TITLE: The effect of dominance rank on the distribution of different types of male-infant-male interactions in Barbary macaques (*Macaca sylvanus*)

SHORT TITLE: Rank and male-infant-male interactions

ABSTRACT

In several cercopithecine species males exhibit a specific type of male-infant-male interaction during which two males briefly manipulate an infant. These interactions typically occur after a male carrying an infant (infant holder) approaches or is approached by another male who is not holding an infant (infant non-holder). The agonistic buffering and relationship management hypotheses explain these interactions as a tool to establish and maintain social bonds among males. Both hypotheses predict that males preferentially use the opportunity to interact and bond with males dominant to themselves. However, the agonistic buffering hypothesis predicts that males preferentially initiate male-infant-male interactions with the highest ranking males available, whereas the relationships management hypothesis predicts that males are more likely to interact with males that are close to them in rank. To test these predictions we collected data on 1,562 male-infant-male interactions during 1,430 hours of focal observation of 12 infants in one group of wild Barbary macaques (*Macaca sylvanus*) in Morocco. Using generalized linear mixed-effect models we found that males preferably initiated interactions with males who were dominant to them. However, we only observed this effect for interactions initiated by the infant holder. In interactions initiated by non-holders, the receiver`s relative rank did not predict the frequency of interactions. Males also initiated more interactions with males close in rank to themselves than distantly-ranked males. Our results support the relationship management hypothesis, but also indicate that the different types of male-infant-male interactions may require different explanations.

INTRODUCTION

Although high maternal investment in offspring is a common feature of mammalian species (Trivers 1972), the extent of male interest in infants and juveniles is highly variable (Maestripieri 1994; van Schaik and Paul 1996). In primates, male-infant interactions range from positive, contributing to the survival of the infant, to negative interactions such as aggression or abuse (Kleindorfer and Wasser 2004; Schino et al. 2003). In some primate species, males exhibit a specific type of infant handling during which two or more individuals simultaneously manipulate an infant. These interactions have been called bridging interactions (Ogawa 1995), triadic male-infant interactions (Taub 1984), agonistic buffering (Deag and Crook 1971), exploitation (Packer 1980), or male-infant-male interactions (Zhao 1996); we use the latter term in our study.

Male-infant-male interactions have been reported in several species of macaques (Bernstein and Cooper 1998; de Waal et al. 1976; Deag and Crook 1971; Estrada and Sandoval 1977; Ogawa 1995; Silk and Samuels 1984), baboons (Busse and Hamilton 1981; Collins 1986; Smuts 1985), mangabeys (Busse and Gordon 1984; Chalmers 1968) and geladas (Dunbar 1984). The behavioural description of male-infant-male interactions is relatively consistent across species: interactions usually last several seconds (or minutes) during which two (rarely more) adult males simultaneously manipulate an infant (lifting it above their heads, nuzzling it, inspecting its genitals, or holding the infant between them) and chatter their teeth (i.e. a fast movement of the jaw that indicates affiliation or submission; Maestripieri 1997). Usually the interaction is initiated by one of the two males that are subsequently involved (hereafter referred

2

49 to as the initiator of the male-infant-male interactions) approaching another male (hereafter

50 referred to as the receiver).

51   The nature of the initiation varies: a) an infant may be picked up by one male (holder)

52 and brought to the other, b) a male without an infant (non-holder) may approach a male with an

53 infant or initiate contact with them, or c) both males may approach or be approached by an

54 infant at the same time and start the interaction simultaneously. In species with extended

55 interactions between males and infants (such as Barbary macaques), male-infant-male

56 interactions may be preceded by dyadic male-infant interaction (e.g. body contact including

57 carrying, cradling, grooming) between the infant and one of the males later involved in a male-

58 infant-male interaction. The role of the infant in the interaction varies from passive, showing

59 some degree of reluctance, or actively seeking the male's presence (Deag 1980; Minge et al.

60 2016).

61   Some males and infants engage in male-infant-male interactions more often than others

62 and individual males may be more likely to participate in interactions with specific infants or

63 with specific male partners (Silk and Samuels 1984; Stein 1984; Taub 1980). The non-random

64 choice of male receivers for male-infant-male interactions led to the formulation of the agonistic

65 buffering hypothesis (Deag and Crook 1971). This hypothesis suggests that, since infants are

66 rarely the target of aggression from adult males, males carry infants to reduce their chances of

67 receiving aggression. Such "extended" protection acts as a "buffer" enabling a male to approach

68 other males, exchange affiliative behaviour with them or reconcile a conflict (Deag 1974; Deag

69 1980). The hypothesis predicts that males prefer to initiate male-infant-male interactions with

70 absolutely or relatively high ranking males, who under other circumstances may be more likely

71 to act aggressively towards subordinates (Deag and Crook 1971). A preference for absolutely

72 or relatively high ranking males as social partners has been observed in olive (*Papio anubis*:

73 Packer 1980) and yellow baboons (*P. cynocephalus*: Stein 1981), bonnet (*Macaca radiata*: Silk

3

and Samuels 1984), Tibetan (*M. thibetana*: Ogawa 1995), and Barbary macaques (*M. sylvanus*: Deag and Crook 1971). Further, the agonistic buffering hypothesis suggests that the occurrence of male-infant-male interactions should be especially high when the tension is increased, such as during and immediately after conflict (Deag and Crook 1971; Paul et al. 1996). However, several studies of different species, including Barbary macaques, do not support this prediction (Ogawa 1995; Smith and Peffer-Smith 1982; Taub 1980).

In Barbary macaques, the use of infants as "anonymous" buffers against aggression has been further questioned with the finding that males prefer to use particular infants. Taub (1980) proposed that male-infant-male interactions represent a subset of male-infant caretaking, which is driven by male effort to invest in his own offspring or maternal relatives (Taub, 1980). However, the main prediction of this hypothesis – that the interacting males share kinship ties with the infant – has never been supported (Ménard et al. 2001; Paul et al. 1996). Instead, several studies support the agonistic buffering hypothesis, which predicts that male-infant-male interactions reduce aggression between males (Deag and Crook 1971). These studies pointed out that males may use male-infant-male interactions to decrease social tension in the long-term; thus, such interactions are not necessarily temporally linked to the current risk of aggression (Paul et al. 1996). Male-infant-male interactions allow males to interact positively with other males, and may thus play an important role in the establishment and maintenance of bonds between males (Kümmerli and Martin 2008; Paul et al. 1996; see also Henkel et al. 2010; Kalbitz et al. 2017), which may help males to avoid conflicts with other males and gain agonistic support in coalitions.

