtained from the 10ktree primate phylogeny version 2 (Arnold et al. 2010). We

235 derived lambda via maximum likelihood estimation as provided in CAPER.

236   All together we ran three models for each sex, with each of these models containing our

237 independent variable (level of IGCC) and the four additional control variables, namely study period

238 length, group size and intra-group contest competition as covariates, and provisioning (2 levels) as

239 confounding factor, which was dummy-coded. In addition, we ran the same analyses separately on

240 the two variables that we used to construct our measure of IGCC (i.e. the frequency of inter-group

241 encounters per day and the proportion of aggressive inter-group encounters for males/females). The

242 results for these models were representative of our overall results and are thus only presented in the

243 supplementary material (electronic supplementary tables S2-S5).

244

245 **RESULTS**

246 *Females*

247 A phylogenetic signal was detected for the standard deviation of the out degree (SDOD; Lambda =

248 0.97) and for density (Lambda = 0.76), but not for the Shannon-Wiener index (SWI; Table 1). The

249 level of IGCC was not significantly related to SWI (Table 1). Conversely, and supporting our

250 predictions, females showed significantly less variation in their number of grooming partners (i.e.

251 lower SDOD; Figure 1) and had significantly denser grooming networks (Figure 2) when levels of

252   IGCC were higher (Table 2). Among the control variables, we found that group size significantly

253   affected SWI (larger groups had less evenly distributed grooming) and SDOD (larger groups had

254   less variation in their number of grooming partners; Table 1). In addition, a higher level of intra-

255   group contest competition resulted in generally denser grooming networks. The other control

256   variables had no significant effect on intra-group affiliation (Table 2).

257

258   *Males*

259   A phylogenetic signal was detected in the model for SWI (lambda = 1) whereas lambda was equal

260   to zero in the models on SDOD and density (Table 2). Contrary to our predictions, the level of

261   IGCC had no significant effect on any of our affiliation measures (Table 2). For the control

262   variables, we found that study period as well as group size affected SWI, i.e. grooming was more

263   evenly distributed the longer the study period and the smaller the group size. Furthermore, group

264   size also affected grooming network density: smaller groups had denser grooming networks than

265   larger groups. The other control variables had no significant effect on grooming distribution.

266

267   **DISCUSSION**

268   In contrast to previous reports (Cheney, 1992; Grueter, 2013), our study is the first to provide partial

269   support for the hypothesis that IGCC affects intra-group affiliation and suggests that the exact

270   nature of this effect is sex specific. In males, the level of IGCC had no significant effect on

271   grooming distribution. In females, the level of IGCC had a positive and significant effect on the

272   variation in the number of grooming partners and on grooming network density, but not on SWI.

273   Our findings on female primates, therefore, corroborate hypotheses from socio-ecological models

274   (Alexander and Borgia 1978; Wrangham 1980; Sterck et al., 1997) and evolutionary biology (Reeve

275   and Hölldobler 2007), and are in line with what has been found, and expected to occur in humans

276   (Haas 1990; West et al. 2006; Choi and Bowles 2007; van Vugt and Park 2009). Because the data

277   available for our analysis were mostly from Old World monkeys, we do not know if these finding

278 also extend to New World Monkeys. In addition, many species of New World monkeys are known

279 to show very little grooming (Dunbar 1991) and intra-group affiliation would have to be measured

280 differently in those species; however, we would expect to find a similar relationship between IGCC

281 and intra-group affiliation using appropriate affiliation measures.

282

283 *Sex differences*

284 By maintaining less varied and denser networks of intra-group affiliation, female primates may be

285 better able to cope with high levels of IGCC. Other things being equal (e.g. group size) females in

286 strongly affiliated groups might more effectively out-compete other groups and access/monopolise

287 resources (e.g. shelter or water) that are essential to maximise their reproductive outputs. The fact

288 that we only found an effect in females but not males is interesting. As males usually take a more

289 active role in aggressive inter-group encounters than females (Majolo et al. 2005; Kitchen and

290 Beehner 2007) and have been reported to have strong social bonds even in species with male

291 dispersal (Silk 1994; Mitani 2009; Schülke et al. 2010; Young et al 2014), a positive effect of IGCC

292 on intra-group affiliation was predicted to occur among males. The lack of support for this

293 prediction in males may be explained by two main factors. Firstly, the benefits and costs of

294 aggressively taking part in inter-group encounters differ between the two sexes. The benefits males

295 can gain from winning an encounter with another group are likely to be highly skewed in favour of

296 the dominant male, whereas in females benefits are expected to be more evenly distributed (Cheney

