



HAL
open science

Social attention biases in juvenile wild vervet monkeys: implications for socialisation and social learning processes

Mathilde Grampp, Cédric Sueur, Erica van de Waal, Jennifer Botting

► **To cite this version:**

Mathilde Grampp, Cédric Sueur, Erica van de Waal, Jennifer Botting. Social attention biases in juvenile wild vervet monkeys: implications for socialisation and social learning processes. *Primates*, 2019, 60 (3), pp.261-275. 10.1007/s10329-019-00721-4 . hal-02194992

HAL Id: hal-02194992

<https://hal.science/hal-02194992v1>

Submitted on 7 Dec 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 **Social attention biases in juvenile wild vervet monkeys; implications for socialisation**
2 **and social learning processes.**

3
4 **Mathilde Grampp^{1,2*}, Cédric Sueur³, Erica van de Waal^{2,4°} & Jennifer Botting^{2,5°}**

5 ¹ Université de Strasbourg, Faculté des Sciences de la Vie, 28 rue Goethe, 67000 Strasbourg, France, ² Inkawu
6 Vervet Project, KwaZulu-Natal, South Africa, ³ Université de Strasbourg, CNRS, IPHC UMR 7178, F-67000
7 Strasbourg, France, ⁴ Department of Ecology and Evolution, University of Lausanne, ⁵ School of Psychology &
8 Neuroscience, University of St Andrews

9 *Corresponding author e-mail address: mathilde.grampp@outlook.fr

10 ° Joint last authors

11
12 **Acknowledgements**

13 We are grateful to the late K. van der Walt for permission to conduct the study in his reserve. The authors would
14 like to thank especially M. Bodin for collecting the focal data in one of the groups (NH), in addition of the other
15 students and volunteers for their assistance in long term data collection at IVP, and the on-site manager A. van
16 Blerk, for his great support. We thank A. Whiten for his useful comments on the manuscript.

17
18 **Abstract**

19 The concept of directed social learning predicts that social learning opportunities for an individual will
20 depend on social dynamics, context and demonstrator identity. However, few empirical studies have examined
21 social attention biases in animal groups. Sex-based and kinship-based biases in social learning and social attention
22 towards females have been shown in a despotic and female philopatric primate: the vervet monkey (*Chlorocebus*
23 *pygerythrus*). The present study examined social attention during the juvenile period. Social attention was
24 recorded through 5-min focal observations during periods of natural foraging. Kin emerged as the most important
25 focus of social attention in juveniles, intensified by biased spatial proximity towards matrilineal related members.
26 The highest-ranking conspecifics were more frequently observed by juveniles than low-ranking ones.

27 Additionally, younger and orphaned juveniles showed higher levels of social attention overall, compared to other
28 age categories. No effect of juvenile's hierarchical rank was detected, suggesting that the social attention variation
29 recorded reflects different biases and stages of social learning and socialisation, rather than social anxiety. Juvenile
30 females tended to exhibit the dominance-based bias more strongly than did males. This might be explained by a
31 greater emphasis on attaining social knowledge during juvenile socialisation in the philopatric sex. Moreover,
32 despite a preferred association between juveniles, social attention was not more often directed to adults, suggesting
33 that adults may be still more often chosen as target of attention independently of their dominance ranks.

34 **Keywords:** Juvenile socialisation, rank acquisition, female philopatry, social learning biases, early social
35 experience, social network.

36

37 **Introduction**

38 Directing visual attention at conspecifics, defined as “social attention”, may serve a number of functions
39 in animals, including group formation and socialisation, or may indicate social anxiety or sexual interest (Chance
40 1967; Caine and Marra 1988; Alberts 1994; Watts 1998; Hrdy and Whitten 1987). Social attention also has an
41 important role in social learning (Heyes 1994; Lonsdorf 2005). Social learning is learning “influenced by
42 observation, or interaction with, another animal (typically a conspecific) or its products” (Heyes 1994, pg 207).
43 Social learning has been found in a wide range of taxa including invertebrates, fish, birds, mammals and primates
44 (Leadbeater and Chittka 2007; Reader et al. 2003; Dawson and Foss 1965; Thornton and Malapert 2009; Dindo
45 et al. 2008; Whiten 2017). Social learning provides information not only about the physical environment (Galef
46 and Whiskin 2008; Magrath and Bennett 2012; Feeney and Langmore 2013), but also about the social
47 environment, and thus has an important function in communication and decision-making (Dugatkin and Godin
48 1993; Cheney and Seyfarth 1990; Anderson et al. 2013; de Waal 1992; Whiten and Byrne 1988). Behavioural
49 traditions within groups appear via social learning (*Pan troglodytes*, Whiten et al. 1999) and therefore studying
50 social attention biases and their effect upon social learning contribute to an understanding of the evolution and
51 dynamics of cultural traits in animal societies (Tomasello 1990).

52 Social attention, and thus opportunities for social learning and patterns of information diffusion, is
53 dependent upon the social structure of a group (Coussi-Korbel and Fragaszy 1995). A number of studies have
54 shown that patterns of behaviour diffusion within a group may vary according to the frequency of demonstration

55 of the behaviour and/or the social relationship between demonstrator and observer (network centrality: Sueur et
56 al. 2011; Dubosq et al. 2016; Claidière et al. 2013; social rank of the demonstrator: Tanaka 1995; observer and
57 demonstrator sexes: Agostini and Visalberghi 2005; affiliation patterns, mother-offspring: Jaeggi et al. 2010;
58 Perry 2009; Lonsdorf 2005, Schuppli et al. 2016; siblings: Schwab et al. 2008a, but see Schwab et al. 2008b).

59 However, directed social learning (Coussi-Korbel and Fragaszy 1995) posits that social attention, and
60 thus social learning, is biased towards specific individuals within a group. Theoreticians suggest that to gather the
61 most useful information, individuals should be selective in when and from whom they obtain social information
62 (Boyd and Richerson 1985). Copying the most successful individuals would theoretically be an adaptive bias
63 (Boyd and Richerson 1985; Laland 2004), allowing the individual to copy the most efficient behaviour.
64 Individuals could also use indirect cues, such as health, size, age, reproductive success, social rank and philopatric
65 sex, which may provide proxies for success (McComb et al. 2001; Brent et al. 2015; Wrangham 1981). Such
66 social learning biases have been found in some species based on the cues of size (*Pungitius pongitius*, Duffy et
67 al. 2009), age (*P. t. verus*, Biro et al. 2003; *Callithrix jacchus*, Schiel and Huber 2006) and sex (*Chlorocebus*
68 *aethiops pygerythrus*, van de Waal et al. 2010; Schiel and Huber 2006). Additionally, studies have found a
69 dominance-based bias in social learning in hens (*Gallus gallus domesticus*, Nicol and Pope 1999; Nicol 2006) and
70 captive chimpanzees (Horner et al. 2010, although rank was entwined with age and previous success; Kendal et
71 al. 2015, but see also Watson et al. 2017) and dominance-based and age-based biases in tufted capuchin monkeys
72 (*Sapajus spp.*, Coelho et al. 2015). Social status has been shown to influence human social attention, by increasing
73 social attention in children (Flynn and Whiten 2012) and the frequency of the gaze cueing phenomenon, whereby
74 human subjects with higher social status guided more often the gaze of their observers (Dalmaso et al. 2011).
75 Nevertheless, in some species of primates, and particularly those living in a structurally despotic type of society,
76 it is difficult to ascertain whether dominance-based biased social learning allows the acquisition of the most
77 valuable information or is a by-product of biased social attention due to social anxiety (Chance 1967; Caine and
78 Marra 1988; Alberts 1994; Watts 1998) or of biased proximity (if social dominance equals centrality within the
79 group; Kanngiesser et al. 2011).

80 Juveniles tend to be active social learners (Lonsdorf and Ross 2012; Matsuzawa et al. 2008; Schiel and
81 Huber 2006). The juvenile period may be a period of brain development and acquisition of crucial behaviours
82 (potentially corresponding to Laland's copy-when-uncertain strategy, 2004). In social species, this transitory
83 period also corresponds to a period of socialisation and social rank acquisition (Lee 1987; Chapais 1992; Cheney
84 and Seyfarth 1990; Pereira 1988; Förster and Cords 2005; Cords et al. 2010; Shimada and Sueur 2014).

85 Vervet monkeys are an interesting species in which to examine social attention and its potential role in
86 both socialisation and social learning. They form matrilineal, nepotistic and despotic groups. Female hierarchical
87 rank is determined by matriline and supported by forming coalitions, whereas fighting abilities are more
88 determinant in males, the dispersing sex (Cheney and Seyfarth 1990). High-ranking females have been not
89 characterized by a greater aggressiveness but rather a higher propensity to make alliances (Cheney and Seyfarth
90 1990). Previous studies have found evidence of social learning abilities in vervet monkeys (van de Waal and
91 Bshary 2011; van de Waal and Whiten 2012) and some studies have revealed similarities in experimental food-
92 processing techniques between mothers and their offspring, suggesting a kinship-bias in observational learning
93 by infants (van de Waal et al. 2012; van de Waal et al. 2014). Van de Waal et al. (2010) revealed a sex-based bias,
94 wherein attention was preferentially directed towards dominant females rather than dominant males engaged in
95 an “artificial fruit” opening task. This preferred social attention may occur because females, as the philopatric sex,
96 may represent an established source of ecological knowledge and thus may generally present a more useful model
97 (van de Waal et al. 2013). Alternatively, sex-based biased social attention towards females may be linked to a
98 higher centrality of females within social networks and to their higher propensity to be chosen as social partners
99 (Cheney and Seyfarth 1990; Wu et al. 2013).

100 A further study of vervet monkey social attention also revealed a bias towards attending to adult females
101 during grooming interactions and foraging bouts (Renevey et al. 2013). Interestingly, considering the despotic
102 type of social dominance and the rank-related attractiveness in grooming interactions in this species (Fairbanks
103 1980), this study did not find any effect of social rank upon social attention. However, Renevey et al. (2013)
104 measured social attention by recording the latency between a subject approaching or being approached within a
105 5m perimeter around a focal individual and the first look directed towards this individual, thereby using a binary
106 response variable of “look” or “no look” within 30sec after the target approached within the perimeter. The
107 absence of effect of social rank on social attention might be due to this protocol that did not consider differences
108 in number of looks that might identify disproportionate attention.

109 The current study examined social attention in wild juvenile vervet monkeys to investigate whether they
110 attend preferentially to certain classes of conspecifics during this period of development and knowledge
111 acquisition. We restricted the focal observations to foraging events - considering the previous results of van de
112 Waal et al. (2014) - to specifically examine the hypothesis of an influence of observational learning on the
113 acquisition of feeding techniques. Given the previous results in the social learning domain (van de Waal et al.
114 2010; van de Waal et al. 2014), we hypothesised that juvenile attention would be biased towards kin, and possibly

115 towards females because of female philopatry (Schiel and Huber 2006). Additionally, age-based biases have been
116 found in social attention in other primates (Biro et al 2003; Schiel and Huber 2006), we therefore hypothesized
117 that the juveniles would preferentially attend to older individuals. Yet, it was unclear whether a bias to attend
118 more to high-ranking individuals would be found here, considering previous results with vervet monkeys
119 (Renevey et al. 2013) and the mixed results on dominance-based bias in other primates (Dindo et al. 2011; Kendal
120 et al. 2015; Watson et al. 2017). Although, we employed a more detailed measure of social attention than
121 previously used with this species (Renevey et al. 2013) to more accurately examine social attention biases.
122 However, because of the despotic style described in previous studies of vervet monkey societies (Cheney and
123 Seyfarth 1990), the rank of the juvenile was expected to be negatively correlated to juvenile social attention
124 because of higher social vigilance in low-ranking individuals (Chance 1967; Alberts 1994). Our sample also
125 contained a number of juvenile orphans (N=9), following multiple group fissions of the lowest three matriline
126 over the preceding three years in one of the groups (BD). The loss of the mother during infancy has been
127 documented as influencing developmental and behavioural patterns in young and adult primates (Lévy et al. 2003,
128 Bastian et al. 2003; Botero et al. 2013; Suomi 1997). We thus additionally hypothesised that we would see
129 differing patterns of social attention between the orphans and the juveniles with mothers currently in the group.

130

131 **Methods**

132 **Study site and subjects**

133 Data come from three groups monitored by the Inkawu Vervet Project (Table 1), a collaboration of the
134 Universities of Neuchâtel, Zurich (Switzerland) and St-Andrews (Scotland) and located on the Mawana Game
135 Reserve, KwaZulu-Natal, South Africa (S 28° 00.327; E 031° 12.348). Social attention data were collected from
136 March to July 2015.

137 **Data collection**

138 We conducted 5min focal samples during foraging, on all the 2yo to 3yo juveniles (N=24) and 3yo to
139 4yo ones (N=19) juveniles (except *Yoog*, not habituated to humans and *Mevr*, who lost her mother in the middle
140 of the study period, in NH and BD respectively). Foraging was defined as the focal individual activity of searching
141 for and consuming food. During the focal samples, the social attention of the focal juvenile was monitored to
142 record all the looks directed towards the individuals present within a 5m radius perimeter around the juvenile.