To emphasize the sole or additional function of the establishment and maintenance of bonds between males, some authors refer to male-infant-male interactions as functioning in coalition formation (e.g. Paul et al. 1996) or relationship management (e.g. Kümmerli and

4

Martin 2008) instead of the narrower agonistic buffering function. According to the relationship management hypothesis (the term we use in this study), males prefer to initiate male-infant-male interactions with group males who: 1) are higher ranking than themselves because these are more valuable social partners than lower-ranking males; 2) are close in rank to themselves because they are more accessible than distantly-ranked males and because bonding with them may be especially important (Kummerli and Martin 2008, Paul et al. 1996): Closely ranked individuals are the most likely competitors and aggressive interactions may be more severe between them as the powers of the opponents are more equal (Preuschoft and van Schaik 2000). To avoid aggression, it may be beneficial for closely ranked males to bond with each other and support each other in coalitionary conflicts (Kuester and Paul 1992).

Barbary macaques are a suitable species to test the agonistic buffering and relationship management hypotheses. Males form clear linear agonistic hierarchies, rarely show counter-aggression (Deag 1974; Preuschoft et al. 1998), and form strong affiliative bonds with other males (Berghänel et al. 2010; Young et al. 2013) that predict coalition formation and attenuate physiological stress response when exposed to stressors (Young et al. 2014). As such, we may expect that specific behavioural strategies evolved in this species to establish and maintain these bonds. Males frequently engage in triadic male-infant-male interactions (Paul et al. 1996; Paul 1999; Whitten 1987; Zhao 1996) that often alternate with positive dyadic infant handling interactions, during which males carry, cradle and groom infants (Paul 1999), despite a polygynandrous mating system. A male may hold an infant for up to an hour, during which he may initiate or receive several male-infant-male interactions. Consequently, males often use the same infants in dyadic and male-infant-male interactions (Paul et al. 1996). Male-infant-male interactions and dyadic infant handling interactions are most frequent during the first six months of an infant's life (Deag 1980; Bergänel et al. 1990).

123   Although numerous studies have focused on the distribution of male-infant-male

124   interactions, the understanding of their function is still limited. Some studies have shown that

125   the dominance rank of the males affects the occurrence and role (i.e. initiator or receiver) of the

126   males involved in the male-infant-male interaction (Kümmerli and Martin 2008; Ogawa 1995;

127   Paul et al. 1996), but the exact relationship between male rank and distribution of male-infant-

128   male interactions differs. A preference for higher ranking receivers depends on: a) how

129   individuals were categorised (e.g. Deag 1980 only found an effect of rank when combining

130   individuals of different age classes, such as adults and subadults) and b) the definition of

131   observed behaviour (e.g. Paul et al. 1996 found that the effect of rank was driven specifically

132   by interactions initiated by the infant holder). In Tibetan macaques the dominant male received

133   many more interactions than other males, and the lowest ranking male initiated many more

134   interactions than the other males in the group (Zhao 1996; Bauer et al. 2014), suggesting that

135   the effect of rank may be driven by one or two individuals rather than reflecting a general

136   tendency to initiate interactions with relatively or absolutely high ranking males. In Barbary

137   macaques, the number of triadic interactions received or initiated by a male was not correlated

138   with his dominance rank (Kümmerli and Martin 2008; Paul et al. 1996; Taub 1980) but

139   depended on the rank difference between the two interacting males (Kümmerli and Martin

140   2008; Paul et al. 1996). Although this difference lead to the formulation of the relationship

141   management hypothesis, only a few studies have directly tested how the rank difference

142   between the males affects the number of their male-infant-male interactions.

143   Here we use a large data set on wild Barbary macaques to test a prediction of the

144   agonistic buffering and relationship management hypotheses: that the number of interactions

145   among initiator-infant-receiver triads is affected by the rank of the receiver. Specifically, we

146   predicted that males initiate more interactions with males who are higher-ranking than

147   themselves than with lower-ranking males, as suggested by both hypotheses. From the agonistic

6

148   buffering hypothesis, we predicted that males would initiate more interactions with a male, the

149   higher his absolute position in the hierarchy. From the relationship management hypothesis, we

150   predicted that more male-infant-male interactions would occur between initiators and receivers,

151   the smaller the rank distance between the two males. Based on the suggestion that the effect of

152   the receiver's rank differs for interactions initiated by the infant holder and by a non-holder

153   (e.g. Paul et al. 1996; Taub 1980), we hypothesised that a male who holds an infant (initiator –

154   holder) have a different motivation to initiate male-infant-male interaction than a male who

155   approaches an existing male-infant dyad (initiator – non-holder); holder-initiated interactions

156   should be motivated by the interaction with the male receiver, whereas initiating non-holders

157   may also be attracted to the infant. Thus, we predicted that the two types of interactions are

158   differentially affected by the rank of the males involved and by the relative role of the identity

159   of the receiver and infant involved in the interactions.

160   **METHODS**

161   **Focal observation**

162   We conducted our study in Ifrane National Park in the Middle Atlas Mountains of

163   Morocco (33-240°N, 005-120°W) with Research Permission from the Haut Commissariat aux

164   Eaux et Forêts et à la Lutte Contre la Désertification of Morocco during two consecutive birth

165   seasons (season 1: April–August 2013, season 2: April–September 2014). We followed one

166   wild non-provisioned group (Green Group) of individually recognized and habituated Barbary

167   macaques that consisted of 7 adult (older than 5 years old) males, 1 subadult (5 years old) male,

168   6 adult females (older than 5 years) and 19-20 juvenile individuals. All adult females gave birth

169   in both seasons, resulting in 6 infants in each season; the 12 infants were followed as focal

170   individuals.

7

171   During 2-hour observation sessions we recorded all interactions between infants and

172   males using focal animal sampling (Altmann 1974). For each interaction we recorded the IDs

173   of the individuals involved and the time at the start and end of interactions (using handheld PCs

174   with Pendragon Forms Version 5.1 (© Pendragon Software Cooperation, U.S.A.). The

175   interactions we recorded included dyadic grooming, carrying, cradling, passive body contact

176   between infants and males, and male-infant-male interactions (for more detailed descriptions

177   of the interactions see Kuběnová et al. 2017; Thierry et al. 2000).

178   We recorded the start of a male-infant-male interaction when both males started teeth

179   chattering while touching the infant at the same time. We recorded the end of an interaction

180   when at least one of the involved males stopped teeth chattering and paying attention to the

181   infant for > 5 seconds. We defined a male as an initiator if he started the interaction by

182   embracing the second male or pulling the infant held by the second male and teeth chattering.

