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1 **NOT LOST IN TRANSLATION: CHANGES IN SOCIAL DYNAMICS IN BONOBOBOS**
2 **AFTER COLONY RELOCATION AND FUSION WITH ANOTHER GROUP**

3 Marta Caselli¹, Beatrice Malaman¹, Giada Cordonì¹, Jean-Pascal Guéry², José Kok³, Elisa
4 Demuru^{4,5}, Ivan Norscia¹

5

6 ¹University of Torino, Department of Life Sciences and Systems Biology, Italy

7 ²La Vallée des Singes, 86700, Romagne, France.

8 ³Ouwehands Dierenpark, 3911AV, Rhenen, the Netherlands.

9 ⁴Laboratoire Dynamique Du Langage, Université de Lyon, CNRS-UMR5596, Lyon, France

10 ⁵ENES Bioacoustics Research Laboratory, University of Saint-Etienne, CRNL, CNRS UMR 5292,
11 Inserm UMR_S, Saint-Etienne, France

12

13 **Corresponding authors:** ivan.norscia@unito.it; elisa.demuru@cnrs.fr

14

15 Marta Caselli ORCID: 0000-0001-8674-8236

16 Giada Cordonì ORCID: 0000-0001-7093-0025

17 Jean-Pascal Guéry ORCID: 0000-0003-4499-3270

18 Elisa Demuru ORCID: 0000-0003-2532-1356

19 Ivan Norscia ORCID: 0000-0002-1618-7717

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24 **Abstract**

25 Animal welfare is affected by both physical and social environment and these aspects can be
26 particularly critical for cognitively and socially-complex species, such as great apes. We observed a
27 captive group of nine bonobos before (April-June 2021) and after relocation (June-August 2022)
28 and we checked whether and to what extent the transfer would affect their social behavior after a
29 stabilization period. The group was transferred from La Vallée des Singes (Romagne, France) to
30 Ouwehands Dierenpark (Rhenen, the Netherlands), where it was merged with the resident bonobo
31 group (N=4). The two zoological parks presented outdoor and indoor facilities that were similar in
32 both size and enrichment quality/quantity. We focused on four behavioral categories: conflict,
33 affiliation (i.e., grooming and sit-in-contact), social play, and socio-sexuality. Via non-parametric
34 tests and social network analyses we investigated whether the frequencies of these behaviors –
35 involving adults and immature subjects - differed: *i*) within the relocated group members before and
36 after transfer; and *ii*) between relocated and resident group members. The transfer did not affect
37 conflict rates within the relocated group and mainly involved inter-group interactions. Nevertheless,
38 the relocated group hierarchical and agonistic networks changed after relocation. Affiliation via
39 grooming and sit-in-contact was higher after relocation and between relocated group members.
40 There was a reorganization of the affiliative social network, possibly to strengthen pre-existing
41 social relationships. Compared to the pre-relocation period, after relocation social play was higher
42 and involved a larger network, particularly involving immature subjects. Hence, social play was
43 probably used by young individuals to enhance new relationships. Adult socio-sexual behaviors
44 were higher before than after relocation and between groups, resulting in a reorganization of the
45 social network for this behavioral category. Socio-sexual behaviors were probably used to enhance
46 new relationships, especially between adults. Overall, via the follow-up before and after
47 relocation/merging, our study was able to highlight that different affiliative patterns – all used to
48 ‘friendly’ relate to others - may have served (at least in part) different functions in the adaptation
49 process. Bonobos adapted their behavior to maintain pre-existing relationships (through grooming)

50 and establish new relationships (through social play in immatures and socio-sexuality in adults).
51 Hence, welfare can be enhanced by ensuring that bonobos are provided with all the environmental
52 and social conditions that allow them to express a wide array of behavioral patterns, necessary to
53 adjust to novelty and avoid social disruption.

54

55 **Keywords**

56 *Pan paniscus*, animal welfare, relocation, social behavior, social assessment

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76 **1. Introduction**

77 One of the main objectives of modern zoos is promoting, assessing and improving the welfare of
78 captive animals (Hughes, 1976; Price and Stoinski, 2007; Linhart et al., 2008; Silk et al., 2009;
79 Maple and Perdue, 2013). Transfers can have a negative impact on animal wellbeing as animals are
80 introduced in new environments and/or groups (Kleinhappel et al., 2016). Nevertheless, transfers
81 are often necessary to meet conservation (e.g., inbreeding avoidance), health or management needs
82 (Linhart et al., 2008; Kleinhappel et al., 2016).

83 Most ethological studies regarding the effect of transfers and physical/social changes focus on non-
84 human primates (e.g., rhesus macaques: O'Neill et al., 1991; cotton-top tamarins: Price, 1992;
85 chimpanzees: Ross et al., 2010; Schel et al., 2013; Neal Webb et al., 2018; bonobos: Pfalzer and
86 Ehret, 1995; lowland gorillas: Ross et al., 2010; Hoff et al., 1996). Regarding the effect of changes
87 in the physical environment, some studies report an increase in affiliative behaviors and a decrease
88 in agonistic behaviors (rhesus macaques: O'Neill et al., 1991; Hanuman langurs: Little and
89 Sommer, 2002) whereas others report no behavioral changes or a decrease/suppression of affiliative
90 behaviors (mandrills: Chang et al., 1999; lowland gorillas: Goerke et al., 1987; chimpanzees: Clarke
91 et al., 1982). As concerns the changes in the social environment, few studies investigated the
92 consequences of the integration of individuals into a pre-existing group or of the fusion of two
93 groups. However, a study on the fusion of two captive chimpanzee groups reported a decrease in
94 aggression and an increase in affiliation, with no complete integration of the two groups (Schel et
95 al., 2013). Another study showed an increase in both affiliative and aggressive behaviors in lowland
96 gorillas (Hoff et al., 1996).