143 During the focal samples, juveniles were most often moving on the ground at a low speed primarily looking for
144 insects and with neighbours often spread out at >3m distance from one another, which allowed the human observer
145 to track their gaze. Eye or head orientation towards another was defined as a look, with a duration which ranged
146 from 1 to 8 sec. Identities of all the individuals inside the 5m perimeter (approaching or being approached by the
147 focal juvenile) during the 5min period were recorded. Additionally, the identity of the nearest neighbour of the
148 focal individual every 30 sec was recorded to measure the spatial proximity between the focal juvenile and its
149 conspecifics.

150 The time between two focal samples of the same individual was a minimum of one hour to ensure
151 independence of the data. Focal individuals were chosen randomly. A total of ten focal bouts per juvenile were
152 recorded in the three groups. The focal data collections were done by only one person at a time, to avoid disruption
153 of the natural social dynamics (M. Bodin in NH and MG in BD and AK groups). Observers had previously passed
154 identification and inter-observer reliability (>80%) tests with long-term field assistants (collecting regularly long-
155 term data) and were able to quickly and reliably identify all group members using facial features.

156 Aggressive interactions were recorded *ad libitum* by human observers following the group every day.
157 These contest data were used to estimate matrilineal (female and offspring) and male hierarchies with the Elo-
158 rating package (Neumann et al. 2011) on R. We used dyadic conflicts with clear winners as indicated by a retreat
159 by the losing individual. The social rank assigned to each individual was either an average of its ranks across four
160 time periods or its rank on the day if the individual's rank varied greatly during the study period (SI, Tables 1-3).

161 **Data analysis**

162 Social attention was estimated by the number of looks towards individuals within a 5m radius perimeter
163 around the focal juvenile, taken continuously during the 5min period and considering each dyad of subjects and
164 targets. Social proximity was estimated by the two following variables (i) the number of times an individual was
165 the nearest neighbour of the juvenile at thirty-second intervals and (ii) the number of focal bouts where an
166 individual was present in the perimeter (0 to 10). This gave us ego-networks (Crossley et al. 2015), for which only
167 relationships or connections of our focal individual (ego) matter. Alters (other individuals) are only connected to
168 ego and not between them, removing the issue of dependence of data (Farine, 2017). Looks outside the perimeter
169 were primarily scored but represented 4.23 % of looks (107 on 2530 looks recorded), so were not included because
170 they were estimated as sometimes inaccurate or often more related to the other's movements than other's
171 behaviours. Vigilance behaviours when looking towards conspecifics or when alarms calls occurred within the

172 groups were scored and represented 1.03 %, 26 on 2530 looks recorded. Some instances of looks towards two
173 individuals in close proximity, or in contact (grooming interactions), thus making impossible for the human
174 observer to identify the exact target of attention were included in the data for each individual of the pair but
175 represented a low percentage of 1.46%, 37 on 2530 looks recorded.

176 Predictor variables were the group, age, rank, sex, age and sex class ratios, and the maternal relatedness
177 of both the subject and the target of attention. The orphan effect was also considered as a binary factor for the
178 juvenile subject behaviour. The age of the juvenile was considered as a factor with two levels: 2yo or 3yo
179 juveniles. The age of the target was also studied as a factor with two levels: immature or adult. The matrilineal
180 relatedness was represented by relatedness coefficients: 0 for non-relatives, 0.5 between mother-offspring (29
181 dyads), 0.25 between siblings (61 dyads) and between aunt/cousin 0.0625 (12 dyads); we did not consider the
182 coefficients 0.125 and 0.03125 because of low numbers of dyads (three and one dyads respectively). Relatedness
183 coefficients were established through our observational knowledge of births. Whilst our observations were able
184 to capture the majority of relationships, it is possible that some additional maternal aunt/cousin relationships, and
185 possibly father-offspring relationships (since males may stay up to 2 years in a same group), may not have been
186 accounted for.

187 We used generalized linear mixed models (GLMMs, Bolker et al 2009) with a negative binomial family
188 to study the effects of the predictors on the following response variables: the number of looks (“social attention”)
189 and the number of times that a given individual was the nearest neighbour of the focal individual (“nearest
190 neighbour”). We used GLMMs, with Poisson family to study the effects of the same variables on spatial proximity,
191 the response variable of the number of focal bouts where a given individual was present within the focal 5m
192 perimeter (“5m perimeter”). Negative binomial models were used to study variables with an over-dispersed
193 distribution. The number of looks and number of times as nearest neighbour were not evenly distributed among
194 group members, but rather strongly influenced by the identities of both the focal and the target. In contrast, the
195 variable of the number of times within the 5m perimeter fits with a Poisson distribution. Identities of the
196 individuals, nested within the identities of the groups, were considered as random factors. Groups’ identities were
197 also tested as fixed factors but did not change anything to results. To control for inter-group demographics, we
198 considered group sex and age ratios (number of individuals in each age/sex class divided by the total number of
199 individuals in the group) as continuous, fixed factors and also considered their interactions with age and sex.
200 Additionally, we ran analyses both with and without the fixed effect of proximity (how often an individual was

201 within a focal individual's 5m perimeter). All two-way interactions were considered in the models; no three-way
202 interactions were considered.

203 For each GLMM, we ran multi-model inferences to compare and rank candidate models according to (i)
204 their respective Akaike information criterion after correction for small sample sizes (AICc) and (ii) normalized
205 Akaike weights (AICw). $\Delta AICc$ is the difference in AICc between one given model and the model with the lowest
206 AIC. The AIC weight indicates the probability of a given model being the best among candidate models. Models
207 with a $\Delta AICc < 4$ were considered equally possible candidates and their statistics averaged. The null model, with
208 only the intercept, was included as a possible candidate, but was never among the models with lowest AICc.
209 Averaged model coefficients and averaged p-values were obtained for models with a $\Delta AICc < 4$ (Pelé et al. 2017;
210 Sueur et al. 2018). Model inference and averaging were carried out with the R package 'MuMIn' (Bartoń 2013).
211 Relative importance of each independent variable (RVI) represents the extent to which each variable explains the
212 variance in the best models ($\Delta AICc < 4$). A RVI of 1 indicates that the variable is present in all best models and
213 plays a major role in explaining the variance of dependent variables. To avoid multicollinearity of predictors, we
214 used the Variance Inflation Factor (VIF) test to calculate a VIF index for each one. However, no variable exceeded
215 a VIF of 3 (Craney and Surles 2002). Statistical analyses were conducted using R Studio 1.0.44 Software (© 2009-
216 2016 RStudio, Inc. version 3.0.1) with α set at 0.05. All the members of the groups were considered in the analyses
217 with the exception of infants (less than one year-old). "S" refers to the subject, the focal juvenile and "T" to the
218 individual target of attention. Because male social ranks fluctuated over time and some of the males transferred
219 to other groups during the study period, we decided to test the aforementioned predictors for social attention
220 without the adult males as target of attention. Additionally, because immature individuals were more often around
221 the juvenile subjects and considering the effect of the sex of the adult target in van de Waal et al. (2010), we
222 decided to exclude immature targets of the dataset in one part of the analyses to see whether the sex of the adult
223 individuals had also an effect on juvenile social attention here. Tables 4 to 7 in the SI summarise the analysed
224 models.

225

226 **Results**

227 **Social attention**

228 Juveniles paid significantly more attention to their matriline members than to other conspecifics
229 (coefficients 0.5 mother and 0.25 siblings, RVI= 1, Table 2; Table 4 in SI; Fig. 1). Additionally, they paid more
230 attention to the individuals who were more often present in the five-meter perimeter (RVI= 1, Table 2; Table 4 in
231 SI). The highest-ranking individuals were significantly more often the targets of juvenile social attention than
232 low-ranking individuals (RVI= 1, Table 2; Table 4 in SI, Fig. 2). Orphaned and 2yo juveniles displayed a higher
233 number of looks than non-orphaned and 3yo juveniles, respectively (RVI= 1 and RVI= 0.98 respectively, Fig. 1;
234 Fig. 3a,b: orphans). The orphan effect had the same RVI and coefficients when we included random factors
235 controlling for group, age or sex of the orphan subjects, compared to not included. Additionally, the age of the
236 subject was still an important factor when the sex ratio was controlled for.

237 Even by excluding the proximity variable (Table 3; Table 5 in SI), the aforementioned predictors
238 remained of high importance. Additionally, older juveniles showed a lower kinship bias towards their mothers
239 than did younger juveniles (interaction between maternal relatedness and age of the subject, RVI= 0.77; Fig. 1).
240 There were no significant sex differences in juvenile social attention. However, there was a trend for juvenile
241 females to pay more attention to the highest-ranking individuals when the proximity variable was not included in
242 the model (sex of the subject, RVI= 0.77 and its interaction with the rank of the target, RVI= 0.49; Fig. 2a). There
243 was no significant effect of the juvenile rank or of its interaction with the target rank (RVI= 0.36 and 0.15 of RVI,
244 respectively). The sex of the target and the group identity were not significant factors predicting social attention
245 (RVI=0.19 and RVI=0.11, respectively). We also checked sex ratio and its interaction with the subject and target
246 sexes, and the variables did not reach any significance and were not included in the best models. The age of the
247 target was not significant when age ratio controlled for and was not included in the best models. The interaction
248 between the sex of the subject and the maternal relatedness was not significant.

249 Considering the importance of the philopatric sex in vervet monkeys (van de Waal et al. 2010) and the
250 hierarchy of males frequently changing, we re-analysed the data excluding dyads in which the groupmate was an
251 adult male (Table 5; Table 7 in SI). The age of the subject, the orphan effect and the maternal relatedness had the
252 same effects on the variance of social attention. However, the effects of the rank of the target and its interaction
253 with the sex of the subject were stronger ($p < 0.01$ vs. $p < 0.001$ and $p = 0.095$ vs. $p = 0.050$, respectively, for datasets
254 with vs. without target males). Hence, the rank of the targets which are matriline members - without the adult
255 males - had a stronger positive effect on social attention, and female subjects tended to show this effect more
256 strongly than did male ones (Fig. 2b).

257 **Social proximity**

258 The identity of the nearest neighbour was strongly influenced by the maternal relatedness (RVI=1, Table
259 4; Table 6 in SI; Fig. 3, the yellow nodes representing matriline members of the subject). The nearest neighbour
260 was more often lower-ranking than the juvenile subject (rank of the target, RVI=0.94). Mothers of 3yo juveniles
261 had significantly less often their mother as nearest neighbour than 2yo juveniles (interaction of age of the subject
262 and maternal relatedness RVI= 0.19). The other predictors (ages, orphan, sex and interactions with group-age/sex
263 ratios) had no significant effect on the variance of the nearest neighbour.

264 Individuals within the perimeter were more often members of the subject's matriline (Table 4, for the
265 relatedness coefficients: 0.5, 0.25 and 0.0625, RVI=1; Table 6 in SI and Fig. 3: for each graph, the yellow nodes
266 represent the matriline members of the subject). Adults were less often in the perimeter when the age ratio was
267 controlled for (Table 4, age the target, RVI=1), and neither the group ratio of the age of the target (Table 4,
268 RVI=0.25) nor its interaction with the age of the target were significant factors (RVI= 0.04). Same-ranked
269 individuals were significantly more often associated within 5m (interaction of the rank of the subject with the rank
270 of the target, RVI=1). Orphans had fewer individuals within 5m (orphan, RVI=1). Despite a high relative
271 importance (RVI=0.90), the age of the subject was not significant, this may be explained by the significance of
272 its interaction with the coefficient 0.5 of the maternal relatedness (RVI= 0.77). Indeed, 3yo juveniles had less
273 often their mothers within a five-meter perimeter, but displayed similar levels of association with their half-
274 siblings as 2yo juveniles. The interaction between the age and the sex of the target had no significant effect on
275 spatial proximity (RVI=0.10). The group identity was not a significant predictor and not selected in the best
276 models.

277

278 **Discussion**

279 In the current study, we examined social attention in juvenile vervet monkeys. A number of factors
280 were found to significantly influence the level and direction of this social attention: most importantly maternal
281 kinship, but also the age and sex of the juvenile subject, the rank of the target of attention and whether or not the
282 subject was an orphan.

283 **Maternal relatedness**

284 Juveniles paid more attention and were more often in the vicinity of their maternal relatives when foraging.
285 As hypothesized, the juvenile vervet monkeys showed a clear kinship bias concerning social attention and the size
286 of this kinship effect was much greater than the other significant parameters ($RVI = 1$). This strong bond with the
287 mother is typical of primate maternal care (Lonsdorf and Ross 2012; Schuppli et al. 2016), and consistent with
288 the nepotistic type of social structure in vervet monkeys (Cheney and Seyfarth 1990). Social attention may have
289 a primarily social function and could be directed towards kin to ensure social cohesion of matriline members and
290 its advantages in a social group (Lee 1987), particularly in juveniles, just after weaning. This is consistent with
291 the results of van de Waal et al. (2014), who showed bias social learning from kin, and results from other primates,
292 including apes (Jaeggi et al. 2010; Schuppli et al. 2016). These last studies showed the importance of the mother
293 in early social learning. The mother-based kinship effect was significantly higher in the 2yo juveniles, compared
294 to the 3yo ones, but the siblings-based kinship effect was similar across ages. These results underline the
295 importance of the siblings as well as the mother in vervet monkeys social structure (Lee 1987) and indicate that
296 siblings may also be key models for social learning (as has been shown in some birds, Schwab et al. 2008a, but
297 see Schwab et al. 2008b). 2yo juveniles had more often their mother as their nearest neighbour than the 3yo
298 juveniles, again underlining the importance of the mother still one year after weaning and its decrease to a level
299 similar to other matriline members with age. Overall, this kinship effect suggests that kinship may have a greater
300 effect on information flow throughout a group than other parameters, with information perhaps more likely to
301 move within, than between matriline. This bias may be reflective of the copy-kin learning strategy of Laland
302 (2004), advantageous because of similar needs between closely related individuals (Cheney and Seyfarth 1990;
303 Schino et al. 2007; Hamilton 1964; Laland 2004) and the “Bonded and Identification-based Observational
304 Learning” between affiliated individuals hypothesized by de Waal (2001).