183   In about 75% of observations, the initiation also involved the initiator approaching to ≤1.5 m

184   of the other male (i.e. the receiver of the interaction). If it was not clear which male started the

185   interaction or if males approached each other and started body contact simultaneously, we

186   recorded the initiator and receiver as unknown.

187   We defined an infant holder as a male who was in body contact (including carrying,

188   cradling and grooming) with the infant right before the male-infant-male interaction started,

189   and an infant non-holder as a male without an infant before the interaction began. In some cases

190   an infant was not held by either of males later involved in the interaction, and we recorded the

191   holder/non-holder categories as unknown. Based on that information we sorted male-infant-

192   male interactions into three categories (see e.g. Ogawa 1995): 1) interactions initiated by the

193   infant holder; 2) interactions initiated by the non-holder; 3) interactions with unknown

194   initiator/receiver or interactions that were not preceded by body contact between the infant and

195   either the initiator or receiver. We included only interactions in the first two categories (with

8

196   clear initiator and holder role) in the analyses. From these, we further excluded interactions that

197   started <20 seconds after the end of the previous interaction of same male-infant-male triad to

198   avoid temporal pseudo-replication. We consider this interval to be sufficient to separate

199   independent interactions given that male-infant-male interactions often occur in fast sequences

200   even when not-involving same male-infant-male triad. From 89 interactions that started within

201   20 seconds from the termination of previous interaction, only 12 (13 %) were performed by the

202   same male-infant-male triad as the previous interaction; these 12 interactions were excluded

203   from the analyses.

204   **Dominance rank**

205   We recorded *ad libitum* (Altmann 1974) any agonistic behaviour between two males

206   which did not involve third parties and had a clear winner and loser, that is, where one male

207   displayed aggressive behaviour (open month, lunge, chase, bite, slap grab, charge, stare,

208   displacement) and the other male displayed submission (present submission flee, retreat; Deag

209   1974; McFarland and Majolo 2011; Wiper and Semple 2007). For each season separately we

210   entered the recorded data into a winner-loser dominance matrix and calculated normalized

211   David's scores (De Vries et al. 2006). The David's score of 7 adult males was based on 124 and

212   114 interactions in seasons 1 and 2, respectively. In season 1 the David's score ranged from -

213   14.5 to 11.8 (median = 0.8) with 3 (14.3%) dyads with unknown and 1 (4.8%) with a two-way

214   relationship). In season 2 the David's score showed the same range as in the previous season

215   (median = 0.7) with 2 (9.5%) dyads with unknown and 4 (19%) dyads with two-way

216   relationship. The change in David's score between seasons (in absolute values) ranged between

217   0 and 9.4 (median = 5.4) for each male. We also assigned ordinal ranks (the integers from 1

218   given to the male with the highest David's score to 7 given to the male with the lowest David's

219   score). Between the seasons, the ordinal ranks of four males remained same, two males changed

220   by 1 position and one male by 2 positions in the hierarchy.

9

221   To assess the importance of males' rank in their role in male-infant-male interactions

222   we used the following rank-based variables: a) *receiver's David's score*, b) *receiver's ordinal*

223   *rank*, c) *David's score distance* (calculated as the absolute value of the difference between

224   David's score of initiator and receiver), d) *ordinal rank distance* (calculated as the absolute

225   value of the difference between the ordinal rank of the initiator and receiver), and e) *hierarchy*

226   *direction*, a binary variable expressing whether the initiator was lower (UP the hierarchy) or

227   higher-ranking (DOWN the hierarchy) than the receiver.

228   **Statistical analysis**

229   We fitted generalized linear mixed-effect models (GLMM) using the lme4 package

230   (Bates et al. 2014) in R 3.1.1 (R Core Team 2014) with the number of interactions for each

231   initiator-infant-receiver triad as the response variable (N = 1,550), assuming a Poisson

232   distribution for the random variation. As primary random effects we included the identities (ID)

233   of the initiator, infant, and receiver. We entered the total observation time of each infant as an

234   offset term to standardize the number of male-infant-male interactions for the duration of focal

235   observations.

236   As fixed effects we included) 1) the binary variable *interaction type* expressing the type

237   of male-infant-male interactions (interactions initiated by holder versus interactions initiated by

238   the non-holder), 2) season, 3) the relative duration of body contact between infant and holder,

239   because by being in body contact with the infant the male may increase his chances of being

240   approached as a receiver of male-infant-male interaction or using the infant to approach another

241   male as an initiator and 4) body contact between the infant and non-holder because the relative

242   duration of body contact of the male-infant dyad is likely to express the strength of their

243   relationship, which may affect the frequency of interactions that the male initiates and receives

244   as a non-holder (Kuběnová et al. 2017). We calculated both variables as the total time   that the

245   infant and each study male (holder or non-holder) were in body contact during all focal

246   observations of the infant, divided by total time of focal observation of the infant.

247   To test whether male rank affected the distribution of infant holder and non-holder

248   initiated male-infant-male interactions, we used the add1 function in R to test the independent

249   marginal effects of the five rank related predictors (see above). We adjusted the significance

250   for the related five rank predictors in a family-wise manner using Holm's correction (Holm

251   1979) to prevent Type I error inflation. In the final model, we included the two rank related

252   predictors which best predicted the frequency of interactions based on likelihood ratio test

253   (LRTs), the interaction terms between *interaction type* (holder versus non-holder initiated

254   interactions) and one rank-related predictor, and interaction terms between the variable

255   *interaction type* and relative duration of body contact of the infant-holder, and infant-non-

256   holder dyad. We computed confidence intervals to quantify the effects of the predictors using

257   the *confint* function in lme4.

258   To analyse whether the motivation to initiate an interaction differed for a male when

259   holding or non-holding an infant we constructed another set of models, comparing the relative

260   importance of infant and receiver IDs between holder and non-holder initiated interactions.

261   First, we tested whether, for both random effects (*infant* as well as *receiver*), it is more

262   parsimonious (and significantly better) to estimate them separately for the two types of male-

263   infant-male interactions. If so, we can conclude that there is a significant difference in the effect

264   of particular identity (*infant* or *receiver*) between the two interaction types. Using a likelihood-

265   ratio test (LRT), we compared a null model estimating random effects *infant* and *receiver*

266   jointly for both types of interactions with models using separate estimates for each interaction

267   type. Second, after finding that the models with separate estimates were more parsimonious,

268   we compared the effect sizes (measured as standard deviations, representing the variation

11

269 among the levels of factor coding the respective random factors) of both random effects

270 estimated separately for both types of interactions.