297 1992; Kitchen and Beehner 2007; Crofooot and Wrangham 2010). This might explain why overall

298 levels of same-sex affiliation are not affected by IGCC in males whereas female affiliation patters

299 are affected. By out-competing another group, every female can potentially gain benefits like access

300 to food and reduced risk of immigration by infanticidal males, although these benefits could be

301 somewhat greater for dominant and/or lactating females (Sterck et al. 1997). Conversely, the main

302 benefits that males can gain during/following aggressive confrontations with other groups are

303 opportunities for extra-group copulations and/or for emigration, and defence of receptive females in

304   their group (Kitchen and Beehner 2007; Crofooot and Wrangham 2010). These benefits are likely to

305   not be shared equally by group males as, for example dominant males often monopolize mating

306   opportunities (e.g. Majolo et al. 2012). Indeed, it has been shown that aggressive participation in

307   inter-group encounters in males largely depends on the age and dominance status of the animals

308   (Majolo et al. 2005; Kitchen and Beehner 2007). Secondly, as all species in our sample are female

309   phylopatric, social relationships among dispersing males may be much more variable and

310   opportunistic than those in females, and be based on other behaviours (e.g. agonistic support) than

311   grooming (Schülke et al. 2012), which for lack of data could not be included into our analysis.

312   IGCC may affect male social relationships but this might not be reflected in the grooming network.

313   Thus, taken together, socio-ecological factors and the different cost/benefits of participation to inter-

314   group confrontations for the two sexes may modulate the effect that IGCC plays on intra-group

315   affiliation and more data are needed to further assess if and how IGCC affects affiliation among

316   males.

317

318   *Confounding variables*

319   The control variables showed that group size was a significant predictor of intra-group affiliation in

320   four of our six models, although the effects of group size on our dependent variables were small in

321   terms of the actual model coefficients. It is well known that group size affects the response of

322   animals to collective action problems as well as the outcome of inter-group encounters (Crofoot and

323   Gilby 2012; Willems and van Schaik, 2015). Group size also affects individual behaviour and has

324   been shown to have fitness consequences for individual animals (Majolo et al., 2008). Therefore,

325   group size is expected to modulate the relationship between IGCC and intra-group affiliation, which

326   is supported by our results. Since all of the species in our dataset are female phylopatric, the

327   relationship between grooming and IGCC may also be affected by kinship, that is, females in

328   species/populations facing a higher level of IGCC might have larger matrilines, which in turn may

329   result in larger and denser grooming networks. In our dataset, we could not control for kin-

330   relationships (as kinship data were not available for most of the study groups in the dataset) but this

331   would be an interesting hypothesis to test in future studies. By including group size into the models,

332   however, we aimed to control for these effects in our analyses.

333

334   *From non-human primate to humans*

335   When comparing the effect of IGCC on intra-group affiliation in humans and non-human animals

336   (Crofoot and Wrangham, 2010), three considerations have to be made. First, unlike many non-

337   human primates, in human hunter-gatherer societies both sexes can disperse and establish long-

338   distance and long-lasting social bonds and co-operative relationships (e.g. Apicella et al. 2012). As

339   such, differences in social structure and inter-individual relatedness in humans societies compared

340   to non-human primates could have an effect on how IGCC affects intra-group affiliation. Second,

341   inter-group conflicts in non-human animals and human warfare may be two behaviourally different

342   phenomena (Crofooot and Wrangham 2010). Human warfare in small scale societies, despite

343   lacking the complex structure, strategic approach and forced recruitment of soldiers typical of

344   military confrontations, is often characterized by social norms (e.g. participation in warfare as a

345   sign of adulthood) and punishment rules (e.g. social isolation or reduced power) that favour

346   individual contribution to aggressive encounters (Haas 1990). These factors should act on limiting

347   the occurrence of free-riding and the risk posed by collective action problems in humans compared

348   to non-human primates (Nunn and Lewis 2001; Crofoot and Gilby 2012; Willems et al. 2013;

349   Willems and van Schaik, 2015). Similarly, the different risk posed by collective action problems can

350   explain why the effect of IGCC on intra-group affiliation appears to be stronger in cooperative

351   breeding birds (Radford 2008a, b, 2011) than in the primate species included in our study. In

352   cooperatively breeding species, group members are often genetically related, share resources with

353   one another (Radford and Fawcett, 2014), and groups are generally small; all conditions that reduce

354   the risk of collective action problems (Willems and van Schaik, 2015). Conversely, our dataset was

355   mostly composed of species living in large groups where the benefits and costs of intense IGCC are

356   likely to be skewed across group members. Third, inter-group conflicts in non-human animals and

357   human warfare may bear different consequences for individual fitness. Deaths resulting from inter-

358   group aggressive confrontations are thought to have been common during the course of human

359   evolution (Haas 1990; Choi and Bowles 2007; but see Fry and Söderberg 2013). Conversely, deaths

360   are relatively rare during inter-group encounters in non-human vertebrates and mostly observed in a

361   small number of species (e.g. lions and anthropoid primates: Packer et al. 1990; Mitani et al. 2010).