305 **Social rank**

306 The rank of the target of attention was an important factor predicting social attention in juveniles, with
307 juveniles directing more social attention towards high-ranking individuals. Considering the despotic nature of the
308 hierarchy in this species, it is plausible that this observed effect may reflect biased social attention because of
309 anxiety - monitoring dominants to anticipate and diminish aggression and thus allow access to high quality
310 resources (Chance 1967; Caine and Marra 1988; Alberts 1994; Watts 1998). Similarly, increasing the number of
311 looks may act as a socially submissive signal and may become a stereotyped display of fear. However, our data
312 does not appear to fully support these hypotheses for a number of reasons. Firstly, the *highest*-ranked rather than
313 *higher*-ranked individuals are more often observed by the juveniles. Secondly, the rank of the juveniles or its

314 interaction with the rank of the target, did not significantly influence the social attention level. These social ranks
315 were established from conflict data, because inherited matrilineal rank may not be representative of the juvenile
316 rank before sexual maturity (Berman 1982), and therefore represent an actual risk of aggression in this population.
317 If anxiety was the cause of increased social attention, lower-ranking juveniles would be expected to show this
318 effect more strongly. Finally, juvenile females tended to exhibit a stronger dominance-based bias compared to
319 males and this trend was more strongly marked when we removed the adult males from the analyses and
320 considered only matriline members as targets. No evidence of sex bias in aggressive interactions was found in the
321 highly detailed study of vervet juvenile behaviour of Raleigh (1979), suggesting instead that increased social
322 attention towards the highest-ranking individuals may provide more benefits to the philopatric sex. Therefore, our
323 results suggest that this biased social attention toward high-ranking individuals is not the result of social anxiety
324 or a tactic to reduce aggression, but instead serves another purpose.

325 Researches on other species revealed biases to copy preferentially high ranked individuals (Nicol &
326 Pope 1999; Kendal et al 2015). Copying high-ranking individuals may allow animals to copy the most successful
327 individuals (Laland 2004; Coelho et al. 2015), if rank is a marker of success. However, it is not clear why dominant
328 females would have better environmental knowledge than lower-ranked females in vervet monkeys. Thus the
329 adaptive benefits of copying the behaviour of the dominant are unclear. Additionally, it should be noted that this
330 increased attention to the highest-ranking individuals may not necessarily result in increased levels of social
331 information transfer. Botting et al. (2018) did not find any dominance-based bias in an experimental social
332 learning task with vervet monkeys, using only female demonstrators. This may suggest a context-dependency of
333 this dominance-based bias, perhaps wherein information about the social, rather than physical, environment is
334 learned.

335 It is also plausible that this rank-biased social attention may function to assist socialisation and rank
336 acquisition. Looking at individuals might be primarily a means of gaining information about others or a first step
337 in the initiation and development of social interaction (Hrdy and Whitten 1987; Wu et al. 2013). Social attention
338 has been shown to vary according to differences in sociability: compared to despotic rhesus macaques, *M. mulatta*,
339 more tolerant species of Barbary macaques, *M. sylvanus*, maintain their level of attention with age (Rosati and
340 Santos 2017). Observing the highest-ranking individuals may help socialisation and rank acquisition in juveniles,
341 to acquire third-party social rank knowledge, improve decision-making and trade grooming for social tolerance
342 or agonistic support, following biological markets theory (Noë and Hammerstein 1994; Carne et al. 2011). Such
343 a dominance-based bias may be particularly relevant for juvenile vervet females, being philopatric and socially

344 central individuals during adulthood, in consonance with sex differences in juvenile sociality observed in male
345 philopatric chimpanzees (Lonsdorf et al. 2014). Interestingly, in this study we found a trend for juvenile females
346 to look more at the highest-ranked individuals, when the proximity was not controlled for and possibly specifically
347 towards matriline members, than adult males. Although Raleigh (1979) did not find any evidence of sex
348 differences in agonistic behaviours among his juvenile vervet subjects, he did find a higher propensity of females
349 to initiate affiliative interactions with non-related conspecifics. The same was true in juvenile female philopatric
350 blue monkeys (Cords et al. 2010). Previous studies have revealed third-party rank relationship knowledge in adult
351 female vervet monkeys, but not in males and juveniles (Borgeaud et al. 2013; Borgeaud et al. 2015). However,
352 the authors did not distinguish between the sexes of the juveniles and the results of the current study suggest that
353 it is plausible that female juveniles, exhibiting more strongly marked attention towards highest-ranked individuals
354 than males, have acquired more elements of hierarchy knowledge than male juveniles and/or exhibit directed
355 socialisation towards the highest-ranking matriline members. However, further researches are needed to test this
356 hypothesis.

357 The rank-based findings in the current study contrast with the findings of a previous study of vervet
358 monkeys (Renevey et al. 2013), which found no effect of rank on social attention. However, given this study used
359 a more detailed method of measuring social attention, these contrasting results may be explained by differences
360 in protocols. Alternatively, they may reflect influences of socio-ecological or cultural variables, which may lead
361 to group differences (Kaburu & Newton-Fisher 2015, Santorelli et al. 2011).

362 **Sex**

363 Juveniles' social attention was not significantly influenced by the sex of the target, nor by the interaction
364 between the subject and target sexes. This is somewhat surprising given previous results in studies of both social
365 attention (Renevey et al 2013) and social learning (van de Waal et al 2010) in vervet monkeys. These studies
366 showed biases towards preferentially attending to adult females. However, Renevey et al (2013) compared social
367 attention directed towards adult females and males, whereas our study included all ages. Our juveniles sample
368 was also biased towards juvenile males and adults were less present around juveniles, which may have obscured
369 the possible sex-based bias. Finally, the effect of the sex of the target was a significant factor predicting juvenile
370 social attention with the dataset containing only adults as targets; adult females were significantly more often
371 observed than adult males (RVI=0.80, see in SI, table 8 and 9).

372 The effect of the sex of the juvenile subject was not a significant factor predicting social attention
373 although the biased sex ratios in the three groups towards the juvenile males and the small number of 3yo females
374 may partially explain this result. However, the subject sex had a relative importance of 77% in the models
375 explaining variation in social attention. Without the proximity variable, the results showed a trend for females to
376 display more dominance-based biased social attention. No differential effect of the maternal relatedness seemed
377 to occur between juvenile males and juvenile females in our study. These results may suggest that sex differences
378 may occur in relation to different socialisation processes, and not pre-existing relationships with matriline
379 members, where young females may look for or engage in more interactions with non-related individuals, and
380 particularly the highest-ranking ones, than do males. This pattern may be consistent with the general rank
381 acquisition in juveniles and adult males after migration. Juvenile females may be already integrated within the
382 matrilineal hierarchy and strongly rely on alliance formation to ensure close social ranks to their mothers. In
383 contrast, social ranks in juvenile males, before migration, may be more flexible and dependent on their physical
384 abilities (Chapais 1992).

385 **Age**

386 The age of the subject was also an important predictor of the number of looks, but not significantly of
387 spatial proximity. Younger juveniles showed overall greater attention to conspecifics, as well as greater attention
388 to the mother. This may support a greater emphasis of social learning in the 2yo juveniles and possibly reflects a
389 critical period of socialisation and social learning. This difference between the two age-classes of juveniles may
390 imply ontogenic changes as found in other primates (Schiel and Huber 2006; Matsuzawa 1994; Lonsdorf et al.
391 2004). We suggest that this finding is not due to more anxiety-based monitoring in the 2yo juveniles as they do
392 not occupy lower social ranks than 3yo, are more often supported by their mother and siblings (Cheney and
393 Seyfarth 1990), and the interaction between the age of the subject and rank of the target was not significant in our
394 models.

395 It has previously been found in chimpanzees that older individuals are preferentially attended to as social
396 models (Biro et al. 2003; Matsuzawa et al. 2008). However, in the current study, adults were less often within the
397 5m perimeter of the juvenile subjects, when controlling by the number of individuals per age categories. This
398 suggests a preferred association between immature individuals, which may ensure higher social tolerance during
399 feeding and potentially allows affiliative interactions, such as social play (Shimada and Sueur, 2014; 2018). The
400 lack of a clear bias toward adults here, compared with results seen in wild chimpanzees, may be due to the

401 complexity of the tasks being learned. Whereas keen attention is required to master skills such as nut-cracking
402 and termite fishing in chimpanzees (Biro et al 2003; Lonsdorf et al 2005), such complex manual manipulation
403 tasks are not seen in vervet monkeys and therefore the role of older, and thus more experienced, individuals as
404 models may be less important.

405 **Orphans**

406 Our sample contained juveniles whose mothers had died or had left the group. 2yo and 3yo orphans
407 displayed significantly greater social attention overall than juveniles still having their mother. The juveniles
408 exhibiting the highest level of social attention in each age class were both orphans (see Fig 3a, b). The interaction
409 between the predictors ‘orphan and rank of the target’ did not reach significance. This suggests that the orphans
410 had an overall increase in social attention. The ego-networks of their social attention illustrate this effect by the
411 larger thickness of their edges. Increased social attention may be associated with social stress; orphaned primates
412 are well-documented as having atypical or anxiety-related behaviours (Goodall 1986; Botero et al. 2013; Suomi
413 1997; Ichise et al. 2006). Mother deprivation may affect social learning skills (Lévy et al. 2003) and the processes
414 of social rank acquisition and maintenance (Bastian et al. 2003). However, the increased social attention found in
415 this study may also reflect adaptive flexibility with a greater emphasis on socialisation, social learning and
416 decision-making in the social domain (Chawarska et al. 2016a), as well as compensating for lack of support from
417 kin, crucial in nepotistic societies (Schino et al. 2007). Our sample size (N=9 orphans) prevented further analyses
418 for possible variations according to the sex, age, rank of the orphans or the presence of siblings, which may provide
419 a better understanding of our results. However, the data from the orphans, as shown on the ego-networks, also
420 underlines the persistence of the importance of siblings in vervet societies after the disappearance of the mother
421 (Fig. 3a,b: *Hipp* to *Heer* and *Vak* to *Vul*; Lee 1987).

422 **Conclusions**

423 In conclusion, matrilineal kinship emerged in this study as the key predictor of social attention in juvenile
424 vervet monkeys, in addition of biased spatial proximity towards kin within the group. This kin-biased based social
425 attention is consistent with previous studies showing that the mother and other matriline members will represent
426 the primary source of information and first social partners in the young vervet monkey’s life (van de Waal et al.
427 2012; van de Waal et al. 2013; van de Waal et al. 2014; Cheney and Seyfarth 1990; Lee 1987). Other predictors
428 had significant, although lesser effects on social attention, such as the age of the subject and rank of the target.
429 Younger juveniles attended more to others than did older juveniles, suggesting a critical period for learning

430 information about the physical and social environments, and juveniles displayed more social attention towards the
431 highest-ranked individuals. Female juveniles tended to attend more to the highest-ranking individuals than males
432 did, likely showing an effect of female philopatry. Finally, orphans exhibited greater attention to conspecifics,
433 potentially underlining the functions and plasticity of social attention in socialisation and social learning
434 processes. These results help illuminate the processes of social integration and information flow dynamics in wild
435 vervet monkeys, with implication for socialisation and social learning processes in wild animals. These social
436 attention biases were revealed from a study in foraging contexts, but may be similar in social contexts given their
437 hypothesised social function.

438

439 **Compliance with Ethical Standards**

440 JB was supported by a grant from the John Templeton Foundation (ID40128 to A. Whiten). EW and the IVP
441 project have received grants from the Swiss National Science Foundation (P300P3_151187 & 31003A_159587)
442 and the Branco Weiss Fellowship-Society in Science-. The authors declare that they have no conflicts of interest.
443 No human participants were included in this study. This study was approved by the University of Strasbourg and
444 was carried out in full accordance with the ethical guidelines and European animal welfare legislation. Animals
445 were habituated to the observers' presence. Every effort was made to ensure the welfare of the animals and
446 minimize disturbance of the groups.