271   For each constructed model we checked homoscedasticity and distribution of residuals

272 using regression diagnostic plots.

273 **ETHICAL NOTE**

274   Our study was observational and non-invasive. All procedures performed in this study

275 were in accordance with the standards of the International Primatological Society for the use

276 of non-human primates in research and adhered the legal requirements of Morocco.

277 **RESULTS**

278   In 1,430 hours of focal observation of 12 infants (50 – 174 hours per infant, median =

279 127, SD = 40) we recorded 2,135 male-infant-male interactions. From these, we excluded 568

280 interactions with unclear initiator / receiver role, 5 interactions that were initiated by an infant

281 approaching both males at the same time and 12 interactions that started <20 seconds after the

282 end of the previous interaction of same male-infant-male triad., giving 1,550 interactions for

283 analysis (Tables 1 & 2).

284 *Table 1. Descriptive statistics for male-infant-male interactions in Barbary macaques based on*

285 *the individuals involved. Data collected April–August 2013 and April–September 2014, Ifrane*

286 *National Park, Middle Atlas, Morocco*

		Per infant	**Initiated by each male**	**Received by each male**	**Per male-male dyad**
Holder initiated	Range	6-157	47-196	54-189	5-75

N=726 (47%)	Median	64	67	86	30
	SD	50	57	54	20
Non-holder initiated	Range	2-150	43-169	64-177	5-109
N=824 (53%)	Median	84	133	124	31
	SD	54	48	40	27

287

288 *Table 2.*

289 *Number of male-infant-male interactions in Barbary macaques based on type. Data collected*

290 *April–August 2013 and April–September 2014, Ifrane National Park in the Middle Atlas,*

291 *Morocco*

.	Interactions together	Up the hierarchy	Down the hierarchy	Holder initiated	Non-holder initiated
Holder initiated	726	489 (67%)	237 (33%)	-	-
Non-holder initiated	824	418 (51%)	406 (49%)	-	-
Hierarchy direction UP	907	-	-	489 (54%)	418 (46%)

Hierarchy direction DOWN	643	-	-	237 (37%)	406 (63%)

292

293 The model improved on the null model after independent addition of the variables *hierarchy*

294 *direction* (UP versus DOWN the hierarchy) and *ordinal rank distance* The model including

295 these two variables further improved when adding the interaction term between *interaction type*

296 (holder versus non-holder initiated interactions) and *hierarchy direction* and between *hierarchy*

297 *direction* and relative duration of body contact of the infant-holder dyad (Table 3)

298 *Table 3. Result of the likelihood ratio test (LRT) testing the effect of predictors on the number*

299 *of interactions among initiator-infant-receiver triads in Barbary macaques (April–August 2013*

300 *and April–September 2014, Ifrane National Park, Middle Atlas, Morocco).* For all predictors

301 df=1.

	χ^2	df	P
Hierarchy direction	13.401	1	**< 0.001**
Ordinal rank distance	6.929	1	<u>**0.008**</u>
David's score of the receiver	0.110	1	0.740
David's score distance	0.463	1	0.496

Interaction type: hierarchy direction	45.662	1	**< 0.001**
Interaction type: Body contact infant-holder	7.607	1	**0.005**
Interaction type: Body contact infant-non-holder	3.783	1	0.052
Ordinal rank distance: Interaction type	0.368	1	0.544
Ordinal rank distance: Hierarchy direction	1.399	1	0.237

302

303   In the resulting final model, the *hierarchy direction*, *interaction type* and their

304 interaction term had a significant effect on the standardized number of interactions, as did the

305 *ordinal rank distance,* duration of body contact between the holder and the infant, and between

306 the non-holder and the infant and interaction terms between both body contacts and *interaction*

307 *type* (Table 4). The main effect of the variable *type* suggests that the frequency of non-holder

308 initiated interactions was 1.43-2.18 times higher than frequency of holder initiated interactions.

309 The main effect of *hierarchy direction* suggests that the frequency of interactions was 1.64-

310 2.50 times higher when the initiator was lower ranking that the receiver (direction was UP the

15

hierarchy) compared to the frequency of interactions initiated by the higher ranking of the two
male (DOWN the hierarchy). However, the interaction term between *hierarchy direction* and
interaction type shows that this concerned only interactions initiated by the holder. For male-
infant-male interactions initiated by the non-holder, the main effect of *hierarchy direction*
(represented by the estimated regression coefficient +703 in Table 4) was compensated by the
interaction term (the estimated regression coefficient -0.708 in Table 4). The effect of
dominance rank, thus, differed for the two types of male-infant-male interactions. When the
initiator held the infant, he was more likely to choose a receiver that was higher ranking than
himself. However, when a male initiated the interaction without an infant (i.e. by approaching
an infant holder) he did not choose the receiver based on his relative rank (Fig. 1).

*Table 4. Summary of the final parameters in a GLMM explaining the number of interactions
among initiator-infant-receiver triads in Barbary macaques (April–August 2013 and April–
September 2014, Ifrane National Park, Middle Atlas, Morocco).*

	Estimate	SE	z	Pr(>IzI)	95% CI
Intercept	-3.362	0.398	-8.452	<0.001	-4.208; -2.557
Season 2014	0.363	0.416	0.874	0.382	-0.525; 1.295
Body contact infant-holder	34.606	1.381	25.060	**<0.001**	**31.906; 37.337**
Body contact infant-non-holder	24.421	1.428	17.108	<0.001	**21.641; 27.221**
Type non-holder initiated	0.569	0.107	5.312	**<0.001**	**0.359; 0.780**
Hierarchy direction UP	0.703	0.107	6.561	**<0.001**	**0.493; 0.915**
Ordinal rank distance	-0.53	0.022	-2.454	**0.014**	**-0.096; -0.010**

|					
Type non-holder initiated: Hierarchy direction UP	-0.708	0.105	-6.713	**<0.001**	**-0.916; -0.501**
Type non-holder initiated: Body contact infant-holder	-4.906	1.628	-3.014	**0.003**	**-8.076; -1.774**
Type non-holder initiated: Body contact infant-non-holder	4.931	1.717	2.872	**0.004**	**1.636; 8.221**