97 The effect of changes in physical and/or social environment can be particularly important when
98 dealing with cognitively and socially-complex species, such as the bonobo (Suntsova and Buzdin,
99 2020; Furuichi, 2011). Bonobos live in multi-male/multi-female communities with fission-fusion
100 dynamics and show male-philopatry, female dispersal and female dominance (Wrangham, 1986).
101 They are generally considered as tolerant and xenophilic (Furuichi 2011), with low levels of overt

102 aggression compared to chimpanzees (Pusey, 2022). During inter-group encounters, wild bonobos
103 can engage in affiliative interactions (Tan et al., 2017), such as grooming, play and socio-sexual
104 behaviors, which are used to establish and/or maintain social relationships (Schroepfer-Walker et
105 al., 2015; Pellis and Iwaniuk, 2000; Demuru et al., 2022). Play can be additionally used as an “ice-
106 breaker strategy” favoring inter-group interactions (Itani, 1990).

107 To our knowledge, only one study investigated the integration of two captive bonobos into a pre-
108 existing group (Pfalzer and Ehret, 1995). This study found no aggression increase after merging and
109 that socio-sexual interactions especially occurred between new and resident group members and no
110 aggression increase (Pfalzer and Ehret, 1995).

111 This study aimed at evaluating the effects of the relocation of an entire bonobo group (hereafter
112 ‘relocated group’) and its fusion with another group (hereafter ‘resident group’) after that a
113 ‘stabilization’ period had passed. Based on the above framework, we formulated the following
114 predictions:

115 Prediction 1 – As affiliation is used to maintain and establish social relationships (Schroepfer-
116 Walker et al., 2015), we expect: 1a) higher levels of affiliation after relocation within the relocated
117 group compared to before relocation, with 1b) a consequent change in the centrality of individuals
118 in the social network of the relocated group; 1c) a higher frequency of affiliative interactions
119 between relocated and resident bonobos (inter-group) than within the relocated group (intra-group).

120 Prediction 2 – Given that social play can be used to establish and maintain social relationships and
121 also as ice-breaker (Itani, 1990, Pellis and Iwaniuk, 2000), we expect: 2a) a higher frequency of
122 play within the members of the relocated group after than before relocation, with 2b) a consequent
123 change in the centrality of individuals; 2c) a higher frequency of play between relocated and
124 resident bonobos (inter-group) than within the relocated group members (intra-group).

125 Prediction 3 – Because bonobos are xenophilic and show relatively low rates of overt aggression
126 (Furuichi, 2011) and aggression is used to establish hierarchy (Vervaecke et al., 2000), we expect:
127 3a) no effect of the relocation on the aggression rates within the relocated group, with 3b) no

128 hierarchy change and 3c) no change in the centrality of individuals; 3d) that the relocation would
129 not increase the aggression level between the relocated and resident group members.

130 Prediction 4 – Because socio-sexual interactions contribute in establishing social relationships
131 (Demuru et al., 2022), we expect: 4a) no effect of the relocation on socio-sexual behaviors within
132 the relocated group members, with 4b) no changes in the centrality of such members; 4c) a higher
133 frequency of socio-sexual behaviors between relocated and resident bonobos (inter-group) than
134 within relocated group members (intra-group).

135

136 **2. Materials and Methods**

137 **2.1 Ethical statement**

138 This study was purely observational. No approval was required from the authors' institution.

139

140 **2.2 Study sites, groups, and data collection**

141 This study was carried out at La Vallée des Singes (VDS; Romagne, France; Fig. 1a) and
142 Ouwehands Dierenpark (OD; Rhenen, the Netherlands; Fig. 1b). At VDS, the bonobo area was
143 composed by two indoor visible enclosure (each of around 100m²) and an external space of natural
144 habitat (around 0.34 ha). The VDS bonobo group (hereafter relocated group) was composed of 9
145 individuals (age range: 2 to 41 years; mean \pm SE: 16.333 \pm 4.327) including adults (2 males and 4
146 females – including one pregnant; age: \geq 12 years); one juvenile female (6 years old); two infants (a
147 3 years old female and a 2 years old male) (Table 1).

148 In October 2021, the VDS group was relocated to OD and merged with the resident group. Here, the
149 bonobo area is very similar to the area at VDS in terms of spaces and naturalistic and artificial
150 enrichment. The area was composed by two indoor enclosures where the individuals were visible
151 (each of around 130m²) and an external space of natural habitat (around 0.33 ha). Both at VDS and
152 OD, the bonobos were free to move from inside to outside (from around 9:30 a.m. to around 5:30-
153 6:30 p.m.) but during bad weather conditions they were kept in the indoor enclosure. Following the

154 relocation, the group composition changed as OD already housed four other bonobos (resident
155 group; 1 adult female, 32 years old; one weaning immature males, 5 years old; 2 juvenile twin
156 males, 11 years old; Table 1), and a pregnant female from VDS gave birth at OD. The resulting new
157 group (hereafter ‘merged group’) was composed of 14 bonobos (Full group info: Table 1).
158 Data were collected in real time from 6 to 4 months prior relocation/merging (VDS, April-June
159 2021), by M.C, and from 8 to 10 months after relocation/merging (OD, June to August 2022), by
160 B.M. after a period of training with M.C. (the period ended when B.M. and M.C. reached more than
161 80% of agreement, Cohen’s Kappa = 0.81). We could not systematically observe the group in the
162 very first months following relocation. Observations were conducted from around 10:00 a.m. to
163 5:30-6:00 p.m. (33.3 and 36.7 hours of observation in 2021 and 2022 respectively; 22.46 ± 0.80 and
164 35.77 ± 0.28 hour/subject, mean \pm SE, in 2021 and 2022 respectively). The identity of individuals
165 was recorded and we carried out observational data collection via two methods: *i*) scan animal
166 sampling (Altmann, 1974) - with a 10-min time window - for common, affiliative behaviors (i.e.
167 grooming and contact-sitting); and *ii*) all-occurrences sampling method (Altmann, 1974) for social
168 play (e.g. rough-and-tumble and play run), agonistic interactions (e.g., avoidance, chase,
169 aggression) and socio-sexual behaviors (e.g., genito-genital rubbing, rump-rump rubbing; full list
170 available in Table S1).