362   Therefore, there might have been stronger evolutionary pressure for an adaptive link between IGCC

363   and intra-group affiliation in the human lineage than in non-human primates or in other

364   phylogenetic taxa.

365   In conclusion, our study provides partial support for the hypothesis that IGCC affects intra-

366   group affiliation, similar to what has been shown in humans and in cooperatively breeding birds.

367   The fact that a link between IGCC and intra-group affiliation was found in females but not in males,

368   suggests different cost/benefit ratios of inter-group encounters for the sexes. The generality of our

369   findings to non-human primate species not included in this study, and to other taxa, is limited by the

370   scarcity and patchiness of data on this topic. When data become available, further studies will be

371   needed to test the effect of factors that we could not analyse here, such as social organization,

372   breeding system, relatedness and participation patterns in inter-group encounters. In addition, data

373   on more species are required and different measures, especially measures involving bond strength,

374   for intra-group affiliation should be explored. Despite the limitations of our study, our analyses

375   suggest for the first time that IGCC has the potential to affect intra-group affiliation in non-human

376   female primates.

REFERENCES

Alexander RD, Borgia G. 1978. Group selection, altruism and the levels of organisation of life. Ann Rev Ecol Sys 9: 449–474.

Apicella CL, Marlowe FW, Fowler JH, Christakis NA. 2012. Social networks and cooperation in hunter-gatherers. Nature 481: 497-501.

Arnold C, Matthews LJ, Nunn CL. 2010. The 10kTrees Website: A new online resource for primate phylogeny. Evol Anthropol 19:114-118.

Aureli F, Schaffner CM, Verpooten J, Slater K, Ramos-Fernandez G. 2006. Raiding parties of male spider monkeys: insights into human warfare? Am J Phys Anthropol 131:486-497.

Borgatti SP, Everett MG, Freeman L. C. 2006. UCInet for Windows: software for social network analysis. Harvard, Massachusetts: Analytic Technologies.

Bowles S. 2009. Did warfare among ancestral hunter-gatherer groups affect the evolution of human social behaviors? Science 324: 1293-1298.

Brown M, Crofoot M. 2013. Social and spatial relations between primate groups. In: Sterling E, Bynum E, Blair M, editors. Primate ecology and conservation. 1st ed. Oxford, UK: Oxford University Press. p. 151-176.

Cheney DL. 1992. Intragroup cohesion and intergroup hostility: the relationship between grooming distributions and intergroup competition among female primates. Behav Ecol 3: 334-345.

Choi JK, Bowles S. 2007. The coevolution of parochial altruism and war. Science 318: 636–640.

Conradt L, List C. 2009. Group decisions in humans and animals: a survey. Phil Trans R Soc B 364: 719-742.

Crofoot MC, Gilby IC. 2012. Cheating monkeys undermine group strength in enemy territory. Proc Natl Acad Sci 109: 501-505.

Crofoot MC, Wrangham R. W. 2010. Intergroup aggression in primates and humans: the case for a unified theory. In: Kappeler PM, Silk J, editors. Mind the gap: tracing the origins of human universals. 1st ed. New York: Springer. p. 171-195

415   Dunbar RIM. 1991. Functional significance of social grooming in primates. Folia Primatol 57:121-

416   131.

417   Erev I, Bornstein G, Galili R. 1993. Constructive intergroup competition as a solution to the free

418   rider problem in the workplace. J Exp Soc Psychol 29:463-478.

419   Fry DP, Söderberg P. 2013. Lethal aggression in mobile forager bands and implications for the

420   origins of war. Science 341: 270-273.

421   Grueter CC. 2013. No effect of inter-group conflict on within-group harmony in non-human

422   primates. Commun Integr Biol 6:e26801.

423   Haas J. 1990. The anthropology of war. Cambridge, UK: Cambridge University Press.

424   Kitchen DM, Beehner JC. 2007. Factors affecting individual participation in group-level aggression

425   among non-human primates. Behaviour 144: 1551–1581.