324

325   *Fig. 1*
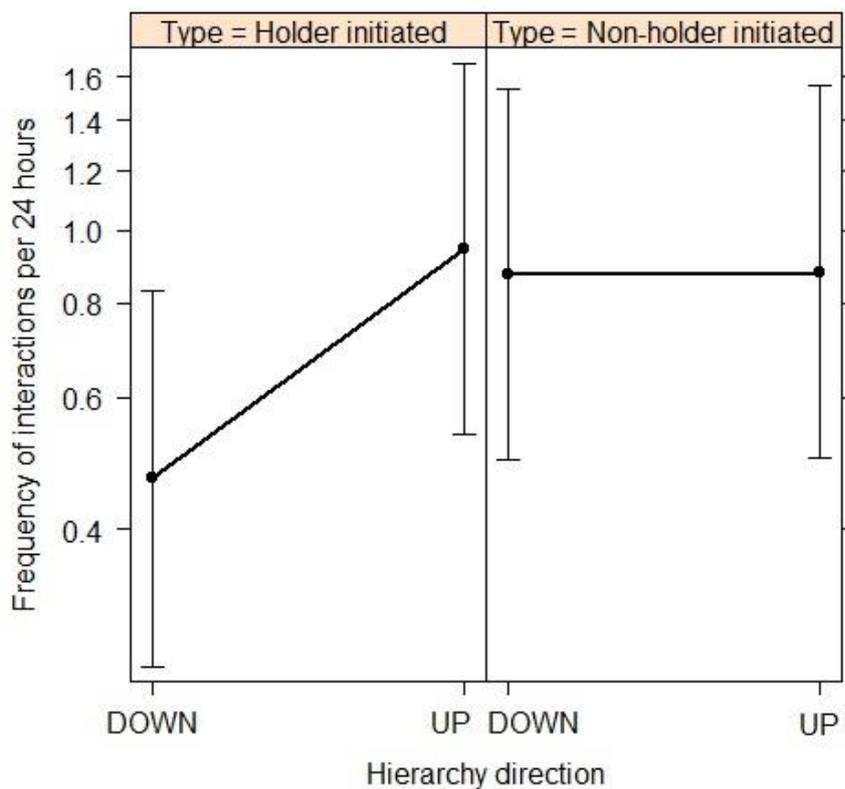
326

327   *Fig. 1. Effect of the interaction between hierarchy direction and type of male-infant-male*

328   *interactions on the frequency of interactions in initiator-infant-receiver triads. Data for*

329   *Barbary macaques, April–August 2013 and April–September 2014, Ifrane National Park,*

The main effect of the variable *ordinal rank distance* suggests that the chance that a male was chosen as a receiver of an interaction increased by 1-9% for every step that males were closer in ordinal ranks (Table 4, Fig. 2). Body contact between holder and infant as well as between non-holder and infant predicts both interactions initiated by the holder and the non-holder, although body contact between holder and infant more strongly affects holder-initiated interactions, whereas body contact between infant and non-holder more strongly affects non-holder initiated interactions.
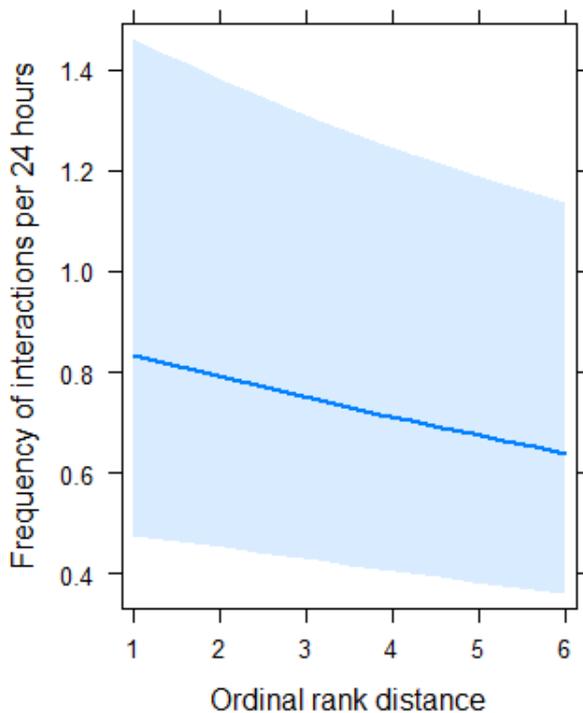
Fig. 2

Fig. 2. Effect of the difference between receiver and initiator ordinal dominance ranks on the frequency of interactions among initiator-infant-receiver triads in Barbary macaques, April–August

18

2013 and April–September 2014, Ifrane National Park, Middle Atlas, Morocco. 95-percent pointwise

344 *confidence intervals are drawn around the estimated effect.*

345   When assessing the effect of infant and receiver IDs on the distribution of holder and

346 non-holder initiated interactions, models with random effect *infant* and *receiver,* estimated

347 separately for the two types of interactions, were both significantly better ($\chi^2 = 6.723$, df = 2, P

348 = 0.010 for *infant*, $\chi^2 = 25.990$, df = 2, P < 0.001 for *receiver*) than models where the random

349 effects were estimated with the observations of either interaction type pooled. In the final model

350 (Table 5), estimating random effects of *infant* and *receiver* separately for the two interaction

351 types, we found that (a) random effects for *infant* were greater than for *receiver*, but also (b) the

352 random effect for *infant* was greater for non-holder initiated male-infant-male interactions than

353 for holder initiated interactions while the random effect for *receiver* was greater for holder

354 initiated than for non-holder initiated interactions, suggesting that the identity of the infant may

355 play a different role in the two types of interaction, and male motivation to initiate an interaction

356 depends on whether an initiator has an infant or not (Table 5).

357 *Table 5. Estimation of random effects (measured as standard deviations) of infant and*

358 *receiver separately for two male-infant-male interaction types in Barbary macaques, April–*

359 *August 2013 and August–September 2014, Ifrane National Park, Middle Atlas, Morocco*

360

Groups	Name	Random effect size
Infant	*Type* holder initiated interactions	0.569
	Type non-holder initiated interactions	0.757
Initiator	(Intercept)	0.421
Receiver	*Type* holder initiated interactions	0.456

Type non-holder initiated interactions	0.373

DISCUSSION

361

362   Our results suggest that receivers of male-infant-male interactions are chosen based on

363   their rank. We found that an initiator was more likely to choose: i) a receiver that was higher

364   ranking than himself than a lower ranking receiver, and ii) a closely ranked receiver over a

365   distantly-ranked receiver. We also found that the effect of receivers' rank and the relative role

366   of the infant's and the receiver's identities differed in holder and non-holder initiated

367   interactions.

368   The importance of relative rank in the distribution of male-infant-male interactions

369   supports the prediction of the agonistic buffering and relationship management hypotheses, that

370   the initiator chooses a partner who represents the greatest potential threat when being

371   approached. We confirmed the result of previous studies of Barbary macaques (Deag 1980;

372   Paul et al. 1996; Taub 1980) and other macaque species (Ogawa 1995; Silk and Samuels 1984)

373   that males preferred to interact with males that were higher ranking than themselves than those

374   that were lower ranking than themselves.