171

172 **2.3 Operational definition and statistical elaboration**

173 We used the frequency of agonistic behaviors (ethogram: Table S1) to fill in different aggression
174 socio-matrices (R “*steepness*” package; CRAN.R - project.org/package=steepness; R version 4.2.1)
175 for the relocated group in 2021 and 2022 to determine individual ranking position via Normalized
176 David's Scores (NDS; de Vries et al., 2006). NDSs were calculated via a dyadic dominance index
177 (Dij). The Dij consists of the observed proportion of wins (Pij) corrected for the chance occurrence
178 of the observer outcome - calculated on the basis of a binomial distribution with each subject having

179 an equal chance of winning or losing in every agonistic encounter (de Vries et al., 2006). To
180 compute hierarchy and NDS, we excluded infants (weaning period).

181 Due to the non-normal distribution of variables (Kolmogorov–Smirnov test: $N_{\text{dyads}} = 36$;
182 $p_{\text{affiliation}_{2021}} < 0.05$; $p_{\text{affiliation}_{2022}} < 0.05$; $p_{\text{play}_{2021}} < 0.05$; $p_{\text{play}_{2022}} < 0.05$; $p_{\text{conflict}_{2021}} < 0.05$;
183 $p_{\text{conflict}_{2022}} < 0.05$; $p_{\text{socio-sexuality}_{2021}} < 0.05$; $p_{\text{socio-sexuality}_{2022}} < 0.05$), we used the non-parametric
184 paired Wilcoxon signed-rank test (Siegel and Castellan, 1988) to compare the frequency of all
185 behavioral categories between the dyads of the relocated group in 2021 at VDS and in 2022 at OD.

186 Due to the non-normal distribution of the behavioral categories (Kolmogorov–Smirnov test: N_{dyads}
187 $= 72$; $p_{\text{affiliation}_{2022}} < 0.05$; $p_{\text{play}_{2022}} < 0.05$; $p_{\text{conflict}_{2022}} < 0.05$; $p_{\text{socio-sexuality}_{2022}} < 0.05$), we used a
188 non-parametric Mann-Whitney test to compare the frequency of behavioral interactions within the
189 dyads of the relocated group and between the relocated and the resident group dyads (Fowler and
190 Cohen, 1986). To account for possible data pseudoreplication (same individuals present in different
191 dyads), we applied a Monte Carlo randomization (10,000 permutations) (Bros and Cowell, 1987).
192 To carry out the above analyses, for each behavioral category the frequency was obtained by
193 considering the number of bidirectional interactions performed within each dyad ($A \rightarrow B + B \rightarrow A$),
194 normalized over the dyad observation time (derived from the scans where both individual of the
195 dyad were present).

196 To obtain the social network of bonobos social behaviors we used the freeware Gephi 0.9.7
197 (www.gephi.org/; dual license CDDL 1.0 and GNU General Public License v3). It includes
198 individuals (nodes) and interindividual connections (directed edges) derived from frequency of
199 dyadic directional interactions (AB if A was the actor and B the receiver; BA if *vice versa*). The
200 node size is based on degree centrality that in our case is the frequency of behaviors made by the
201 actor on the receiver and *vice versa* (Golbeck, 2013; Saqr et al., 2018). Because sit-in-contact is not
202 directional, only grooming was considered for the affiliation network. Via this software we
203 extracted the eigenvector centrality values, to measure the centrality of each individual of the group.

204 The algorithm measures the transitive influence of nodes: high-scoring nodes and low-scoring
205 nodes contribute differently (more the high-scoring and less the low-scoring nodes respectively) to
206 the final score of each node (Ruhnau, 2000). To evaluate whether the centrality of individuals of the
207 relocated group had changed from 2021 to 2022, we carried a correlation of the individual
208 eigenvector centrality values between 2021 and 2022. Due to the small sample size ($N_{\text{individuals}} = 9$,
209 not testable for normality), we applied a non-parametric Spearman's rank correlation (Fowler and
210 Cohen, 1986).

211 In case of multiple comparisons involving the same data (i.e., the comparison between the
212 frequency of dyadic interactions within the members of the relocated group in: 2021 vs 2022 and
213 2022 vs 2022 with the new individuals) the level of probability was adjusted according to
214 Bonferroni correction (Sedgwick, 2012).

215

216 **3. Results**

217 As concerns Prediction 1, we found a significant difference in the frequency of affiliative behaviors
218 (i.e., grooming and sit-in-contact) within the relocated group between 2021 and 2022, with the
219 highest frequency recorded in 2022 (Wilcoxon signed-rank test via Monte Carlo randomization:
220 $N_{\text{dyads}} = 36$, $Z = -3.186$, $p = 0.001$; Fig. 2a). With respect to the grooming network, we found no
221 correlation in the eigenvector centrality values of the relocated group members between 2021 and
222 2022 (Spearman's rank correlation: $N_{\text{individuals}} = 9$, $\rho(7) = 0.536$, $p = 0.137$; Fig. 2b). Moreover, we
223 found that the frequency of grooming/sit-in-contact behaviors was significantly higher within the
224 members of the relocated group than between the relocated group members and the resident group
225 members (Mann-Whitney test via Monte Carlo randomization: $N_{\text{relocated_group_dyads}} = 36$, $N_{\text{relocated_}}$
226 $\text{and_resident_group_members_dyads}} = 36$, $U = 334.500$, $Z = -3.533$, $p < 0.001$; Fig. 2a).

227 For Prediction 2, we found that the frequency of social play within the relocated group members
228 (intra-group) was significantly higher in 2022 than in 2021 (Wilcoxon signed-rank test via Monte
229 Carlo randomization: $N_{\text{dyads}} = 36$, $Z = -2.589$, $p = 0.008$; Fig. 3a). We found a positive correlation in

230 the eigenvector centrality values of the relocated group members between 2021 and 2022
231 (Spearman's rank correlation: $N_{\text{individuals}} = 9$, $\rho(7) = 0.825$, $p = 0.006$; Fig 3b). Moreover, we found
232 no significant difference in the frequency of play between the members of the relocated group
233 (intra-group) and between the relocated group members and the resident group members (inter-
234 group) (Mann–Whitney test via Monte Carlo randomization: $N_{\text{relocated_group_dyads}} = 36$, $N_{\text{relocated_}$
235 $_and_resident_group_members_dyads} = 36$, $U = 559.500$, $Z = -1.065$, $p = 0.292$; Fig. 3a).