426   Majolo B, Ventura R, Koyama NF. 2005. Sex, rank and age differences in the Japanese macaque

427   (*Macaca fuscata yakui*) participation in inter-group encounters. Ethology 111:455-468.

428   Majolo B, de Bortoli Vizioli A. & Schino G (2008). Costs and benefits of group living in primates:

429   group size effects on behaviour and demography. *Animal Behaviour*, 76: 1235-1247.

430   Majolo B, Lehmann J, de Bortoli Vizioli A, Schino G. 2012. Fitness-related benefits of dominance

431   in primates. Am J Phys Anthropol 147: 652-660.

432   Miller N, Garnier S, Hartnett AT, Couzin ID. 2013. Both information and social cohesion determine

433   collective decisions in animal groups. Proc Natl Acad Sci 110: 5263-5268.

434   Mitani JC. 2009. Male chimpanzees form enduring and equitable social bonds. Anim Behav77:633-

435   640.

436   Mitani JC, Watts DP, Amsler SJ. 2010. Lethal intergroup aggression leads to territorial expansion in

437   wild chimpanzees. Curr Biol 20: R507-508.

438   Nunn CL, Lewis RJ. 2001. Cooperation and collective action in animal behavior. In: Noë r, van

439   Hooff JARAM, Hammerstein P, editors. Economics in nature. 1st ed. Cambridge, UK:

440   Cambridge University Press. p. 42-66

441 Orme CDL, Freckleton RP, Thomas GH, Petzoldt T, Fritz SA, Isaac NJB. 2012. CAPER:

442   comparative analyses of phylogenetics and evolution in R. Package version 0.5. Available at

443   http://cran.r-project.org/web/packages/caper/index.html. Accessed May 30th, 2013.

444 Packer C, Scheel D, Pusey AE. 1990. Why lions form groups: food is not enough. Am Nat 136: 1-

445   19.

446 Polizzi di Sorrentino E, Schino G, Massaro L, Visalberghi E, Aureli F. 2012 Between-group hostility

447   affects within-group interactions in tufted capuchin monkeys. Anim Behav 83: 445-451.

448 Puurtinen M, Mappes T. 2009. Between-group competition and human cooperation. Proc R Soc B

449   267: 355-360.

450 R Development Core Team 2011. A language and environment for statistical computing. R

451   Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/. ISBN

452   3-900051-07-0.

453 Radford AN. 2008a. Duration and outcome of intergroup conflict influences intragroup affiliative

454   behaviour. Proc R Soc B 275: 2787-2791.

455 Radford AN. 2008b. Type of threat influences postconflict allopreening in a social bird. Curr Biol

456   18: R114-115.

457 Radford AN. 2011. Preparing for battle? Potential intergroup conflict promotes current intragroup

458   affiliation. Biol Lett 7: 26-29.

459 Radford AN, Fawcett TW. 2014. Conflict between groups promotes later defense of a critical

460   resource in a cooperatively breeding bird. Curr Biol 24: 2935-2939.

461 Reeve HK, Hölldobler B. 2007. The emergence of a superorganism through intergroup competition.

462   Proc Natl Acad Sci 104: 9736 - 9740.

463 Rubenstein DI. 1986: Ecology and sociality in horses and zebras. In: Rubenstein DI, Wrangham

464   RW, editors. Ecological determinants of social evolution. 1st ed. Princeton: Princeton

465   University Press. p. 282-302

466 Schülke O, Bhagavatula J, Vigilant L, Ostner J. 2010. Social bonds enhance reproductive success in

467   male macaques. Curr Biol 220: 2207-2210.

468   Silk J. 1994. Social relationships of male bonnet macaques: male bonding in a matrilineal society.

469   Behaviour 130:271-291.

470   Sterck EHM, Watts DP, van Schaik CP. 1997. The evolution of female social relationships in

471   nonhuman primates. Behav Ecol Sociobiol 41: 291-309.

472   Tan JHW, Bolle F. 2007. Team competition and the public goods games. Econom Lett 96: 133-139.

473   van Vugt M, Park JH. 2009. Guns, germs, and sex: how evolution shaped our intergroup

474   psychology. Soc Personal Psychol Compass 3: 927-938.

475   Ventura R, Majolo B, Koyama NF, Hardie S, Schino G. 2006. Reciprocation and interchange in wild

476   Japanese macaques: Grooming, co-feeding and agonistic support. Am J Primatol 68: 1138-

477   1149.