447

448 **References**

- 449 Alberts SC (1994) Vigilance in young baboons: effects of habitat, age, sex and maternal rank on glance rate. *Anim Behav*
450 47:749-755.
- 451 Agostini I, Visalberghi E (2005). Social influences on the acquisition of sex-typical foraging patterns by juveniles in a group
452 of wild tufted capuchin monkeys (*Cebus nigrinus*). *Am J Primatol* 65:335-351.
- 453 Anderson JR, Takimoto A, Kuroshima H, Fujita K (2013) Capuchin monkeys judge third-party reciprocity. *Cognition*
454 127:140-146.
- 455 Bartoń K (2013) MuMIn: Multi-model inference. R package version 1.9. 13. The Comprehensive R Archive Network
456 (CRAN). Vienna. Austria.3
- 457 Bastian ML, Sponberg AC, Suomi SJ, Higley JD (2003) Long-term effects of infant rearing condition on the acquisition of
458 dominance rank in juvenile and adult rhesus macaques (*Macaca mulatta*). *Dev Psychobiol* 42:44-51.

- 459 Bastian M., Heymann S., Jacomy M. (2009). Gephi: an open source software for exploring and manipulating networks.
 460 International AAAI Conference on Weblogs and Social Media.
- 461 Berman CM (1982) The ontogeny of social relationships with group companions among free-ranging infant rhesus monkeys
 462 I. Social networks and differentiation. *Anim Behav* 30:149-162.
- 463 Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White JSS (2009) Generalized linear mixed
 464 models: a practical guide for ecology and evolution. *Trends in ecology & evolution* 24:127-135.
- 465 Biro D, Inoue-Nakamura N, Tonooka R, Yamakoshi G, Sousa C, Matsuzawa T (2003) Cultural innovation and transmission
 466 of tool use in wild chimpanzees: evidence from field experiments. *Anim Cogn* 6:213–223.
- 467 Borgeaud C, van de Waal E, Bshary, R. (2013) Third-party ranks knowledge in wild vervet monkeys (*Chlorocebus aethiops*
 468 *pygerythrus*). *PLoS One* 8:e58562.
- 469 Borgeaud C, Alvino M, van Leeuwen K, Townsend SW, Bshary R (2015) Age/sex differences in third-party rank
 470 relationship knowledge in wild vervet monkeys, *Chlorocebus aethiops pygerythrus*. *Anim Behav* 102:277-284.
- 471 Borgeaud C, Bshary R (2015) Wild vervet monkeys trade tolerance and specific coalitionary support for grooming in
 472 experimentally induced conflicts. *Curr Biol* 25:3011-3016.
- 473 Botero M, MacDonald SE, Miller RS (2013) Anxiety-related behaviour of orphan chimpanzees (*Pan troglodytes*
 474 *schweinfurthii*) at Gombe National Park, Tanzania. *Primates* 54:21-26.
- 475 Botting J, Whiten A, Grampp M, van de Waal E (2018) Field experiments with wild primates reveal no consistent
 476 dominance-based bias in social learning. *Anim Behav* 136:1-12.
- 477 Boyd R, Richerson PJ (1985) Culture and the evolutionary process. University of Chicago Press. Chicago.
- 478 Brent LJJ, Franks DW, Foster EA, Balcomb KC, Cant MA, Croft DP (2015) Ecological Knowledge, Leadership, and the
 479 Evolution of Menopause in Killer Whales. *Curr Biol* 25:746–750.
- 480 Caine NG, Marra SL (1988) Vigilance and social organization in two species of primates. *Anim Behav* 36:897-904.
- 481 Carne C, Wiper S, Semple S (2011) Reciprocation and interchange of grooming, agonistic support, feeding tolerance, and
 482 aggression in semi-free-ranging Barbary macaques. *Am J Primatol* 73:1127-1133.
- 483 Chapais B (1992) The role of alliances in social inheritance of rank among female primates. In: Harcourt AH, de Waal FBM
 484 (ed) *Coalitions and Alliances in Humans and Other Mammals*. Oxford University Press. USA.
- 485 Chawarska K, Macari S, Powell K, DiNicola L, & Shic F (2016a) Enhanced social attention in female infant siblings at risk
 486 for autism. *J Am Acad Child Adolesc Psychiatry* 55:188-195.
- 487 Chawarska K, Ye S, Shic F, Chen L (2016b) Multilevel Differences in Spontaneous Social Attention in Toddlers with
 488 Autism Spectrum Disorder. *Child Develop* 87:543–557.
- 489 Chance MR (1967) Attention structure as the basis of primate rank orders. *Man* 2:503-518.
- 490 Cheney DL, Seyfarth RM (1990) *How Monkeys See the World: Inside the Mind of Another Species*. University of Chicago
 491 Press. Chicago.
- 492 Cheney DL, Lee PC, Seyfarth RM (1981) Behavioural correlates of non-random mortality among free-ranging female vervet

- 493 monkeys. Behav Ecol Sociobiol 9:153-161.
- 494 Claidière N, Messer EJE, Hoppitt W, Whiten A (2013) Diffusion Dynamics of Socially Learned Foraging Techniques in
495 Squirrel Monkeys. Curr Biol 23:1251–1255.
- 496 Coelho CG, Falótico T, Izar P, Mannu M, Resende BD, Siqueira JO, Ottoni EB (2015) Social learning strategies for nut-
497 cracking by tufted capuchin monkeys (*Sapajus spp.*). Anim Cogn 18:911-919.
- 498 Cords M, Sheehan M.J, Ekernas LS (2010) Sex and age differences in juvenile social priorities in female philopatric,
499 nondespotic blue monkeys. Am J Primatol 72:193–205.
- 500 Coussi-Korbel S, Frigaszy DM (1995) On the relation between social dynamics and social learning. Anim Behav 50:1441–
501 1453.
- 502 Craney TA, Surlis JG (2002) Model-dependent variance inflation factor cutoff values. Quality Engineering 14:391-403.
- 503 Crossley, N., Bellotti, E., Edwards, G., Everett, M. G., Koskinen, J., & Tranmer, M. (2015). Social network analysis for ego-
504 nets: Social network analysis for actor-centred networks. Sage.
- 505 Dalmaso M, Pavan G, Castelli L, Galfano G (2011) Social status gates social attention in humans. Biol Lett rsbl20110881.
- 506 Dawson BV, Foss BM (1965) Observational learning in Budgerigars. Anim Behav 13:470-474.
- 507 de Waal FBM (1992) Intentional deception in primates. Evolutionary Anthropology: Issues, News, and Reviews 1:86-92.
- 508 de Waal FBM (2001) The Ape and The Sushi Master: Cultural Reflections of a Primatologist “the Urge to be like others” pp
509 224. New York: Basic Books.
- 510 Dindo M, Thierry B, Whiten A (2008) Social diffusion of novel foraging methods in brown capuchin monkeys (*Cebus*
511 *apella*). Proc R Soc Lond B 275:187–193.
- 512 Dindo M, Leimgruber KL, Ahmed R, Whiten A, de Waal F (2011) Observer choices during experimental foraging tasks in
513 brown capuchin monkeys (*Cebus apella*). Am J Primatol 73:920-927.
- 514 Dubosq J, Romano V, Sueur C, MacIntosh AJJ (2016) Network centrality and seasonality interact to predict lice load in a
515 social primate. Scient Rep 6.
- 516 Duffy GA, Pike TW, Laland KN (2009) Size-dependent directed social learning in nine-spined sticklebacks. Anim Behav
517 78:371–375.
- 518 Dugatkin LA, Godin J-G.J (1993) Female mate copying in the guppy (*Poecilia reticulata*): age-dependent effects. Behav
519 Ecol 4:289–292.
- 520 Fairbanks LA (1980) Relationships among adult females in captive vervet monkeys: testing a model of rank-related
521 attractiveness. Anim Behav 28:853-859.
- 522 Farine, D. R. (2017). A guide to null models for animal social network analysis. Methods in ecology and evolution, 8(10),
523 1309-1320.
- 524 Feeney WE, Langmore NE (2013) Social learning of a brood parasite by its host. Biol Lett 9:20130443.
- 525 Flynn E, Whiten A (2012) Experimental “Microcultures” in Young Children: Identifying Biographic, Cognitive, and Social
526 Predictors of Information Transmission. Child Develop 83:911–925.

- 527 Förster S, Cords M (2005) Socialisation of infant blue monkeys (*Cercopithecus mitis stuhlmanni*): Allomaternal interactions
528 and sex differences. *Behaviour* 142:869–896.
- 529 Galef BG, Whiskin EE (2008) ‘Conformity’ in Norway rats? *Anim Behav* 75:2035–2039.
- 530 Giraldeau LA, Lefebvre L (1987) Scrounging prevents cultural transmission of food-finding behaviour in pigeons. *Anim*
531 *Behav* 35:387-394.
- 532 Goodall J (1986) *The chimpanzees of Gombe: patterns of behaviour*. Harvard University Press. Cambridge.
- 533 Hamilton WD (1964) The genetical evolution of social behaviour. *J Theor Biol* 7:17-52.
- 534 Heyes CM (1994) Social learning in animals: categories and mechanisms. *Biological Reviews* 69: 207-231.
- 535 Horner V, Proctor D, Bonnie KE, Whiten A, de Waal FBM (2010) Prestige Affects Cultural Learning in Chimpanzees. *PLoS*
536 *one* 5:e10625.
- 537 Hrdy SB, Whitten PL (1987) Patterning of sexual activity. In: Cheney DL, Seyfarth RM, Smuts R, Wrangham R, Wrangham
538 RW, Struhsaker TT (ed) *Primate societies*. University of Chicago Press. Chicago. pp 370-384.
- 539 Ichise M, Vines DC, Gura T, Anderson GM, Suomi SJ, Higley JD, Innis RB (2006) Effects of early life stress on [11C]
540 DASB positron emission tomography imaging of serotonin transporters in adolescent peer-and mother-reared
541 rhesus monkeys. *J Neurosci* 26:4638-4643.
- 542 Jaeggi AV, Dunkel LP, Van Noordwijk MA, Wich SA, Sura AAL, van Schaik CP (2010) Social learning of diet and
543 foraging skills by wild immature Bornean orangutans: implications for culture. *Am J Primatol* 72:62–71.
- 544 Kaburu SS, & Newton-Fisher NE (2015) Egalitarian despots: hierarchy steepness, reciprocity and the grooming-trade model
545 in wild chimpanzees, *Pan troglodytes*. *Anim Behav* 99:61-71.
- 546 Kanngiesser P, Sueur C, Riedl K, Grossmann J, Call J (2011). Grooming network cohesion and the role of individuals in a
547 captive chimpanzee group. *Am J Primatol* 73:758-767.
- 548 Kano F, Hirata S, Call J (2015) Social attention in the two species of Pan: Bonobos make more eye contact than
549 chimpanzees. *PLoS one* 10:e0129684.
- 550 Kendal R, Hopper LM, Whiten A, Brosnan SF, Lambeth SP, Schapiro SJ, Hoppitt W (2015) Chimpanzees copy dominant
551 and knowledgeable individuals: implications for cultural diversity. *Evol Hum Behav* 36:65–72.
- 552 Laland KN (2004) Social learning strategies. *Anim Learn Behav* 32:4–14.
- 553 Leadbeater E, Chittka L (2007) Social Learning in Insects — From Miniature Brains to Consensus Building. *Curr Biol*
554 17:R703–R713.
- 555 Lee PC (1987) Sibships: Cooperation and competition among immature vervet monkeys. *Primates* 28:47-59.
- 556 Lévy F, Melo AI, Galef BG, Madden M, Fleming AS (2003). Complete maternal deprivation affects social, but not spatial,
557 learning in adult rats. *Dev Psychobiol* 43:177-191.
- 558 Lonsdorf EV, Eberly LE, Pusey AE (2004) Sex differences in learning in chimpanzees. *Nature* 428:715–716.
- 559 Lonsdorf EV (2005) Sex differences in the development of termite-fishing skills in the wild chimpanzees, *Pan troglodytes*
560 *schweinfurthii*, of Gombe National Park, Tanzania. *Anim Behav* 70:673–683.