236 Regarding Prediction 3, from a descriptive point of view, we found low level of agonistic
237 interaction at intra-group level between the member of the relocated group in 2021 and 2022 (0.024
238 ± 0.007 and 0.031 ± 0.009 mean \pm SE before and after relocation respectively) and, after the
239 relocation, a higher frequency of inter-group aggression - between relocated and resident group
240 members - (0.084 ± 0.019 mean \pm SE) than intra-group aggression - between relocated group
241 members - (0.031 ± 0.009 mean \pm SE). We found that the difference in the frequency of agonistic
242 interactions within the members of the relocated group between 2021 and 2022 was not significant
243 (Wilcoxon signed-rank test via Monte Carlo randomization: $N_{\text{dyads}} = 36$, $Z = -1.027$, $p = 0.311$; Fig.
244 4a). We found no correlation in the eigenvector centrality values of the relocated group members
245 between 2021 and 2022 (Spearman's rank correlation: $N_{\text{individuals}} = 9$, $\rho(7) = 0.653$, $p = 0.057$; Fig
246 4b). Moreover, we found no correlation in the NDS of the relocated group members between 2021
247 and 2022 (Spearman's rank correlation: $N_{\text{individuals}} = 7$, $\rho(5) = 0.378$, $p = 0.403$) resulting in a
248 change of the female at the top of the hierarchy, while the hierarchical order of the other subjects
249 remains more or less unchanged (see Table 2 for details). Finally, we found a significantly higher
250 frequency of agonistic interactions between the relocated group members and the resident group
251 members (inter-group) than between the relocated group members (intra-group) (Mann–Whitney
252 test via Monte Carlo randomization: $N_{\text{relocated_group_dyads}} = 36$, $N_{\text{relocated_and_resident_group_members_dyads}} = 36$,
253 $U = 313.500$, $Z = -3.771$, $p = 0.000$; Fig. 4a).

254 Concerning prediction 4, the frequency of socio-sexual behaviors within the members of the
255 relocated group was significantly higher in 2021 than in 2022 (Wilcoxon signed-rank test via Monte

256 Carlo randomization: $N_{\text{Dyads}} = 36$, $Z = -2.687$, $p = 0.007$; Fig. 5a). We also found no correlation in
257 the eigenvector centrality values of the relocated group members between 2021 and 2022
258 (Spearman's rank correlation: $N_{\text{Individuals}} = 9$, $\rho(7) = 0.092$, $p = 0.814$; Fig 5b). Moreover, we
259 found a significantly higher frequency of socio-sexual interactions between the relocated group
260 members and the resident group members than within the members of the relocated group (Mann-
261 Whitney test via Monte Carlo randomization: $N_{\text{relocated_group_dyads}} = 36$,
262 $N_{\text{relocated_and_resident_group_members_dyads}} = 36$, $U = 441.000$, $Z = -2.338$, $p = 0.019$; Fig. 5a).

263

264 **4. Discussion**

265 Our results show that the relocation of the VDS bonobo group and its merging with the resident
266 group led to social reorganization. We found: 1) that individuals of the relocated group affiliated
267 (via grooming and sit-in-contact) more frequently after than before relocation (Prediction 1a
268 confirmed) - with a change in the grooming network centrality of individuals (Prediction 1b
269 confirmed) - and that grooming/sit-in-contact behaviors were more frequent between relocated
270 group members (intra-group) than between relocated and resident group members (inter-group)
271 (Prediction 1c not confirmed); 2) higher frequencies of social play after than before relocation
272 (Prediction 2a confirmed) - without a change in the centrality of individuals (Prediction 2b not
273 confirmed) - and no difference in the comparison of social play frequency between relocated group
274 members (intra-group), and between relocated and resident group members (inter-group)
275 (Prediction 2c not confirmed); 3) no difference in the frequency of agonistic interactions between
276 the members of the relocated group (intra-group) after and before relocation (Prediction 3a
277 confirmed) - with a change in the dominance rank and individual centrality (Prediction 3b and 3c
278 not confirmed) - and lower aggression levels between the relocated group members (intra-group)
279 than between relocated and resident group members (inter-group) (Prediction 3d not confirmed); 4)
280 lower frequencies of socio-sexual behaviors after than before relocation (Prediction 4a not
281 confirmed) - with a change in the centrality of individuals (Prediction 4b confirmed) - and lower

282 frequencies of socio-sexual behaviors between the relocated group members (intra-group) than
283 between relocated and resident group members (inter-group) (Prediction 4c confirmed).

284

285 *4.1 Affiliative behaviors*

286 Rates of affiliation (i.e., grooming and sit-in-contact) were higher after relocation than before,
287 especially between the individuals of the relocated group. These results are in line with a previous
288 study about the effects of the fusion of two chimpanzee groups. The authors reported an increase of
289 intra-group affiliation levels, but no change with respect to the level of affiliation between the two
290 groups (Schel et al., 2013).

291 The increase of intra-group affiliation level could suggest that affiliative behaviors, such as
292 grooming and contact-sitting, may be used to maintain pre-existing relationships at least when
293 group merging is involved. The fact that affiliative interactions could be used preferentially to
294 maintain old (rather than to enhance new) relationships, may also be informed by the change in the
295 individual centrality within the grooming social network, which was extended to more individuals
296 within the relocated group after the transfer.