375   Results on the importance of the absolute rank of the male for male-infant-male

376   interactions are inconsistent and differ among species. Previous studies of Barbary macaques

377   found that the number of triadic interactions received or initiated was not correlated with male

378   dominance rank (Kümmerli and Martin 2008; Paul et al. 1996; Taub 1980) but depended on the

379   rank difference between the males (Kümmerli and Martin 2008; Paul et al. 1996). In contrast,

380   in Tibetan macaques, high-ranking males were more frequently chosen as recipients in bridging

381   interactions than low-ranking males were (Ogawa 1995). In bonnet macaques male dominance

382   rank was significantly negatively correlated with the number of triadic interactions received but

20

unrelated to the number of triadic interactions initiated (Silk and Samuels 1984). Supporting previous studies of Barbary macaques (Kümmerli and Martin 2008; Paul et al. 1996; Taub 1980) males in our study did not choose the receivers based on their absolute rank.

The importance of the rank distance between males in male-infant-male interactions is emphasized in the relationship management hypothesis (Paul et al 1996). This hypothesis was originally suggested to explain male-infant-male interactions in Barbary macaques, but its support remains scarce. (Kümmerli and Martin 2008; Paul et al. 1996). Male Barbary macaques form strong affiliative bonds with other males (Berghänel et al. 2010; Young et al. 2013) that predict coalition formation (Berghänel et al. 2011). Given the high occurrence of coalitionary conflicts among male Barbary macaques (Bissonnette et al. 2009; Widdig et al. 2000), males may use male-infant-male interactions to bond with closely ranking males. Closely ranking individuals are the most likely and dangerous competitors in conflict (Preuschoft and van Schaik 2000; Silk 1994), but may also be preferential allies in coalitionary conflicts. A male may be reluctant to provide support to a much lower-ranking recruiter, who cannot effectively reciprocate in future. It may be thus advantageous for a recruiter to target closely ranking males, whose support is relatively effective and also likely (Paul et al 1996, Silk 1994). These criteria for the choice of specific social partners govern the distribution of grooming (Seyfarth 1976), affect the formation of social bonds (Mitani 2009) and the distribution of aggressive interactions (Silk 1994).

Our study confirmed that males are more likely to initiate male-infant-male interactions with other males the closer their position in the hierarchy was. However, we also found that this relationship depended on the variable used to describe a male's position in the hierarchy. A preference for closely ranked males emerged when assessing males' position in the hierarchy as their position in the hierarchy, but not when using David's scores. This might suggest that

21

408   ordinal ranks measure better than David's score how males assess their relative position in the

409   hierarchy. Given the high consistency of dominance-submissive interactions between dyads

410   (only xx % of reversals), the distribution of David's scores is mainly determined by the

411   frequency of interactions of different male-male dyads. It is possible that males choose their

412   social partners based on the general patterns of the interactions of the dyads (who in the dyad

413   is dominant / submissive) but the frequency of the dominant-submissive interactions is less

414   important. It is also possible that the distribution of David's scores is affected by sampling bias

415   (i.e. ad libitum data collection of dominance-submissive interactions between males).

416   We also found that the preference for relatively higher ranking receivers applied only to

417   interactions where the initiator is also the holder of the infant. Previous studies have suggested

418   that interactions may be categorised according to whether the male initiating the interaction is

419   a holder or non-holder (Collins 1986; Ogawa 1995; Paul et al. 1996; Zhao 1996), and that the

420   effect of rank may differ for those categories. Infant holder males may preferably initiate

421   interactions with higher ranking males than themselves (Paul et al. 1996), and males who

422   initiate interactions with relatively higher ranking males, may be mainly infant holders (Taub

423   1980). However, the potential differences in the underlying patterns have rarely been

424   thoroughly tested.

425   The lack of an effect of rank in interactions initiated by a non-holder might seem to

426   contradict the agonistic buffering and relationship management hypotheses (Deag 1980; Paul

427   et al. 1996). The original formulation of the agonistic buffering hypothesis describes "the

428   deliberate use of a baby as a "buffer" in a situation where an approach without the buffer would

429   lead to the increased likelihood of an aggressive response by a dominant male" (Deag 1980, p.

430   55); thus, this hypothesis implies a focus on interactions initiated by the infant holder.

431   Formulated to broaden the context of male-infant-male interactions, the relationship

432   management hypothesis seeks to explain both types of interactions (initiated by holder and non-

22

holder), which can both serve males to bond with others. As bonding with lower ranking males

may also be profitable (e.g. in the context of coalition formation: Bissonnette et al. 2009;

Widdig et al. 2000), the relationship management hypothesis does not preclude interactions

where an initiator is higher ranking compared to a receiver. However, based on the prediction

that bonds with higher ranking males are more beneficial (e.g. stronger coalition partners),

males should be more interested in bonding with males who are higher ranking than themselves

than with males who are lower ranking than themselves, and interactions going up the hierarchy

should thus prevail, regardless of who holds the infant (Paul et al. 1996). However, only infant

holders chose higher ranking males as receivers of interactions in our study.

The different effect of rank in the two types of interactions deserves some interpretation.

First, it is possible that the difference is the results of constrains, such as limited access to

different males and infants. For example, infants are limited resources (Kümmerli and Martin

2008) and carrying infants may be costly (Henkel et al. 2010), so an infant holder may want to

use the infant "strategically" and will tend to initiate interactions specifically with higher

ranking individuals. In contrast non-holders may be less selective, willing to invest in bonding

with any males, even lower ranking ones. Second, other mechanisms besides the relationship

management may explain male-infant-male interactions and slightly different explanations may

apply to the two types of interactions.

The agonistic buffering and relationship management hypotheses assume that a male

always initiates an interaction to interact with another male. However, in non-holder initiated

interactions, the initiator may be attracted by both the receiver and the infant. If this is the case,

the relative roles of infant identity and male identity should differ in both types of interactions.

When comparing random effects of infants and receiver across both types of interactions, we

found that the random effect for *infant* was greater for male-infant-male interactions initiated

by non-holder than for those initiated by holder, while the random effect for *receiver* was

23

458   greater for holder-initiated interactions than for non-holder initiated interactions. Although this

459   does not directly compare the relative importance of the predictors between the two types of

460   interactions, it suggests that whereas a male holding an infant chooses a receiver based on his

461   identity, rank and the strength of the relationship with the infant (Kuběnová et al. 2017), for an

462   initiating non-holder, the identity of an infant also motivates his approach. This suggests that

463   males are attracted to specific infants and at least some male-infant-male interactions may be

464   driven by such attraction, rather than male motivation to interact with another male.