- 561 Lonsdorf EV, Ross SR (2012) Socialisation and development of behaviour. In: Mitani JC, Call J, Kappeler PM, Palombit
 562 RA, Silk JB (ed) The evolution of primate societies. University of Chicago Press. Chicago. pp 245-268.
- 563 Lonsdorf EV, Anderson KE, Stanton MA, Shender M, Heintz MR, Goodall J, Murray CM (2014) Boys will be boys: sex
 564 differences in wild infant chimpanzee social interactions. *Anim Behav* 88:79–83.
- 565 Magrath RD, Bennett TH (2012) A micro-geography of fear: learning to eavesdrop on alarm calls of neighbouring
 566 heterospecifics. *Proc R Soc Lond B* 279:902–909.
- 567 Matsuzawa T (1994) Field experiments on use of stone tools by chimpanzees in the wild. In: Wrangham RW (ed)
 568 Chimpanzee cultures. Harvard University Press. Cambridge. pp 351-370.
- 569 Matsuzawa T, Biro D, Humle T, Inoue-Nakamura N, Tonooka R, Yamakoshi G (2008) Emergence of Culture in Wild
 570 Chimpanzees: Education by Master-Apprenticeship. In: Matsuzawa T (ed) Primate Origins of Human Cognition
 571 and Behaviour. Springer. Tokyo. pp 557–574
- 572 McComb K, Moss C, Durant SM, Baker L, Sayialel S (2001) Matriarchs as Repositories of Social Knowledge in African
 573 Elephants. *Science* 292:491–494.
- 574 Neumann C, Duboscq J, Dubuc C et al. (2011) Assessing dominance hierarchies: validation and advantages of progressive
 575 evaluation with Elo-rating. *Anim Behav* 82:911–921.
- 576 Nicol CJ (2006) How animals learn from each other. *Applied Animal Behaviour Science* 100:58–63.
- 577 Nicol CJ, Pope SJ (1999) The effects of demonstrator social status and prior foraging success on social learning in laying
 578 hens. *Anim Behav* 57:163–171.
- 579 Noë R, Hammerstein P (1994) Biological markets: supply and demand determine the effect of partner choice in cooperation,
 580 mutualism and mating. *Behav Ecol Sociobiol* 35:1–11.
- 581 Pelé M, Bellut C, Debergue E, Gauvin C, Jeanneret A, Leclere T, Nicolas L, Pontier F, Zausa D, Sueur C (2017) Cultural
 582 influence of social information use in pedestrian road-crossing behaviours. *R Soc Open Science* 4:160739.
- 583 Pereira ME (1988) Effects of age and sex on intra-group spacing behaviour in juvenile savannah baboons, *Papio*
 584 *cynocephalus cynocephalus*. *Anim Behav* 36:184–204.
- 585 Pereira ME, Fairbanks LA (1993) Juvenile Primates: Life History, Development and Behaviour, with a New Foreword.
 586 University of Chicago Press. Chicago.
- 587 Perry S (2009) Conformism in the food processing techniques of white-faced capuchin monkeys (*Cebus capucinus*). *Anim*
 588 *Cogn* 12:705–716.
- 589 Raleigh MJ, Flannery JW, ERVIn FR (1979) Sex differences in behaviour among juvenile vervet monkeys (*Cercopithecus*
 590 *aethiops sabaues*). *Behav Neural Biol* 26:455-465.
- 591 Reader SM, Kendal JR, Laland KN (2003) Social learning of foraging sites and escape routes in wild Trinidadian guppies.
 592 *Anim Behav* 66:729–739.
- 593 Renevey N, Bshary R, van de Waal E (2013) Philopatric vervet monkey females are the focus of social attention rather
 594 independently of rank. *Behaviour* 150:599-615.

- 595 Rosati AG, Santos LR (2017) Tolerant Barbary macaques maintain juvenile levels of social attention in old age, but despotic
596 rhesus macaques do not. *Anim Behav* 130:199-207.
- 597 Santorelli CJ, Schaffner CM, Campbell CJ, Notman H, Pavelka MS, Weghorst JA, Aureli F (2011) Traditions in spider
598 monkeys are biased towards the social domain. *PLoS one* 6:e16863.
- 599 Schiel N, Huber L (2006) Social influences on the development of foraging behaviour in free-living common marmosets
600 (*Callithrix jacchus*). *Am J Primatol* 68:1150-1160.
- 601 Schino G, di Sorrentino EP, Tiddi B (2007) Grooming and coalitions in Japanese macaques (*Macaca fuscata*): partner choice
602 and the time frame reciprocation. *J Comp Psychol* 121:181.
- 603 Schuppli C, Meulman EJ, Forss SI, Aprilinayati F, van Noordwijk MA, van Schaik CP (2016) Observational social learning
604 and socially induced practice of routine skills in immature wild orang-utans. *Anim Behav* 119:87-98.
- 605 Schwab C, Bugnyar T, Schloegl C, Kotrschal K (2008a) Enhanced social learning between siblings in common ravens,
606 *Corvus corax*. *Anim Behav* 75:501–508.
- 607 Schwab C, Bugnyar T, Kotrschal K (2008b) Preferential learning from non-affiliated individuals in jackdaws (*Corvus*
608 *monedula*). *Behav Proc* 79:148-155.
- 609 Shimada M, Sueur C (2014) The importance of social play network for infant or juvenile wild chimpanzees at Mahale
610 Mountains National Park, Tanzania. *Am J Primatol* 76:1025–1036.
- 611 Shimada, M., & Sueur, C. (2018). Social play among juvenile wild Japanese macaques (*Macaca fuscata*) strengthens their
612 social bonds. *American journal of primatology*, 80(1), e22728.
- 613 Sosa S (2018) Social Network Analysis. In: Vonk J, Shackelford TK (ed) *Encyclopedia of Animal Cognition and Behavior*.
614 Springer.
- 615 Sterck EHM, Watts DP, Schaik CP van (1997) The evolution of female social relationships in nonhuman primates. *Behav*
616 *Ecol Sociobiol* 41:291–309.
- 617 Sueur C, Jacobs A, Amblard F, Petit O, King AJ (2011a) How can social network analysis improve the study of primate
618 behaviour? *Am J Primatol* 73:703–719.
- 619 Sueur C, Petit O, De Marco A, Jacobs AT, Watanabe K, Thierry B (2011b) A comparative network analysis of social style in
620 macaques. *Anim Behav* 82:845-852.
- 621 Sueur C, Kuntz C, Debergue E, Keller B, Robic F, Siegwalt-Baudin F, Richer C, Ramos A, Pelé M (2018) Leadership linked
622 to group composition in Highland cattle (*Bos taurus*): Implications for livestock management. *Appl Anim Behav*
623 *Sci* 198:9-18.
- 624 Suomi SJ (1997) Early determinants of behaviour: evidence from primate studies. *Brit Med Bull* 53:170-184.
- 625 Tanaka I (1995) Matrilineal distribution of louse egg-handling techniques during grooming in free-ranging Japanese
626 macaques. *Am J Phys Anthropol* 98:197–201.
- 627 Thelen MH, Frautschi NM, Roberts MC, Kirkland KD, Dollinger SJ (1981) Being imitated, conformity, and social
628 influence: An integrative review. *J Res Pers* 15:403–426.

- 629 Thornton A, Malapert A (2009) Experimental evidence for social transmission of food acquisition techniques in wild
630 meerkats. *Anim Behav* 78:255–264.
- 631 Tomasello M (1990) Cultural transmission in the tool use and communicatory signalling of chimpanzees? In: Parker S,
632 Gibson K (ed) *Language and Intelligence in Monkeys and Apes: Comparative Developmental Perspectives*.
633 Cambridge University Press. England. pp 274
- 634 van de Waal E, Renevey N, Favre CM, Bshary R (2010) Selective attention to philopatric models causes directed social
635 learning in wild vervet monkeys. *Proc R Soc Lond B* 277:2105-2111.
- 636 van de Waal E, Bshary R (2011) Social-learning abilities of wild vervet monkeys in a two-step task artificial fruit
637 experiment. *Anim Behav* 81:433–438.
- 638 van de Waal E, Whiten A (2012) Spontaneous emergence, imitation and spread of alternative foraging techniques among
639 groups of vervet monkeys. *PLoS one* 7:e47008.
- 640 van de Waal E, Krützen M, Hula J, Goudet J, Bshary R (2012) Similarity in food cleaning techniques within matriline in
641 wild vervet monkeys. *PLoS one* 7:e35694.
- 642 van de Waal E, Borgeaud C, Whiten A (2013) Potent social learning and conformity shape a wild primate's foraging
643 decisions. *Science* 340:483-485.
- 644 van de Waal E, Bshary R, Whiten A (2014) Wild vervet monkey infants acquire the food-processing variants of their
645 mothers. *Anim Behav* 90:41–45.
- 646 Watts DP (1998) A preliminary study of selective visual attention in female mountain gorillas (*Gorilla gorilla beringei*).
647 *Primates* 39:71-78.
- 648 Watson KK, Werling DM, Zucker NL, Platt ML (2010) Altered Social Reward and Attention in Anorexia Nervosa. *Front*
649 *Psychol* 1.
- 650 Watson SK, Reamer LA, Mareno MC, Vale G, Harrison RA, Lambeth SP, Schapiro SJ, Whiten A (2017) Socially
651 transmitted diffusion of a novel behaviour from subordinate chimpanzees. *Am J Primatol* 79.
- 652 Whiten A, Byrne RW (1988) Tactical deception in primates. *Behavioural and Brain Sciences* 11:233–244.
- 653 Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama Y, Tutin CEG, Wrangham RW, Boesch C (1999)
654 Cultures in chimpanzees. *Nature* 399:682–685.
- 655 Whiten A (2017) A second inheritance system: The extension of biology through culture. *Interface Focus* 7:20160142.
- 656 Wrangham RW (1981) Drinking competition in vervet monkeys. *Anim Behav* 29:904-910.
- 657 Wu DWL, Bischof WF, Kingstone A (2013) Looking while eating: The importance of social context to social attention.
658 *Scient Rep* 3.
- 659

660 **Tables**661 **Table 1** Details of group compositions in NH, BD and AK groups.

	Group size	Immature*/adult individuals	Adults	Ratios ♀/♂			
				Juvenile subjects		Orphans	
				2 years-old	3	2	3
AK	33	17/16	10/6	1/8	1/2	0/2	0/1
BD	45	24/21	13/8	5/5	0/7	1/3	0/1
NH	45	26/19	12/7	2/3	2/7	0/0	0/1
Total	121	65/56	35/21	8/16	3/16	1/5	0/3

662 *over 1 year-old and less than 4 year-old

663

664 **Table 2** Predictors of social attention in juveniles including the proximity variable (five-meter perimeter
665 composition), obtained from combined group models. Significant predictors are displayed in bold, for the selected
666 best models ($\Delta AIC_c < 4$). *s*: subject, *T*: target. Variables are presented from the highest to the lowest relative variable
667 importance (RVI).

Parameter	Estimate	P-value	Relative importance
Orphan S	0.355	<0.001	1
Maternal relatedness			
0.5(mother)	0.755	<0.0001	1
0.25(siblings)	0.500	<0.001	
0.0625(cousins)	0.504	0.07	
Five-meter perimeter	0.971	<0.0001	1
Rank T	0.375	<0.0001	1
Age s (3)	-0.200	0.013	0.98
Rank s	-0.101	0.190	0.51
Sex s ♂	-0.084	0.324	0.49
Orphan s * Rank T	0.171	0.284	0.34
Sex s ♂ * Rank T	-0.180	0.209	0.19
Age s x Maternal relatedness			
3-years old * 0.5	-0.702	<u>0.07</u>	0.13
3-years old * 0.25	0.085	0.745	
3-years old * 0.0625	0.301	0.618	
Rank s * Rank T	-0.042	0.762	0.10

668

669

670 **Table 3** Predictors of social attention in juveniles from combined group models, without the proximity variable.
 671 Significant predictors are displayed in bold, for the selected best models ($\Delta AIC_c < 4$). *s*: *subject*, *T*: *target*. Variables
 672 are presented from the highest to the lowest relative variable importance (RVI).

Parameter	Estimate	P-value	Relative importance
Age s (3)	-0.168	0.049	1
Orphan s	0.308	0.001	1
Maternal relatedness			
0.5(mother)	1.218	<0.0001	1
0.25(siblings)	0.935	<0.0001	
0.0625(cousins)	0.782	0.014	
Rank T	0.288	<0.01	1
Sex s ♂	-0.119	0.162	0.77
Age s x Maternal relatedness			
3-years old * 0.5	-1.187	<0.01	0.77
3-years old * 0.25	-0.054	0.853	
3-years old * 0.0625	0.412	0.533	
Sex s ♂ * Rank T	-0.263	0.095	0.49
Rank s	-0.061	0.433	0.36
Sex T	-0.067	0.542	0.19
Rank s * Rank T	0.199	0.182	0.15
Group			0.11
BD	0.021	0.867	
NH	-0.134	0.318	
Orphan s * Rank T	0.156	0.377	

673

674 **Table 4** Predictors of spatial proximity in juveniles from combined group models. Significant predictors are
 675 displayed in bold, for the selected best models ($\Delta AIC_c < 4$). *s*: *subject*, *T*: *target*. Variables are presented from the
 676 highest to the lowest relative variable importance (RVI).

	Parameter	Estimate	P-value	Relative importance
<i>Nearest neighbour</i>	Maternal relatedness			1
	0.5(mother)	1.863	<0.0001	
	0.25(siblings)	1.240	<0.0001	
	0.0625(cousins)	1.005	0.015	
	Rank T	-0.314	0.034	0.94
	Rank s	0.091	0.269	0.61
	Rank T * Rank s	0.294	0.076	0.43
	Age s	-0.044	0.619	0.39
	Group			0.27
	BD	-0.313	0.103	
	NH	-0.151	0.437	

	Age s * Maternal relatedness			0.19
	3-years old * 0.5	-1.320	0.016	
	3-years old * 0.25	-0.207	0.572	
	3-years old * 0.0625	0.499	0.572	
	Sex s	-0.028	0.762	0.18
	Orphan	0.020	0.846	0.17
	Age T	0.777	<0.0001	1
	Orphan s	-0.188	0.0046	1
	Maternal relatedness			1
	0.5	1.107	<0.0001	
	0.25	0.540	<0.0001	
	0.0625	0.491	0.018	
	Rank s	0.068	0.183	1
	Rank T	0.119	0.146	1
	Rank T * Rank s	0.438	<0.0001	1
	Age s	-0.052	0.351	0.85
<i>Five-meter perimeter</i>	Age s * Maternal relatedness			0.71
	3-years old * 0.5	-0.564	0.031	
	3-years old * 0.25	-0.172	0.319	
	3-years old * 0.0625	0.641	0.109	
	Sex s ♂	-0.051	0.365	0.51
	Sex s * Rank T	-0.1660	0.106	0.30
	Ratio Age T	0.103	0.509	0.24
	Sex T ♂	0.010	0.903	0.23
	Age T * Sex T ♂	0.211	0.208	0.09
	Age T * Ratio Age T	-0.026	0.937	0.02

677

678 **Table 5** Predictors of social attention in juveniles from combined group models, without the proximity variable
679 and without adult males. Significant predictors are displayed in bold, for the selected best models ($\Delta AICc < 4$). *s*:
680 *subject*, *T*: *target*. Variables are presented from the highest to the lowest relative variable importance (RVI).