297

298 *4.2 Social play*

299 Our results suggest that social play was used to establish – more than to maintain – social
300 relationships (Pellis and Iwaniuk, 2000). Indeed, the frequency of social play in the relocated group
301 increased after merging but social play rates were comparable between the relocated group
302 members (intra-group) and between relocated and resident group members (inter-group). Another
303 non-exclusive possible explanation for the increment of social play rates after relocation could be
304 the role of play in reducing social tension (Cordoni and Palagi, 2016; Yamanashi et al., 2018). Such
305 tension could have been possibly caused by the new environment and by the presence of new
306 individuals in the group. Indeed, bonobos use play during tense situations, such as pre-feeding, to
307 reduce mild stress (Palagi et al., 2006).

308 Moreover, we found that immature individuals kept leading social play within the relocated group
309 and maintained their centrality in an expanded social play network after relocation. The fact that
310 social play between relocated and resident group members mostly involved immature subjects is in
311 line with a previous study on inter-group encounters (Itani, 1990). The author reported that social
312 play interactions occurred between immature subjects, which preferred play as ice-breaker with
313 outgroup members (Itani, 1990). Moreover, previous studies reported that social play can be used as
314 social assessment between unknown individuals (Thompson, 1998; Pellis and Iwaniuk, 2000;
315 Cordoni and Palagi, 2011) Overall, after relocation the social play network was expanded within
316 the relocated group and at the same time extended to the members of the resident bonobos
317 (originally outgroup members), thus indicating the double function of play in reinforcing existing
318 relationships and in establishing new ones.

319

320 *4.3 Agonistic behaviors*

321 After the group transfer, the overall aggression frequency did not change. The fact that aggression
322 levels were not affected by the relocation is in line with the coping model (de Waal, 1989). The
323 coping model tries to explain how social species use behavioral mechanism to buffer intra-group
324 aggressions (de Waal, 1989). Even though in the study bonobos the aggression rates were
325 comparable before and after relocation, a redistribution of agonistic interactions within the relocated
326 group occurred after the transfer and was accompanied by a hierarchy variation and a change of the
327 dominant female (Table 2). This result is likely related to the introduction of outgroup members
328 (Sapolsky, 1993). Moreover, our social-network analysis on the agonistic interactions between the
329 relocated and the resident group members revealed that the majority of agonistic interactions
330 involved the males and females of the relocated group and the two juveniles (but almost adult)
331 males of the resident group. Consistently, Itani (1990) reported that inter-group aggression mostly
332 occurred between males and between females and males whereas females interacted mostly through
333 socio-sexual behaviors rather than via direct aggression (Itani, 1990). In general, our results on

334 agonistic behaviors show that even if bonobos are considered a xenophilic species (Furuichi, 2011),
335 the integration of two different groups can lead to social and hierarchical reorganization.

336

337 *4.4 Socio-sexual behaviors*

338 After relocation, socio-sexual behaviors decreased within the transferred group - with a change in
339 the centrality of individuals - and most socio-sexual contacts occurred between relocated and
340 resident group members. These results underline the role that socio-sexual behaviors can have in
341 enhancing new relationships. Socio-sexual contacts can be flexibly used to regulate social tension
342 (de Waal, 1990) and also to maintain and establish relationships and alliances (Moscovice et al.,
343 2015; Demuru et al., 2022). Genito-genital rubbing can occur preferentially during the maximum
344 swelling phase and last longer between weakly bonded females (Hohmann and Fruth 2000; Demuru
345 et al., 2022; Annichiarico et al., 2020). During the pre-relocation, socially stable period, socio-
346 sexual interactions probably worked as a “social-glue” to maintain social relationships and
347 alliances. In the period of social instability that possibly followed group merging (as it usually
348 occurs in apes after merging; Von Rohr et al., 2012), it is possible that the study bonobos decreased
349 socio-sexual interactions with familiar subjects to divert them preferentially toward unfamiliar
350 individuals, so as to regulate social tension and establish new alliances.

351

352 *4.5 Conclusions*

353 To our knowledge this is the first study that investigated the behavioral and relational variation in a
354 group of bonobos after its relocation and fusion with another group. This study highlights that
355 bonobos are able to adopt different measures to cope with relocation and merging with new
356 individuals. In particular, bonobos preferentially used grooming/sit-in-contact affiliation to maintain
357 pre-existing social relationships, social play as social assessment strategy and to enhance new
358 relationships (especially involving immature subjects as social bridge), and socio-sexual
359 interactions to enhance inter-group relationships. As a possible result, aggression levels did not

360 increase after relocation even though the group composition change led to a hierarchy
361 reorganization, with a new dominant female from the relocated group. Clearly, some of the
362 observed differences may be due to the change in the environmental setting or to the fact that a
363 pregnant female gave birth after relocation. However, the new infant was not able to engage in
364 independent interactions during the study period and the facilities of the two zoos (VDS and OD)
365 are strikingly similar – also in terms of environmental enrichments - so the transfer and merging
366 probably account for most of the observed behavioral changes. On a broader perspective, our study
367 points toward the importance of considering the impact that relocations of captive social animals
368 could have not only on physical welfare, but also on social behavior, which represents an important
369 aspect to maintain and improve animal welfare. Long-term behavioral observations are needed to
370 understand the time scale needed to reach partial or complete integration of different groups.

371

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377

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387 **REFERENCES**

388 Altmann, J., 1974. Observational study of behavior: sampling methods. *Behaviour*. 49(3-4), 227-
389 266. <https://doi.org/10.1163/156853974X00534>

390 Annicchiarico, G., Bertini, M., Cordoni, G., Palagi, E., 2020. Look at me while having sex! Eye-to-
391 eye contact affects homosexual behaviour in bonobo females. *Behaviour* 157, 949-970.
392 <https://doi.org/10.1163/1568539X-bja10034>

393 Bros, W.E., Cowell, B.C., 1987. A technique for optimizing sample size (replication). *J. Exp. Mar.*
394 *Biol. Ecol.* 114(1), 63-71. [https://doi.org/10.1016/0022-0981\(87\)90140-7](https://doi.org/10.1016/0022-0981(87)90140-7)