465   In summary, our results suggest that relationship management among males is an

466   effective, but non-exclusive explanation for male-infant-male interactions in Barbary macaques

467   and that the motivation to initiate interaction may differ depending on whether the infant is held

468   by the initiator or receiver of the interaction. Males holding an infant are more likely to interact

469   with males who are higher ranking than and closely ranked to themselves, suggesting that

470   relationship management is important during holder initiated interactions. However, males do

471   not prefer to initiate interactions with higher ranking males when in the role of non-holder. We

472   suggest that this is because non-holders initiate interactions to interact with other males (as

473   reflected by the preference for closely ranked receivers) but also with the infant. This

474   combination of motivations may compromise the non-holders's choice of higher-ranking

475   receivers. The role of infants in the initiators' choice of holder-infant dyads is supported by our

476   finding that the role of infant's identity was greater for non-holder initiated male-infant-male

477   interactions than for holder initiated interactions. Heterogeneity of male-infant-male interactions

478   may explain some ambiguity in conclusions of previous research on male motivation to get

479   involved in male-infant-male interactions, because the role of rank may be obscured if we

480   consider all interactions together. Future studies of this subject should pay attention to different

481   types of interactions (e.g. initiated by holder versus non-holder) and to their broader context

482   (e.g. which male-male or male-infant interactions preceded or followed each male-infant-male

24

interaction). Explaining the function of male-infant-male interactions in Barbary macaques but also in other primate species may contribute to our understanding of the complexity and evolution of other types of male infant care in different taxa, including human.

BIBLIOGRAPHY

Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour*, *49*(3), 227–266.

Bauer, B., Sheeran, L. K., Matheson, M. D., Li, J.-H., & Wagner, R. S. (2014). Male Tibetan macaques'(Macaca thibetana) choice of infant bridging partners. *Zoological Research* *35*(3): 222-230.

Berghänel, A., Schülke, O., & Ostner, J. (2010). Coalition formation among Barbary macaque males: the influence of scramble competition. *Animal Behaviour*, *80*(4), 675–682.

Berghänel, A., Ostner, J., Schröder, U., & Schülke, O. (2011). Social bonds predict future cooperation in male Barbary macaques, Macaca sylvanus. *Animal Behaviour*, *81*(6), 1109–1116.

Bernstein, I. S., & Cooper, M. A. (1998). Ambiguities in the behavior of Assamese macaques. *Am J Primatol*, *45*, 170–171.

Bissonnette, A., de Vries, H., & van Schaik, C. P. (2009). Coalitions in male Barbary macaques, Macaca sylvana: strength, success and rules of thumb. *Animal Behaviour*, *78*(2), 329–335.

Busse, C. D., & Gordon, T. P. (1984). Infant carrying by adult male mangabeys (Cercocebus atys). *American Journal of Primatology*, *6*(3), 133–141.

Busse, C., & Hamilton, W. J. (1981). Infant carrying by male chacma baboons. *Science*, *212*(4500), 1281–1283.

Chalmers, N. R. (1968). The social behaviour of free living mangabeys in Uganda. *Folia primatologica*, *8*(3–4), 263–281.

Clutton-Brock, T. H., & Isvaran, K. (2006). Paternity loss in contrasting mammalian societies. *Biology Letters*, *2*(4), 513–516.

Collins, D. A. (1986). Interactions between adult male and infant yellow baboons (Papio c. cynocephalus) in Tanzania. *Animal Behaviour*, *34*(2), 430–443.

De Vries, H., Stevens, J. M., & Vervaecke, H. (2006). Measuring and testing the steepness of dominance hierarchies. *Animal Behaviour*, *71*(3), 585–592.

de Waal, F. B., van Hooff, J. A., & Netto, W. J. (1976). An ethological analysis of types of agonistic interaction in a captive group of Java-monkeys (Macaca fascicularis). *Primates*, *17*(3), 257–290.

Deag, J. M. (1974). A study of the social behavior and ecology of the wild Barbary macaque, Macaca sylvanus, L. 1758. *Unpublished doctoral Dissertation, University of Bristol*.

Deag, J. M. (1980). Interactions between males and unweaned Barbary macaques: Testing the agonistic buffering hypothesis. *Behaviour*, 54–81.

Deag, J. M., & Crook, J. H. (1971). Social behaviour and 'agonistic buffering'in the wild barbary macaque Macaca sylvana L. *Folia Primatologica*, *15*(3–4), 183–200.

Dunbar, R. I. M. (1984). Infant-use by male gelada in agonistic contexts: Agonistic buffering, progeny protection or soliciting support? *Primates*, *25*(1), 28–35.

Estrada, A., & Sandoval, J. M. (1977). Social relations in a free-ranging troop of stumptail macaques (Macaca arctoides): Male-care behaviour I. *Primates*, *18*(4), 793–813.

Henkel, S., Heistermann, M., & Fischer, J. (2010). Infants as costly social tools in male Barbary macaque networks. *Animal Behaviour*, *79*(6), 1199–1204.

530 Holm, S. (1979). A simple sequentially rejective multiple test procedure. *Scandinavian*

531 *Journal of Statistics*, *6*, 65-70.

532 Hrdy, S. B. (1976). Care and exploitation of nonhuman primate infants by conspecifics other

533 than the mother. *Advances in the Study of Behavior*, *6*, 101–158.

534 Kalbitz, J., Schülke, O., & Ostner, J. (2017). Triadic male-infant-male interaction serves in

535 bond maintenance in male Assamese macaques. *PloS one*, *12*(10), e0183981.

536 Kleiman, D. G., & Malcolm, J. (1981). The evolution of male parental investment in

537 mammals. In D. J. Gubernick, O. H. Klopfer (Eds)*, Parental care in mammals* (pp.

538 347–387). New York: Plenum Press.

539 Kleindorfer, S., & Wasser, S. (2004). Infant handling and mortality in yellow baboons (Papio

540 cynocephalus): evidence for female reproductive competition? *Behavioral Ecology*

541 *and Sociobiology*, *56*(4), 328–337.

542 Kuběnová, B., Konečná, M., Majolo, B., Šmilauer, P., Ostner, J., & Schülke, O. (2017).

543 Triadic awareness predicts partner choice in male–infant–male interactions in Barbary

544 macaques. *Animal cognition*, *20*(2), 221–232.

545 Kümmerli, R., & Martin, R. D. (2008). Patterns of infant handling and relatedness in Barbary

546 macaques (Macaca sylvanus) on Gibraltar. *Primates*, *49*(4), 271–282.