478   West SA, Gardner A, Shuker DM, Reynolds T, Burton-Chellow M, Sykes EM, Guinnee MA,

479   Griffin AS. 2006. Cooperation and the scale of competition in humans. Curr Biol 16: 1103–

480   1106.

481   Wey T, Blumstein DT, Shen W, Jordán F. 2008. Social network analysis of animal behaviour: a

482   promising tool for the study of sociality. Anim Behav 75: 333-344.

483   Willems EP, Hellriegel B, van Schaik CP. 2013. The collective action problem in primate territory

484   economics. Proc R Soc B 280:20130081.

485   Willems EP, van Schaik CP. (2015). Collective action and the intensity of between-group

486   competition in nonhuman primates. Behav Ecol 26: 625-631.

487   Wilson EO, Bossert WH. 1971. A primer in population biology. Boston, Massachusetts: Sinauer

488   Associates.

489   Wrangham RW. 1980. An ecological model of female-bonded primate groups. Behaviour 75:262-

490   300.

491   Young C, Majolo B, Heistermann M, Schülke O, Ostner J (2014). Responses to social and

492   environmental stress are attenuated by strong male bonds in wild macaques. Proc Natl Acad Sci

493   201411450.

494

495   Table 1: PGLS results on the effect of the level of IGCC and of the control variables on the three

496   measures of intra-group affiliation among females (n=25; significant results in bold).

Independent variables	Model No. - Dependent variables								
	Model #1 - SWI			Model #2 - SDOD			Model #3 - Density		
	Lambda = 0			Lambda = 0.97			Lambda = 0.76		
	Estimate ± *SE*	*t*	*P*	Estimate ± *SE*	*t*	*P*	Estimate ± *SE*	*t*	*P*
Level of IGCC	0. 12±0.36	0.34	0.74	**-18.67±4.56**	**-4.10**	**<0.001**	**0.32±0.14**	**2.26**	**<0.03**
Study period	0.14±0.08	1.75	0.10	-0.12±1.12	-0.11	0.92	0.06±0.04	1.58	0.12
Provisioning	-0.03±0.21	0.14	0.89	-4.27±2.96	-1.44	0.17	0.05±0.083	0.57	0.58
Group size	**-0.01±0.00**	**-3.21**	**<0.01**	**-0.07±0.02**	**-2.91**	**<0.01**	-0.00±0.09	0.03	0.97
Level of intra-group contest competition	-0.10±0.18	-0.56	0.58	-0.97±2.52	-0.39	0.70	**0.07±0.00**	**-4.62**	**<0.001**
Intercept	**1.59±0.31**	**5.07**	**<0.001**	16.99±12.06	1.41	0.18	**0.60±0.24**	**2.51**	**0.02**

497

498

499 Table 2: PGLS results on the effect of the level of IGCC and of the control variables on the three

500 measures of intra-group affiliation among males (n=19; significant results in bold). [f] denotes the

501 model for which the Lilliefors normality test was significant (indicating that the model residuals

502 were not normally distributed)

Independent variables	Model No. - Dependent variables								
	Model #1[f] - SWI			Model #2 - SDOD			Model #3 - Density		
	Lambda = 1			Lambda = 0			Lambda = 0		
	Estimate ± *SE*	*t*	*P*	Estimate ± *SE*	*t*	*P*	Estimate ± *SE*	*t*	*P*
Level of IGCC	-1.95±2.76	-0.71	0.49	161.33±157.90	1.02	0.33	-0.05±0.20	-0.24	0.81
Study period	**6.95±2.56**	**2.71**	**<0.02**	-63.88±133.84	-0.48	0.64	-0.19±0.17	-1.10	0.29
Provisioning	1.54±0.84	1.82	0.09	77.57±102.0	0.75	0.46	-0.23±0.13	-1.71	0.11
Group size	**-0.04±0.00**	**23.59**	**<0.001**	-4.40±2.79	-1.58	0.14	**-0.01±0.00**	**-2.26**	**<0.05**
Level of intra-group contest competition	-0.49±0.64	0.76	0.46	-7.59±79.62	-0.09	0.93	0.22±0.10	2.08	0.06
Intercept	-6.04±8.17	0.74	0.47	317.85±219.48	1.45	0.17	**0.81±0.28**	**2.83**	**<0.02**

503

504   **Figure 1:** Scatter plots showing the relationship between the level of IGCC (ln-transformed), on the

505   y axis, and the standard deviation of out degree (SDOD) among female primates.

506

507   **Figure 2:** Scatter plots showing the relationship between the level of IGCC (ln-transformed) and

508   the density of grooming networks among female primates.