395 Chang, T.R., Forthman, D.L., Maple, T.L., 1999. Comparison of confined mandrill (*Mandrillus*
396 *sphinx*) behavior in traditional and “ecologically representative” exhibits. *Zoo Biol.*18(3), 163-176.
397 [https://doi.org/10.1002/\(SICI\)1098-2361\(1999\)18:3<163::AID-ZOO1>3.0.CO;2-T](https://doi.org/10.1002/(SICI)1098-2361(1999)18:3<163::AID-ZOO1>3.0.CO;2-T)

398 Clarke, A.S., Juno, C.J., Maple, T.L., 1982. Behavioral effects of a change in the physical
399 environment: A pilot study of captive chimpanzees. *Zoo Biol.* 1(4), 371-380.
400 <https://doi.org/10.1002/zoo.1430010411>

401 Cordoni, G., Palagi, E., 2011. Ontogenetic trajectories of chimpanzee social play: similarities with
402 humans. *PLoS One*, 6(11), e27344. <https://doi.org/10.1371/journal.pone.0027344>

403 Cordoni, G., Palagi, E., 2016. Aggression and hierarchical steepness inhibit social play in adult
404 wolves. *Behaviour*, 153(6-7), 749-766. <https://doi.org/10.1163/1568539X-00003326>

405 de Vries, H., Stevens, J.M., Vervaecke, H., 2006. Measuring and testing the steepness of dominance
406 hierarchies. *Anim. Behav.* 71(3), 585–592. <https://doi.org/10.1016/j.anbehav.2005.05.015>

407 De Waal, F.B.M., 1989. *Peacemaking among primates*. Harvard University Press, Cambridge, MA

408 de Waal, F.B.M., 1990. Sociosexual behavior used for tension regulation in all age and sex
409 combinations among bonobos, in: Federman, J.R. (Eds.), *Pedophilia*. Springer, New York, NY, pp.
410 378-393. https://doi.org/10.1007/978-1-4613-9682-6_15

411 Demuru, E., Caselli, M., Guéry, J. P., Michelet, C., Alexieff, F., Norscia, I., 2022. Female bonobos
412 show social swelling by synchronizing their maximum swelling and increasing bonding. *Sci.*
413 *Rep.* 12(1), 1-11. <https://doi.org/10.1038/s41598-022-22325-7>

414 Fowler J., Cohen L., 1996., *Statistics for ornithologists*. British Trust for Ornithology, Thetford,
415 UK.

416 Furuichi, T., 2011. Female contributions to the peaceful nature of bonobo society. *Evol. Anthropol.*
417 20(4), 131-142. <https://doi.org/10.1002/evan.20308>

418 Goerke, B., Fleming, L., Creel, M., 1987. Behavioral changes of a juvenile gorilla after a transfer to
419 a more naturalistic environment. *Zoo Biol.* 6(4), 283-295. <https://doi.org/10.1002/zoo.1430060403>

420 Golbeck, J., 2013. Network structure and measures, in: Kaufmann, M. (Eds), *Analyzing the social*
421 *web*. Elsevier, Waltham, MA, pp. 25–44. <https://doi.org/10.1016/B978-0-12-405531-5.00003-1>

422 Hoff, M.P., Hoff, K.T., Horton, L.C., Maple, T.L., 1996. Behavioral effects of changing group
423 membership among captive lowland gorillas. *Zoo Biol.* 15(4), 383-393.
424 [https://doi.org/10.1002/\(SICI\)1098-2361\(1996\)15:4<383::AID-ZOO3>3.0.CO;2-7](https://doi.org/10.1002/(SICI)1098-2361(1996)15:4<383::AID-ZOO3>3.0.CO;2-7)

425 Hohmann, G., Fruth, B., 2000. Use and function of genital contacts among female bonobos. *Anim.*
426 *Behav.*, 60(1), 107-120. <https://doi.org/10.1006/anbe.2000.1451>

427 Hughes, B.O., 1976. Behaviour as index of welfare, in: Proceedings of the Fifth European Poultry
428 Conference, Malta. pp. 1005-1018.

429 Itani, G., 1990. Relations between unit-groups of bonobos at Wamba, Zaire: encounters and
430 temporary fusions. *ASM*. 11(3), 153-186.

431 Kleinhappel, T.K., John, E.A., Pike, T.W., Wilkinson, A., Burman, O.H., 2016. Animal welfare: a
432 social networks perspective. *Sci. Prog.* 99(1), 68-82.
433 <https://doi.org/10.3184/003685016X14495640902331>

434 Linhart, P., Adams, D.B., Voracek, T., 2008. The international transportation of zoo animals:
435 conserving biological diversity and protecting animal welfare. *Vet. Ital.*, 44(1), 49-57.

436 Little, K.A., Sommer, V., 2002. Change of enclosure in langur monkeys; implications for the
437 evaluation of environmental enrichment. *Zoo Biol.* 21, 549–559. <https://doi.org/10.1002/zoo.10058>

438 Maple, T.L., Perdue, B.M., 2013. Environmental Enrichment, in: Maple, T.L., Perdue, B.M. (Eds),
439 Zoo Animal Welfare. Springer, Berlin, DE, pp. 95-117. [https://doi.org/10.1007/978-3-642-35955-](https://doi.org/10.1007/978-3-642-35955-2_6)
440 [2_6](https://doi.org/10.1007/978-3-642-35955-2_6)

441 Moscovice, L.R., Deschner, T., Hohmann, G., 2015. Welcome back: responses of female bonobos
442 (*Pan paniscus*) to fusions. *PloS one*, 10(5), e0127305. <https://doi.org/10.1371/journal.pone.0127305>

443 Neal Webb, S.J., Hau, J., Schapiro, S.J., 2018. Captive chimpanzee (*Pan troglodytes*) behavior as a
444 function of space per animal and enclosure type. *Am. J. Primatol.*, 80(3), e22749.
445 <https://doi.org/10.1002/ajp.22749>

446 O'Neill, P.L., Novak, M.A., Suomi, S.J., 1991. Normalizing laboratory-reared rhesus macaque
447 (*Macaca mulatta*) behavior with exposure to complex outdoor enclosures. *Zoo Biol.* 10(3), 237-
448 245. <https://doi.org/10.1002/zoo.1430100307>