Parameter	Estimate	P-value	Relative importance
Age s (3)	-0.200	0.045	1
Orphan s	0.312	0.005	1
Maternal relatedness			1
0.5(mother)	1.14	<0.0001	
0.25(siblings)	0.887	<0.0001	
0.0625(cousins)	0.725	0.022	
Rank T	0.369	<0.001	1
Sex s ♂	-0.116	0.254	0.75
Age s x Maternal relatedness			0.73
3-years old * 0.5	-1.178	<0.01	
3-years old * 0.25	-0.047	0.871	

3-years old * 0.0625	0.450	0.494	
Sex s ♂ * Rank T	-0.333	<u>0.050</u>	0.56
Rank s	-0.042	0.642	0.52
Orphan s * Rank T	0.165	0.387	0.30
Rank s * Rank T	0.304	0.059	0.38

681

682 **Figures captions**

683 **Fig. 1** Social attention according to relatedness coefficients in the two age-classes of focal juveniles (named Observer): 2
684 years-old and 3 years-old. Social attention as measured by average of number of looks at others across 10 focal bouts per
685 juvenile. Maternal relatedness coefficients: 0.5= mother; 0.25= half-siblings; 0.0625= cousins/aunts; 0= unrelated.

686 Social attention towards matriline members of 0.0625 (maternal cousins/aunts) and 0.25 (half-siblings) relatedness
687 coefficients, is higher than towards non-matrilineal related individuals, independently of the age of the subject. Social attention
688 towards the focal juvenile's mother is higher than towards non-matrilineal group members and for 2 year-old than 3 year-old
689 subjects.

690

691 **Fig. 2a,b** Interaction between sex of the focal juveniles (named Observer) and rank of the target on social attention. Social
692 attention as measured by average of number of looks at others across 10 focal bouts per juvenile. Target rank: 0.05= (0, 0.1];
693 0.15= (0.1, 0.2] ... 0.95= (0.9, 1), 0=lowest ranked individuals; 1=highest ranked individuals. **a** With all target individuals. **b**
694 With target adult males removed.

695 The rank of the target influenced significantly the levels of juvenile social attention, with a trend of females showing this effect
696 more strongly. Removing all target adult males, led to a greater effect of the target rank on juvenile social attention.

697

698 **Fig. 3a,b,c,d** Social ego-networks of the two highest and lowest levels of social attention in the 2yo (highest: a. and lowest:
699 c.) and the 3yo focal juveniles (b. and d.).

700 Social attention as measured by the average of looks at others across the ten focal bouts. These social ego-networks are also
701 the two highest and lowest levels of social attention corrected by social proximity (number of times within the perimeter)
702 across ages (highest: a. and b., lowest: c. and d.). The central nodes represent the subjects/observers: the focal juveniles (O).
703 The target individuals (T) are positioned according to the data of proximity (number of times as the focal nearest neighbour
704 when present within the 5m perimeter) and the strength of the edges represents the number of looks of O towards T across ten
705 focal bouts of a 5min period. Males and females have names with three or four letters respectively. Adults have names with
706 capital letters. The green gradient represents the group social hierarchy. Lower-ranking individuals of the focal juvenile are
707 represented by white nodes, whereas higher-ranking ones by green nodes. Largest nodes are the highest-rated individuals in
708 each group (Elo-rating >0.8), wherein the darkest green nodes with names in white represent the alpha males and females.

709 Yellow nodes are the matriline members of the focal juvenile. Symbols indicate: □, the juvenile's mother (0.5 relatedness
710 coefficient); °, the juvenile's maternal sibling(s) (0.25) and * the maternal aunts/cousins (0.0625).

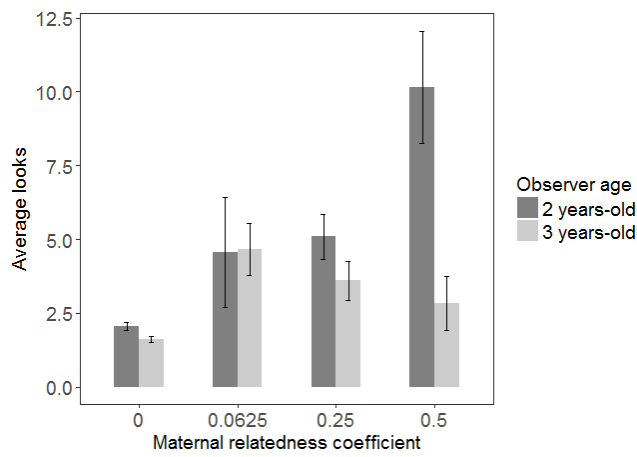
711 **a** Highest level of attention in the 2yo juveniles: *Hipp*, an orphaned female from BD (social rank: 0.534).
712 *Hipp* exhibited the highest attention towards the alpha female (*OULI*), yet only within 5m during one focal bout. She also
713 showed high attention towards her older half-sister (*HEER*); the two highest-ranked juvenile males (*Ogi* and *Poe*); the beta
714 male (*CHE*); and 2yo females, often within 5m (*Mevr* and *Nurk*).

715 **b** Highest level of social attention in the 3yo juveniles: *Vak*, an orphaned male from BD (social rank: 0.037).
716 *Vak* showed high attention towards two high-ranked adult females (*ASIS* and *HEER*) and with a lesser effect towards his half-
717 sibling (*Vul*) and one high-ranking juvenile male (*Ogi*).

718 **c** Lowest level of social attention in the 2yo juveniles: *Xian*, a female from NH (social rank: 0.594).
719 *Xian* exhibited social proximity and attention towards her maternal siblings (*Xer* and *Xala*) but only proximity to her mother
720 (*XAIX*).

721 **d** Lowest level of social attention in the 3yo juveniles: *Jun*, a male from NH (social rank: 0.445).
722 We used Gephi 0.9.2 (Bastian et al., 2009; <https://gephi.org/>) to do these figures.
723

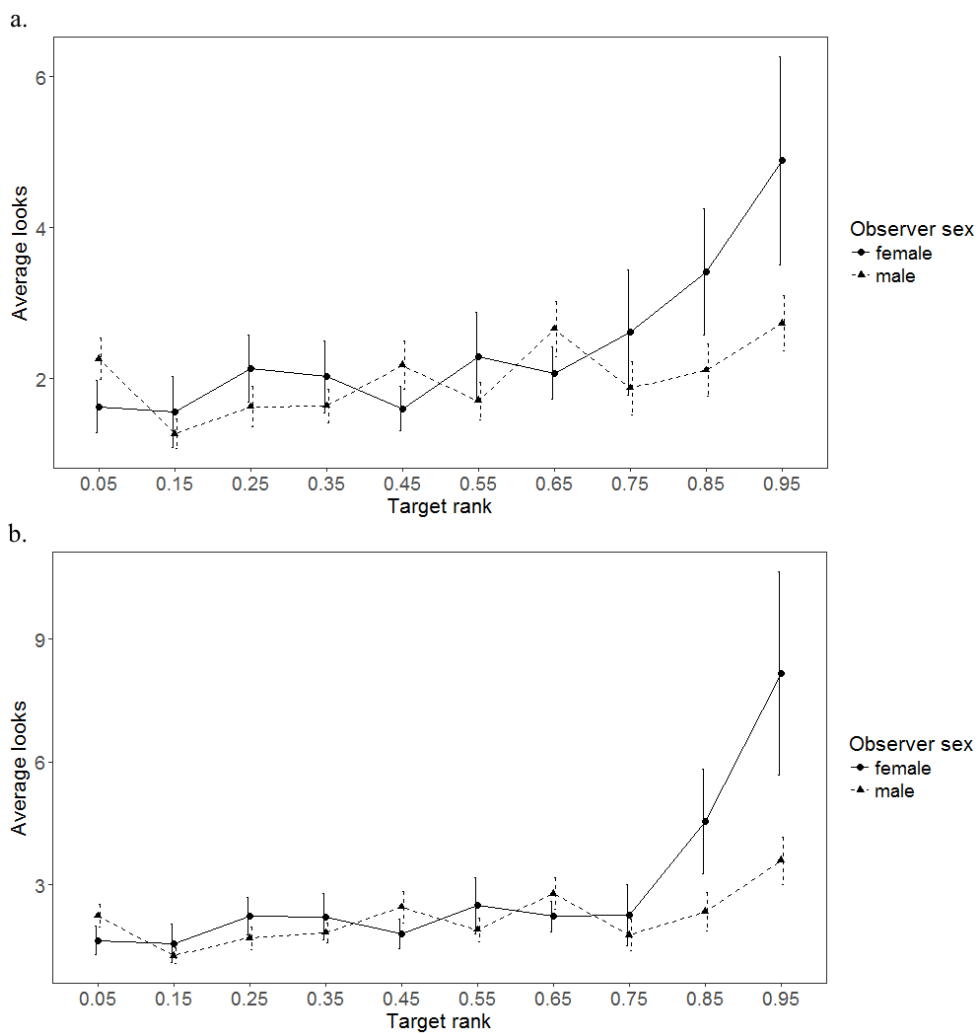
724 **Figures**



725

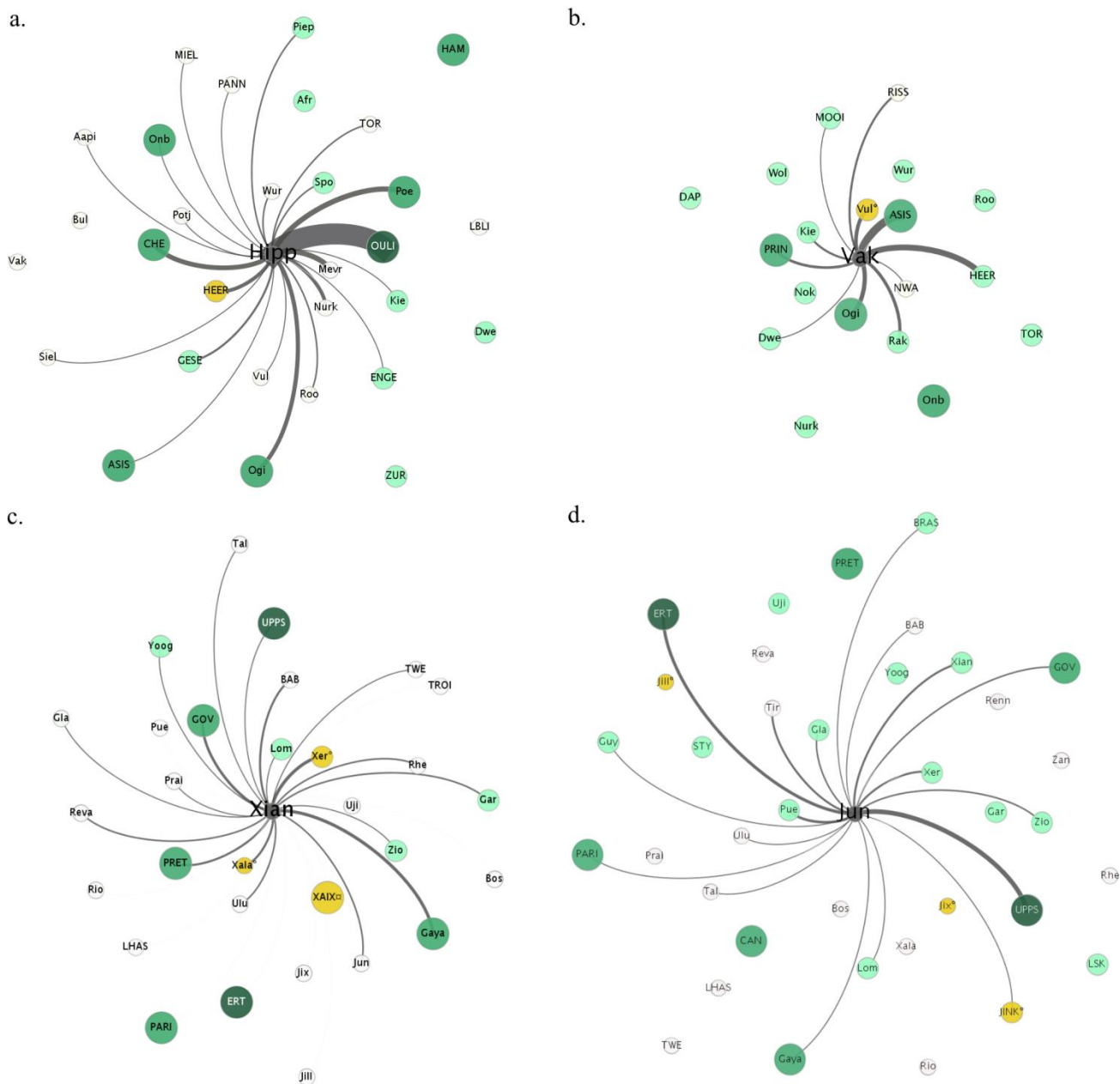
726 **Fig. 1**

727



729 **Fig. 2a,b**

730



731

732 **Fig. 3a,b,c,d**

733

734 **Supplementary material**

735 **Table 1** Dominance ranks given according to Elo-ratings in AK group, study period from 01/05/2015 (May) to
 736 03/08/2015 (August). *Names in italic are names of the focal juveniles.*