547 Maestripieri, D. (1994). Social structure, infant handling, and mothering styles in group-living

548 Old World monkeys. *International Journal of Primatology*, *15*(4), 531–553.

549 Maestripieri, D. (1997). Gestural communication in macaques: Usage and meaning of

550 nonvocal signals. *Evolution of communication*, *1*(2), 193–222.

551

552 McFarland, R., & Majolo, B. (2011). Grooming coercion and the post-conflict trading of

553 social services in wild Barbary macaques. *PLoS One*, *6*(10), e26893.

27

554   Ménard, N., von Segesser, F., Scheffrahn, W., Pastorini, J., Vallet, D., Gaci, B., et al. (2001).

555   Is male-infant caretaking related to paternity and/or mating activities in wild Barbary

556   macaques (Macaca sylvanus)? *Comptes rendus de l'Académie des sciences. Série III,*

557   *Sciences de la vie*, *324*(7), 601.

558   Minge, C., Berghänel, A., Schülke, O., & Ostner, J. (2016). Patterns and Consequences of

559   Male–Infant Relationships in Wild Assamese Macaques (Macaca assamensis).

560   *International journal of primatology*, *37*(3), 350–370.

561   Mitani, J. C. (2009). Male chimpanzees form enduring and equitable social bonds. *Animal*

562   *Behaviour*, *77*(3), 633–640.

563   Ogawa, H. (1995). Bridging behavior and other affiliative interactions among male Tibetan

564   macaques (Macaca thibetana). *International journal of primatology*, *16*(5), 707–729.

565   Packer, C. (1980). Male care and exploitation of infants in Papio anubis. *Animal Behaviour*,

566   *28*(2), 512–520.

567   Paul, A. (1999). The socioecology of infant handling in primates: Is the current model

568   convincing? *Primates*, *40*(1), 33–46.

569   Paul, A., Kuester, J., & Arnemann, J. (1996). The sociobiology of male-infant interactions in

570   Barbary macaques, Macaca sylvanus. *Animal Behaviour*, *51*(1), 155–170.

571   Preuschoft, S., & van Schaik, C. P. (2000). Dominance and communication. In F. Aureli, F.

572   B. M. de Waal (Eds), *Natural Conflict Resolution* (pp. 77–105). Berkeley: University

573   of California Press.

574   Schino, G., Speranza, L., Ventura, R., & Troisi, A. (2003). Infant handling and maternal

575   response in Japanese macaques. *International journal of primatology*, *24*(3), 627–638.

576   Schülke, O., Bhagavatula, J., Vigilant, L., & Ostner, J. (2010). Social bonds enhance

577   reproductive success in male macaques. *Current Biology*, *20*(24), 2207–2210.

578   Seyfarth, R. M. (1976). Social relationships among adult female baboons. *Animal Behaviour*,

579   *24*(4), 917–938.

580   Silk, J. B. (1994). Social relationships of male bonnet macaques: male bonding in a

581   matrilineal society. *Behaviour*, *130*(3), 271–291.

582   Silk, J. B., & Samuels, A. (1984). Triadic interactions among Macaca radiata: Passports and

583   buffers. *American Journal of Primatology*, *6*(4), 373–376.

584   Smith, E. O., & Peffer-Smith, P. G. (1982). Triadic interactions in captive Barbary macaques

585   (Macaca sylvanus, Linnaeus, 1758):"Agonistic buffering"? *American Journal of*

586   *Primatology*, *2*(1), 99–107.

587   Smuts, B. B. (1985). *Sex and friendship in baboons*. Aldine.

588   Stein, D. M. (1981). *The nature and function of social interactions between infant and adult*

589   *male yellow baboons (Papio cynocephalus)*. PhD thesis, University of Chicago.

590   Stein, D. M. (1984). *The sociobiology of infant and adult male baboons* (Vol. 5). Ablex

591   Publishing Corporation.

592   Taub, D. M. (1980). Testing the 'agonistic buffering'hypothesis. *Behavioral Ecology and*

593   *Sociobiology*, *6*(3), 187–197.

594   Taub, D. M. (1984). Male caretaking behavior among wild Barbary macaques (Macaca

595   sylvanus). In D. M. Taub (Ed.), Primate Paternalism (pp 20–55). New York, Van

596   Nostrand Reinhold.

597   Thierry, B. (2000). Covariation of conflict management patterns across macaque species.

In F. Aureli, F. B. M. de Waal (Eds), *Natural Conflict Resolution* (pp. 106–128). Berkeley: University of California Press.

Thierry, B., Bynum, E., Baker, S., Kinnaird, M., Matsumura, S., Muroyama, Y., Watanabe, K. (2000). The social repertoire of Sulawesi macaques. *Primate Research*, *16*, 203–226.

Trivers, R. (1972). *Parental investment and sexual selection* (Vol. 136). Biological Laboratories, Harvard University.

Van Schaik, C. P., & Paul, A. (1996). Male care in primates: does it ever reflect paternity? *Evolutionary Anthropology: Issues, News, and Reviews: Issues, News, and Reviews*, *5*(5), 152–156.

Whitten, P. L. (1987). Infants and adult males. *Primate societies*. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth & T. T. Struhsaker (Eds.), Primate Societies (pp 343–357). Chicago: University of Chicago Press.

Widdig, A., Streich, W. J., Tembrock, G., & others. (2000). Coalition formation among male Barbary macaques(Macaca sylvanus). *American Journal of Primatology*, *50*(1), 37–51.

Wiper, S. M., & Semple, S. (2007). The function of teeth chattering in male Barbary macaques (Macaca sylvanus). *American Journal of Primatology*, *69*(10), 1179–1188.

Woodroffe, R., & Vincent, A. (1994). Mother's little helpers: patterns of male care in mammals. *Trends in Ecology & Evolution*, *9*(8), 294–297.

Young, C., Hähndel, S., Majolo, B., Schülke, O., & Ostner, J. (2013). Male coalitions and female behaviour affect male mating success independent of dominance rank and female receptive synchrony in wild Barbary macaques. *Behavioral Ecology and Sociobiology*, *67*(10), 1665–1677.

621   Young, C., Majolo, B., Heistermann, M., Schülke, O., & Ostner, J. (2014). Responses to

622   social and environmental stress are attenuated by strong male bonds in wild macaques.

623   *Proceedings of the National Academy of Sciences*, *111*(51), 18195–18200.

624   Zhao, Q.-K. (1996). Male-infant-male interactions in Tibetan macaques. *Primates*, *37*(2),

625   135–143.