449 Palagi, E. Paoli, T. Tarli, S.B., 2006. Short-term benefits of play behavior and conflict prevention in
450 *Pan paniscus*. *Int. J. Primatol.* 27(5), 1257-1270. <https://doi.org/10.1007/s10764-006-9071-y>

451 Pellis, S.M., Iwaniuk, A.N., 2000. Adult–adult play in primates: comparative analyses of its origin,
452 distribution and evolution. *Ethology*, 106(12), 1083-1104. <https://doi.org/10.1046/j.1439-0310.2000.00627.x>

454 Pfalzer, S., Ehret, G., 1995. Social integration of a bonobo mother and her dependent daughter into
455 an unfamiliar group. *Primates*. 36(3), 349-360. <https://doi.org/10.1007/BF02382858>

456 Price, E.C., 1992. Adaptation of captive-bred cotton-top tamarins (*Saguinus oedipus*) to a natural
457 environment. *Zoo Biol.*, 11(2), 107-120. <https://doi.org/10.1002/zoo.1430110206>

458 Price, E.E., Stoinski, T.S., 2007. Group size: Determinants in the wild and implications for the
459 captive housing of wild mammals in zoos. *App. Anim. Behav. Sci.*, 103(3-4), 255-264.
460 <https://doi.org/10.1016/j.applanim.2006.05.021>

461 Pusey, A.E., 2022. Warlike chimpanzees and peacemaking bonobos. *PNAS*. 119(31), e2208865119.
462 <https://doi.org/10.1073/pnas.220886511>

463 Ross, S.R., Wagner, K.E., Schapiro, S.J., Hau, J., Lukas, K.E., 2011. Transfer and acclimatization
464 effects on the behavior of two species of African great ape (*Pan troglodytes* and *Gorilla gorilla*
465 *gorilla*) moved to a novel and naturalistic zoo environment. *Int. J. Primatol.* 32(1), 99-117.
466 <https://doi.org/10.1007/s10764-010-9441-3>

467 Ruhnau, B., 2000. Eigenvector-centrality—a node-centrality?. *Soc. Netw.* 22(4), 357-365.
468 [https://doi.org/10.1016/S0378-8733\(00\)00031-9](https://doi.org/10.1016/S0378-8733(00)00031-9)

469 Sapolsky, R.M., 1993. The physiology of dominance in stable versus unstable social hierarchies, in
470 Mason, W.A., Mendoza, S.P. (Eds.), *Primate social conflict* (pp. 171–204). State University of New
471 York Press. New York, NY, pp. 171-204.

472 Saqr, M., Fors, U., Nouri, J., 2018. Using social network analysis to understand online Problem-
473 Based Learning and predict performance. *PLoS One*. 13(9), e0203590. <https://doi.org/10.1371/journal.pone.0203590>

475 Schel, A.M., Rawlings, B., Claidiere, N., Wilke, C., Wathan, J., Richardson, J., ... , Slocombe, K.,
476 2013. Network analysis of social changes in a captive chimpanzee community following the
477 successful integration of two adult groups. *Am. J. Primatol.* 75(3), 254-266.
478 <https://doi.org/10.1002/ajp.22101>

479 Schroepfer-Walker, K., Wobber, V., Hare, B., 2015. Experimental evidence that grooming and play
480 are social currency in bonobos and chimpanzees, in: Hare, B., Yamamoto, S. (Eds), *Bonobo*
481 *Cognition and Behaviour*, Leiden, NL, pp. 299-316.

482 Sedgwick, P., 2012. Multiple significance tests: the Bonferroni correction. *Bmj.* 344, e509.
483 <https://doi.org/10.1136/bmj.e509>

484 Siegel, S., Castellan, N. J., 1988. *Nonparametric Statistics for the Behavioural Sciences*, second ed.
485 McGraw-Hill Book Company, New York. <https://doi.org/10.1177/014662168901300212>

486 Silk, J.B., Beehner, J.C., Bergman, T.J., Crockford, C., Engh, A.L., Moscovice, L.R., ... , Cheney, D.
487 L., 2009. The benefits of social capital: close social bonds among female baboons enhance offspring
488 survival. *Proc. Royal Soc. B.* 276(1670), 3099-3104. <https://doi.org/10.1098/rspb.2009.0681>

489 Suntsova, M.V., Buzdin, A.A., 2020. Differences between human and chimpanzee genomes and
490 their implications in gene expression, protein functions and biochemical properties of the two
491 species. *BMC Genom.*, 21(7), 1-12. <https://doi.org/10.1186/s12864-020-06962-8>

492 Tan, J., Ariely, D., Hare, B., 2017. Bonobos respond prosocially toward members of other
493 groups. *Sci. rep.* 7(1), 1-11. <https://doi.org/10.1038/s41598-017-15320-w>

494 Thompson, K.V., 1998. Self assessment in juvenile play, in Bekoff, M., Byers, J.A. (Eds.), *Animal*
495 *play: Evolutionary, comparative, and ecological perspectives*, Cambridge University Press,
496 Cambridge, UK, pp. 183–204. <https://doi.org/10.1017/CBO9780511608575.010>

497 Vervaecke, H., De Vries, H.A.N., Van Elsacker, L., 2000. Dominance and its behavioral measures in
498 a captive group of bonobos (*Pan paniscus*). *Int. J. Primatol.* 21, 47-68.
499 <https://doi.org/10.1023/A:1005471512788>

500 Von Rohr, C.R., Koski, S.E., Burkart, J.M., Caws, C., Fraser, O.N., Ziltener, A., Van Schaik, C.P.,
501 2012. Impartial third-party interventions in captive chimpanzees: a reflection of community
502 concern. *PloS one*, 7(3), e32494. <https://doi.org/10.1371/journal.pone.0032494>

503 Wrangham, R.W., 1986. 16. Ecology and Social Relationships in Two Species of Chimpanzee, in
504 Rubenstein, D.I., Wrangham, R.W. (Eds), *Ecological aspects of social evolution*, Princeton
505 University Press, Princeton, NJ, pp. 352-378.