Name	Age	Sex	For May month	For June	For July	For August	Rank
GAGA	>6	f	1	1	1	1	1
GUGU	>6	f	0.966	0.965	0.965	0.965	0.965
ELT	>6	m	0.933	0.931	0.931	0.931	0.931
<i>Gele</i>	2	f	0.900	0.896	0.896	0.896	0.897
GHAN	>6	f	0.866	0.862	0.862	0.862	0.863
INHL	>6	f	0.833	0.827	0.827	0.827	0.828
<i>Gho</i>	2	m	0.800	0.793	0.793	0.793	0.794
Hib	4	m	0.766	x	x	x	0.766
<i>Hwa</i>	3	m	0.733	0.724	0.758	0.758	0.743
HAMB	>6	f	0.700	0.685	0.689	0.655	0.682
UMZ	>6	m	0.666	0.413	0.586	0.551	≠
Inkw	1	f	0.633	0.655	0.655	0.620	0.640
<i>Ubu</i>	3	m	0.600	0.620	0.620	0.586	0.606
FUD	>6	m	0.566	0.551	0.724	0.724	≠
<i>Unw</i>	2	m	0.533	0.586	0.517	0.482	0.529
<i>Hey</i>	2	m	0.500	0.310	0.310	0.275	0.348
NKOS	>6	f	0.466	0.517	0.482	0.689	≠
HLEK	>6	f	0.433	0.482	0.448	0.448	0.452
ISIL	>6	f	0.400	0.448	0.413	0.413	0.418
VOL	>6	m	0.366	0.758	0.551	0.517	≠
Ilon	1	f	0.333	0.379	0.379	0.344	0.382
<i>Nyo</i>	2	m	0.300	0.275	0.241	0.206	0.255
<i>Hol</i>	2	m	0.266	0.344	0.344	0.310	0.316
NDON	>6	f	0.233	0.206	0.206	0.172	0.204
<i>Idwa</i>	3	m	0.200	0.241	0.275	0.241	0.239
<i>Hlo</i>	2	m	0.166	0.172	0.172	0.103	0.153
Mba	1	m	0.133	0.137	0.137	0.068	0.118
MAMO	>6	f	0.100	0.103	0.103	0.137	0.110
<i>Iji</i>	2	m	0.066	0.034	0.068	0.034	0.05
Mvu	4	m	0.033	x	x	x	0.033
<i>Mun</i>	2	m	0	0	0.034	0	0.008
NMA (New male 1)	>6	m	x	x	0	0.379	≠
NWM (New male 2)	>6	m	x	x	x	x	0.001
WOLFIE	>6	m	x	x	x	x	0.001

738 **Table 2** Dominance ranks given according to Elo-ratings in BD group, study period from 21/03/2015 (March) to
 739 29/07/2015 (July). *Names in italic are names of the focal juveniles.* Social ego-networks of underlined focal
 740 individuals in Fig.3.

Name	Age	Sex	For					Rank
			March month	For April	For May	For June	For July	
OULI	>6	f	1	1	1	1	1	1
MAD	>6	m	0.976	0.976	0.976	0.975	0.897	0.960
ASIS	>6	f	0.953	0.953	0.952	0.951	0.974	0.956
CHE	>6	m	0.928	0.926	0.906	0.930	0.948	0.927
<i>Ogi</i>	3	m	0.883	0.906	0.857	0.853	0.846	0.869
PRIN	>6	f	0.860	0.883	0.880	0.878	0.871	0.874
<i>Onb</i>	2	m	0.837	0.860	0.809	0.804	0.692	0.800
<i>Poe</i>	3	m	0.813	0.744	0.833	0.829	0.820	0.807
NEU	>6	m	0.790	0.813	0.905	0.902	0.923	0.866
Dwe	4	m	0.767	0.837	0.761	0.780	0.769	0.782
HEER	>6	f	0.744	0.604	0.619	0.560	0.307	≠
GESE	>6	f	0.720	0.790	0.619	0.756	0.743	0.727
ZUR	>6	m	0.697	0.767	0.785	0.609	0.794	0.730
Afr	4	m	0.674	0.674	0.666	0.658	x	0.668
ENGE	>6	f	0.651	0.627	0.595	0.682	0.641	0.639
SNOR	>6	f	0.627	0.581	0.571	0.585	0.615	0.595
NUMB	>6	f	0.604	0.558	0.547	0.487	0.512	0.541
<i>Piep</i>	2	f	0.581	0.651	0.714	0.731	0.717	0.678
Kie	4	m	0.558	0.697	0.690	0.707	x	0.663
TOR	>6	m	0.511	0.488	0.476	0.512	0.538	0.505
DAP	>6	m	0.488	0.534	0.238	0.268	0.461	≠
<i>Spo</i>	3	m	0.465	0.465	0.642	0.634	0.666	0.574
<u><i>Hipp</i></u>	2	f	0.534	0.511	0.5	0.536	0.589	0.534
<i>Nok</i>	3	m	0.441	0.441	0.452	0.121	0.179	0.326
<i>Akk</i>	3	m	0.418	0.418	0.428	0.439	0.564	0.453
<i>Siel</i>	2	f	0.395	0.395	0.404	0.414	0.435	0.408
MIEL	>6	f	0.372	0.186	0.190	0.146	0.128	0.204
MOOI	>6	f	0.348	0.372	0.523	x	x	0.414
Potj	1	f	0.325	0.348	0.380	0.390	0.410	0.370
Rak	2	m	0.302	0.325	0.333	0.317	0.333	0.322
Aapi	1	f	0.279	0.279	0.285	0.292	0.282	0.283
Roo	3	m	0.255	0.255	0.261	0.463	0.487	0.344
Wol	4	m	0.232	0.209	0.214	0.243	x	0.224
Bul	2	m	0.209	0.162	0.166	0.219	0.256	0.202
Mevr	2	f	0.186	0.116	0.119	0.341	0.358	0.224
<i>Alsi</i>	2	f	0.162	0.302	0.357	0.365	0.384	0.314

PANN	>6	f	0.139	0.139	0.142	0.097	0.153	0.134
<i>Nurk</i>	2	f	0.116	0.232	0.309	0.195	0.230	0.216
<i>Wur</i>	2	m	0.093	0.093	0.023	0	0	0.041
<i>Vul</i>	2	m	0.069	0.069	0.095	0.170	0.205	0.121
<u><i>Vak</i></u>	3	m	0.046	0.046	0.047	0.024	0.025	0.037
RISS	>6	f	0.023	0.023	0	0.048	0.051	0.029
LBLI	>6	f	0	0	0.071	0.073	0.076	0.044
NWA (New male)	>6	m	x	x	x	x	0.102	0.102
HAM	>6	m	0.930	0.720	x	x	x	0.825

741

742 **Table 3** Dominance ranks given according to Elo-ratings in NH group, study period from 02/04/2015 (April) to
743 03/08/2015 (August). *Names in italic are names of the focal juveniles.* Social ego-networks of underlined focal
744 individuals in Fig. 3.

Name	Age	Sex	For April month	For May	For June	For July	For August	Rank
UPPS	>6	f	1	1	1	1	1	1
ERT	>6	m	0.977	0.977	0.976	0.928	0.928	0.957
GENE	>6	f	0.954	0.954	0.953	0.976	0.952	0.957
<i>Gaya</i>	3	f	0.931	0.931	0.930	0.952	0.976	0.944
CAN	>6	m	0.909	0.909	0.906	0.833	0.761	≠
GOV	>6	m	0.886	0.886	0.860	0.857	0.857	0.869
STY	>6	m	0.863	0.840	0.837	0.33	0.261	≠
XAIX	>6	f	0.840	0.795	0.790	0.809	0.880	0.822
PRET	>6	f	0.818	0.818	0.818	0.904	0.904	0.851
LSK	>6	m	0.795	0.500	0.511	x	x	≠
PARI	>6	f	0.772	0.863	0.883	0.880	0.714	0.822
ZARA	>6	f	0.750	0.772	0.767	0.785	0.833	0.781
<i>Gar</i>	2	m	0.727	0.704	0.674	0.690	0.595	0.678
Yoog	2	f	0.704	0.750	0.720	0.738	0.619	0.706
Bras	4	f	0.681	0.727	0.697	0.714	0.642	0.692
<i>Zio</i>	3	m	0.659	0.681	0.651	0.666	0.809	0.693
<i>Xer</i>	3	m	0.636	0.659	0.627	0.595	0.500	0.603
<u><i>Xian</i></u>	2	f	0.613	0.636	0.604	0.642	0.476	0.594
<i>Lom</i>	3	m	0.590	0.590	0.744	0.761	0.785	0.699
Guy	4	m	0.568	0.613	x	x	x	0.590
Uji	1	m	0.545	0.568	0.581	0.571	0.666	0.586
<i>Pue</i>	3	m	0.522	0.545	0.558	0.547	0.690	0.572
Gla	1	m	0.500	0.522	0.534	0.523	0.452	0.506
JINK	>6	f	0.477	0.477	0.465	0.476	0.571	0.493
<u><i>Jun</i></u>	3	m	0.454	0.454	0.441	0.452	0.428	0.445
<i>Zan</i>	1	m	0.431	0.431	0.395	0.404	0.357	0.403
BAB	>6	m	0.409	0.409	0.488	0.500	0.547	0.470

Rio	4	m	0.386	0.363	0.418	0.428	0.380	0.395
Prai	1	f	0.363	0.340	0.348	0.357	0.285	0.338
Jill	2	f	0.340	0.318	0.116	0.071	0.071	0.187
JAKA	>6	f	0.318	0.295	0.325	0.309	0.214	0.292
Xala	1	f	0.295	0.272	0.302	0.285	0.190	0.268
Ulu	3	m	0.272	0.386	0.372	0.380	0.738	0.429
TWE	>6	m	0.250	0.250	0.255	0.619	0.523	0.379
TROI	>6	f	0.227	0.227	0.232	0.190	0.333	0.241
LHAS	>6	f	0.204	0.204	0.186	0.142	0.404	0.228
Jix	1	m	0.181	0.181	0.162	0.238	0.166	0.195
Tir	2	m	0.159	0.159	0.209	0.166	0.238	0.186
Bos	1	m	0.136	0.136	0.139	0.119	0.119	0.129
Tal	3	m	0.113	0.113	0.279	0.214	0.142	0.172
ROMA	>6	f	0.090	0.090	0.093	0.095	0.095	0.092
BOGO	>6	f	0.068	0.068	0.069	0.261	0.309	0.155
Renn	1	f	0.045	0.045	0.046	0.047	0.047	0.046
Reva	3	f	0.022	0.022	0.023	0.023	0	0.018
Rhe	2	m	0	0	0	0	0.023	0.004

745

746 **Table 4** Best models selected to explain the variance of number of looks in table 2 in the main text.

1	Age of observer
2	Age of target
3	Orphan
4	Sex of observer
5	Sex of target
6	Maternal relatedness
7	Rank of observer
8	Ratio age of target
9	Rank of target
10	Age of observer * Maternal relatedness
11	Age of target * Sex of observer
12	Age of target * Ratio age of target
13	Sex of observer * Rank of target
14	Rank of target * Rank of observer

747

Component of models	df	Δ AICc	Weight
1/2/3/6/7/9/10/14	17	0	0.16
1/2/3/4/6/7/9/10/13/14	19	1.19	0.09
1/2/3/4/6/7/9/10/14	18	1.43	0.08
1/2/3/6/7/8/9/10/14	18	1.65	0.07
1/2/3/5/6/7/9/10/14	18	2.00	0.06
2/3/4/6/7/9/13/14	15	2.09	0.05
1/2/3/6/7/9/14	14	2.41	0.05
1/2/3/5/6/7/9/10/11/14	19	2.47	0.05
1/2/3/4/6/7/9/13/14	16	2.66	0.04
2/3/6/7/9/14	13	2.70	0.04
1/2/3/4/6/7/8/9/10/13/14	20	2.83	0.04
1/2/3/4/6/6/8/9/10/14	19	3.09	0.03
1/2/3/4/5/6/7/9/10/13/14	20	3.20	0.03
2/3/4/6/7/9/14	14	3.28	0.03
1/2/3/4/5/6/7/9/10/14	19	3.43	0.03
2/3/4/6/7/8/9/13/14	16	3.56	0.03

1/2/3/5/6/7/8/9/10/14	19	3.63	0.03
1/2/3/6/7/8/9/10/12/14	19	3.68	0.02
1/2/3/4/5/6/7/9/10/11/13/14	21	3.72	0.02
1/2/3/4/6/7/9/14	15	3.77	0.02
1/2/3/6/7/8/9/14	15	3.83	0.02
1/2/3/4/5/6/7/9/10/11/14	20	3.92	0.02

748

749 **Table 5** Best models selected to explain the variance of number of looks in table 3 in the main text.