506 Yamanashi, Y., Nogami, E., Teramoto, M., Morimura, N., Hirata, S., 2018. Adult-adult social play
507 in captive chimpanzees: Is it indicative of positive animal welfare?. *App. Anim. Behav. Sci.* 199,
508 75-83. <https://doi.org/10.1016/j.applanim.2017.10.006>

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511 **TABLES**

512 **Table 1**

513 Full description of the group composition during the study period.

Relocated group			Resident group		
Subject	Sex	Year of birth	Subject	Sex	Year of birth
Lisala	Female	1980	Eja	Female	1990
Kutu	Female	1998	Azibo	Male	2011
Lingoye	Female	2007	Ayubu	Male	2011
Omanga	Female	2008	Bakari	Male	2017
Luebo	Male	2006			
Bondo	Male	1991			
Visola	Female	2015			
Nginga	Female	2018			
Maiko	Male	2019			
Malembe	Male	2022			

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516 **Table 2**

517 Hierarchy of the relocated group in 2021 and 2022

Hierarchy of the relocated group in 2021	Hierarchy of the relocated group in 2022
Omanga	Lisala
Kutu	Kutu
Lisala	Lingoye
Bondo	Luebo
Lingoye	Omanga
Luebo	Bondo
Visola	Visola

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525 **FIGURES**

526 **Figure 1**

527 Satellite photos of bonobo enclosure at a) VDS and b) OD. The red line outlines the boundary of the
528 enclosure, and the dotted part identifies the indoor enclosure.

529 **Figure 2**

530 a) Violin plot of the frequency of affiliative behaviors (grooming/sit in contact) within the relocated
531 group members in 2021 (red color) and 2022 (green color) and between the relocated and resident
532 group members (blue color) with the corresponding mean and standard error of the behavioral
533 frequency; b) social network of grooming interactions and number of involved dyads (same colors
534 as figure a)

535 **Figure 3**

536 a) Violin plot of the frequency of play behaviors within the relocated group members in 2021 (red
537 color) and 2022 (green color) and between the relocated and resident group members (blue color)
538 with the corresponding mean and standard error of the behavioral frequency; b) social network of
539 play behaviors and number of involved dyads (same colors as figure a)

540 **Figure 4**

541 a) Violin plot of the frequency of agonistic behaviors within the relocated group members in 2021
542 (red color) and 2022 (green color) and between the relocated and resident group members (blue
543 color) with the corresponding mean and standard error of the behavioral frequency; b) social
544 network of agonistic behaviors and number of involved dyads (same colors as figure a)

545 **Figure 5**

546 a) Violin plot of the frequency of socio-sexual behaviors within the relocated group members in
547 2021 (red color) and 2022 (green color) and between the relocated and resident group members

548 (blue color) with the corresponding mean and standard error of the behavioral frequency; b) social
549 network of socio-sexual behaviors and number of involved dyads (same colors as figure a)

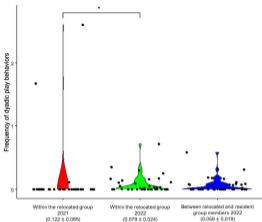
a



b



a



b

Interactions within the relocated group in 2021

Adult-adult 0 on 15 (0%)
 Immature-adult 0 on 18 (0%)
 Immature-immature 3 on 3 (100%)
 Total 3 on 36 (8.3%)



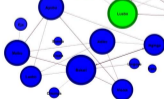
Interactions within the relocated group in 2022

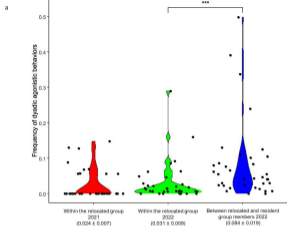
Adult-adult 5 on 15 (33.3%)
 Immature-adult 13 on 18 (72.2%)
 Immature-immature 3 on 3 (100%)
 Total 21 on 36 (58.3%)



Interactions between the relocated and the resident group members

Adult-adult 2 on 10 (11.1%)
 Immature-adult 10 on 15 (66.7%)
 Immature-immature 3 on 3 (100%)
 Total 15 on 36 (41.7%)

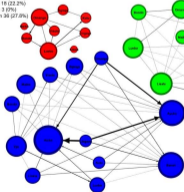




b

Interactions within the relocated group in 2021

Adult-adult 6 on 15 (40%)
 Immature-adult 4 on 15 (22.2%)
 Immature-immature 0 on 3 (0%)
 Total 10 on 36 (27.8%)



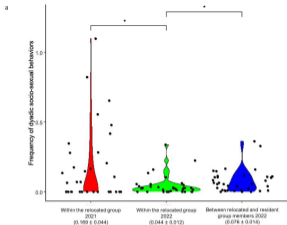
Interactions within the relocated group in 2022

Adult-adult 14 on 15 (93.3%)
 Immature-adult 13 on 15 (72.2%)
 Immature-immature 2 on 3 (66.7%)
 Total 29 on 36 (80.6%)



Interactions between the relocated and the resident group members

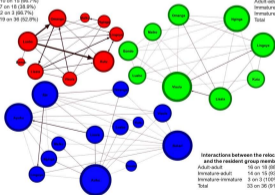
Adult-adult 16 on 18 (88.9%)
 Immature-adult 15 on 15 (100%)
 Immature-immature 3 on 3 (100%)
 Total 34 on 36 (94.4%)



b

Interactions within the relocated group in 2021

Adult-adult 10 on 15 (66.7%)
 Immature-adult 7 on 16 (38.8%)
 Immature-immature 2 on 3 (66.7%)
 Total 19 on 34 (52.8%)



Interactions within the relocated group in 2022

Adult-adult 9 on 15 (60%)
 Immature-adult 14 on 18 (77.8%)
 Immature-immature 3 on 3 (100%)
 Total 26 on 36 (72.2%)

Interactions between the relocated and the resident group members

Adult-adult 16 on 18 (88.9%)
 Immature-adult 14 on 15 (93.3%)
 Immature-immature 3 on 3 (100%)
 Total 33 on 36 (91.7%)