1	Age of observer
2	Orphan
3	Sex of observer
4	Sex of target
5	Group's identity
6	Maternal relatedness
7	Rank of observer
8	Rank of target
9	Group ratio of sex of target
10	Maternal relatedness * Age of observer
11	Orphan observer * Rank of target
12	Sex of observer * Rank of target
13	Rank of observer * Rank of target

750

Component of models	df	Δ AICc	Weight
1/2/3/6/8/10/12	17	0	0.05
1/2/3/6/8/10	16	0.41	0.04
1/2/6/8/10	15	0.44	0.04
1/2/3/6/8/12	14	1.10	0.03
1/2/3/6/8/10/11/12	18	1.21	0.03
1/2/3/6/7/8/10/12	18	1.43	0.02
1/2/3/6/8/9/10/12	18	1.48	0.02
1/2/3/4/6/8/10/12	18	1.55	0.02
1/2/3/6/7/8/10	17	1.89	0.02
1/2/6/8/10/11	16	1.91	0.02
1/2/3/6/7/8/10/12/13	19	1.91	0.02
1/2/3/6/8/10/11	17	1.91	0.02
1/2/3/6/8/9/10	17	1.97	0.02
1/2/6/8/9/10	16	2.01	0.02
1/2/3/4/6/8/10	17	2.03	0.02
1/2/4/6/8/10	16	2.07	0.02
1/2/3/5/6/8/10/12	19	2.09	0.02
1/2/3/6/7/8/10/13	18	2.10	0.02
1/2/3/6/8/11/12	15	2.13	0.02
1/2/6/7/8/10	16	2.18	0.02
1/2/3/6/8/9/12	15	2.36	0.02
1/2/3/6/8	13	2.39	0.02
1/2/6/7/8/10/13	17	2.41	0.02
1/2/3/6/7/8/12	15	2.47	0.01
1/2/3/5/6/8/10	18	2.58	0.01
1/2/3/4/6/8/12	15	2.61	0.01
1/2/6/8	12	2.65	0.01
1/2/3/6/8/9/10/11/12	19	2.68	0.01
1/2/3/6/7/8/10/11/12	19	2.69	0.01
1/2/5/6/8/10	17	2.74	0.01
1/2/3/4/6/8/10/11/12	19	2.79	0.01
1/2/3/6/7/8/10/11/12/13	20	2.97	0.01
1/2/3/6/7/8/9/10/12	19	3.01	0.01
1/2/3/4/6/7/8/10/12	19	3.05	0.01
1/2/3/5/6/8/12	16	3.06	0.01
1/2/3/6/7/8/12/13	16	3.29	0.01
1/2/3/6/7/8/10/11/13	19	3.33	0.01
1/2/3/6/8/9/11/12	16	3.41	0.01

1/2/3/5/6/7/8/10/12	20	3.42	0.01
1/2/3/5/6/8/10/11/12	20	3.43	0.01
1/2/3/6/7/8/10/11	18	3.44	0.01
1/2/3/6/7/8/9/10/12/13	20	3.44	0.01
1/2/3/6/8/9/10/11	18	3.46	0.01
1/2/6/8/9/10/11	17	3.46	0.01
1/2/3/4/6/7/8/10/12/13	20	3.50	0.01
1/2/3/6/7/8/9/10	18	3.52	0.01
1/2/3/5/6/8/9/10/12	20	3.52	0.01
1/2/3/4/6/8/10/11	18	3.53	0.01
1/2/6/7/8/10/11/13	18	3.54	0.01
1/2/4/6/8/10/11	17	3.54	0.01
1/2/3/4/6/7/8/10	18	3.54	0.01
1/2/3/4/6/8/9/10/12	19	3.55	0.01
1/2/3/6/7/8/11/12	16	3.55	0.01
1/2/3/4/6/8/11/12	16	3.59	0.01
1/2/3/4/5/6/8/10/12	20	3.66	0.01
1/2/6/7/8/10/11	17	3.67	0.01
1/2/3/6/7/8/9/10/13	19	3.68	0.01
1/2/3/4/6/7/8/10/13	19	3.70	0.01
1/2/3/6/8/9	14	3.73	0.01
1/2/3/6/7/8/11/12/13	17	3.76	0.01
1/2/6/7/8/9/10	17	3.79	0.01
1/2/3/6/8/11	14	3.79	0.01
1/2/3/6/7/8/9/12	16	3.80	0.01
1/2/3/6/7/8	14	3.82	0.01
1/2/4/6/7/8/10	17	3.83	0.01
1/2/3/5/6/7/8/10	19	3.85	0.01
1/2/3/5/6/7/8/10/12/13	21	3.89	0.01
1/2/3/4/6/8	14	3.94	0.01
1/2/6/8/9	13	3.96	0.01
1/2/6/8/11	13	3.97	0.01
1/2/3/5/6/8/9/10	19	3.98	0.01
1/2/3/4/6/7/8/12	16	3.99	0.01
1/2/6/7/8/9/10/13	18	4.00	0.01

751

752 **Table 6** Best models selected to explain the variance of the proximity variables: the nearest neighbour's identity
753 and the five-meter perimeter composition, respectively, in table 4 in the main text.

1	Age of observer
2	Orphan
3	Sex of observer
4	Group
5	Maternal relatedness
6	Rank of observer
7	Rank of target
8	Age of observer * Maternal relatedness
9	Rank of target * Rank of observer

754

Component of models	df	Δ AICc	Weight
5/6/7/9	12	0	0.08
5/7	10	0.13	0.08
5/6/7	11	1.13	0.05
4/5/6/7/9	14	1.34	0.04
1/2/6/7/8/9	16	1.37	0.04
1/5/6/7/9	13	1.38	0.04
4/5/7	12	1.44	0.04
1/5/7	11	1.89	0.03
3/5/6/7/9	13	1.91	0.03
2/5/6/7/9	13	1.97	0.03
1/5/7/8	14	1.98	0.03
3/5/7	11	2.03	0.03

2/5/7	11	2.15	0.03
1/5/6/7	12	2.46	0.02
1/5/6/7/8	15	2.47	0.02
4/5/6/7	13	2.47	0.02
5	9	2.55	0.02
1/4/5/6/7/9	15	2.84	0.02
1/4/5/6/7/8/9	18	3.00	0.02
3/5/6/7	12	3.06	0.02
2/5/6/7	12	3.11	0.02
3/4/5/6/7/9	15	3.14	0.02
3/4/5/7	13	3.24	0.02
1/4/5/7	13	3.27	0.02
2/4/5/6/7/9	15	3.29	0.02
1/2/5/6/7/8/9	17	3.34	0.02
1/2/5/6/7/9	14	3.37	0.02
1/3/5/6/7/9	14	3.40	0.02
1/3/5/6/7/8/9	17	3.41	0.02
2/4/5/7	13	3.45	0.02
1/4/5/7/8	16	3.54	0.01
5/6	10	3.70	0.01
2/3/5/6/7/9	14	3.85	0.01
1/3/5/7	12	3.87	0.01
1/2/5/7	12	3.91	0.01
1/4/5/6/7	14	3.92	0.01
4/5	11	3.92	0.01
1/5/8	13	3.96	0.01
1/3/5/7/8	15	3.99	0.01

755

756

1	Age of observer
2	Age of target
3	Orphan
4	Sex of observer
5	Sex of target
6	Maternal relatedness
7	Rank of observer
8	Ratio age of target
9	Rank of target
10	Age of observer * Maternal relatedness
11	Age of target * Sex of observer
12	Age of target * Ratio age of target
13	Rank of target * Rank of observer

757

Component of models	df	Δ AICc	Weight
1/2/3/6/7/9/10/13	17	0	0.22
1/2/3/4/6/7/9/10/13	18	1.43	0.11
1/2/3/6/7/8/9/10/13	18	1.65	0.10
1/2/3/5/6/7/9/10/13	18	2.00	0.08
1/2/3/6/7/9/13	14	2.41	0.07
1/2/3/5/6/7/9/10/11/13	19	2.47	0.06
2/3/6/7/9/13	13	2.70	0.05
1/2/3/4/6/7/8/9/10/13	19	3.09	0.04
2/3/4/6/7/9/13	14	3.28	0.04
1/2/3/4/5/6/7/9/10/13	19	3.43	0.04
1/2/3/5/6/7/8/9/10/13	19	3.63	0.04
1/2/3/6/7/8/9/10/12/13	19	3.68	0.04
1/2/3/4/6/7/9/13	15	3.77	0.03
1/2/3/6/7/8/9/13	15	3.83	0.03
1/2/3/4/5/6/7/9/10/11/13	20	3.92	0.03

758

759 **Table 7** Best models selected to explain the variance of number of looks in table 5 in the main text (without
760 proximity variable and the target adult males).

1	Age of observer
2	Orphan
3	Sex of observer
4	Maternal relatedness
5	Rank of observer
6	Rank of target
7	Maternal relatedness * Age of observer
8	Orphan observer * Rank of target
9	Sex of observer * Rank of target
10	Rank of target * Rank of observer

761

Component of models	df	Δ AICc	Weight
1/2/3/4/6/7/9	17	0	0.11
1/2/3/4/5/6/7/9/10	19	0.83	0.07
1/2/3/4/6/9	14	0.92	0.07
1/2/4/6/7	15	1.07	0.07
1/2/4/5/6/7/10	17	1.21	0.06
1/2/3/4/6/7/8/9	18	1.44	0.06
1/2/3/4/6/7	16	1.56	0.05
1/2/3/4/5/6/7/10	18	1.75	0.05
1/2/3/4/5/6/7/8/9/10	20	1.79	0.05
1/2/3/4/5/6/7/9	18	1.90	0.04
1/2/3/4/5/6/9/10	16	1.93	0.04
1/2/3/4/6/8/9	15	2.16	0.04
1/2/4/5/6/7/8/10	18	2.43	0.03
1/2/3/4/5/6/8/9/10	17	2.67	0.03
1/2/4/6/7/8	16	2.75	0.03
1/2/3/4/5/6/9	15	2.76	0.03
1/2/3/4/5/6/7/8/10	19	3.02	0.02
1/2/4/5/6/7	16	3.11	0.02
1/2/3/4/6/7/8	17	3.27	0.02
1/2/4/6	12	3.34	0.02
1/2/3/4/5/6/7/8/9	19	3.36	0.02
1/2/3/4/5/6/7	17	3.52	0.02
1/2/4/5/6/10	14	3.65	0.02
1/2/3/4/6	13	3.69	0.02

762

763 **Table 8** Predictors of social attention in juveniles, without immature target individuals, obtained from combined
764 group models. Significant predictors are displayed in bold, for the selected best models (Δ AICc<4). *O*: observer,
765 *T*: target.

Parameter	Estimate	P-value	Relative importance	Best models (Δ AICc<4)
Maternal relatedness			1	19
0.5(mother)	1.240	<0.0001		
Rank T	0.584	0.0001	1	19
Sex T ♂	-0.375	0.027	0.80	13
Age O (3)	-0.117	0.434	0.70	13
Sex O ♂	-0.078	0.607	0.67	12
Sex O ♂ * Rank T	-0.595	0.033	0.57	9
Age O x Maternal relatedness			0.45	7
3 years-old * 0.5	-1.331	<0.01		

Group				0.12	4
	BD	-0.157	0.441		
	NH	-0.262	0.220		

766

767 **Table 9** Best models selected to explain the variance of number of looks in table 8 of the supplementary material,
768 only with adult target individuals.

1	Age of observer
2	Sex of observer
3	Sex of target
4	Group's identity
5	Maternal relatedness
6	Rank of target
7	Maternal relatedness * Age of observer
8	Sex of observer * Rank of target

769

Component of models	df	$\Delta AICc$	Weight
1/2/3/5/6/7/8	16	0	0.14
1/3/5/6/7	14	0.21	0.13
2/3/5/6/8	12	0.30	0.12
1/2/3/5/6/8	13	0.64	0.10
1/2/3/5/6/7	15	1.96	0.05
1/3/5/6	11	2.11	0.05
2/3/4/5/6/8	14	2.17	0.05
3/5/6	10	2.21	0.05
1/5/6/7	13	2.30	0.04
2/5/6/8	11	2.48	0.04
1/2/5/6/7/8	15	2.51	0.04
1/2/5/6/8	12	2.91	0.03
1/2/3/4/5/6/7/8	18	3.19	0.03
2/3/5/6	11	3.24	0.03
1/2/3/4/5/6/8	15	3.50	0.02
1/3/4/5/6/7	16	3.59	0.02
1/2/3/5/6	12	3.74	0.02
1/5/6	10	3.92	0.02
5/6	9	3.95	0.02

770