Social attention biases in juvenile wild vervet monkeys; implications for socialisation

2 and social learning processes.

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

- ¹Université de Strasbourg, Faculté des Sciences de la Vie, 28 rue Goethe, 67000 Strasbourg, France, ²Inkawu
- 6 Vervet Project, KwaZulu-Natal, South Africa, ³ Université de Strasbourg, CNRS, IPHC UMR 7178, F-67000
- 7 Strasbourg, France, ⁴Department of Ecology and Evolution, University of Lausanne, ⁵School of Psychology &
- 8 Neuroscience, University of St Andrews
- 9 *Corresponding author e-mail address: mathilde.grampp@outlook.fr
- 10 ° Joint last authors

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Abstract

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

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

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

Introduction

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

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

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

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

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

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

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

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

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

Methods

Study site and subjects

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

Data collection

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

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

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

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

Data analysis

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

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

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

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

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

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

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Results

Social attention

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

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

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

Social proximity

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

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

Discussion

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

Maternal relatedness

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

Social rank

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

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

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

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

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

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

Sex

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

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

Age

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

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

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

Orphans

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

Conclusions

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

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

Compliance with Ethical Standards

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660 <u>Tables</u>

Table 1 Details sf group compositions in NH, BD and AK groups.

•	Group Immature*/adult size individuals Adu			Ratios ♀/♂				
		Immature*/adult	Juvenile subjects		Orphans			
		Tidates	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	

^{*}over 1 year-old and less than 4 year-old

Table 2 Predictors sf social attention in juveniles including the proximity variable (five-meter perimeter composition), obtained from combined group models. Significant predictors are displayed in bold, for the selected best models (ΔAICc<4). *s: subject, T: target*. Variables are presented from the highest to the lowest relative variable 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	1
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	0.07	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

Table 3 Predictors of social attention in juveniles from combined group models, without the proximity variable. Significant predictors are displayed in bold, for the selected best models (ΔAICc<4). *s: 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)	-0.168	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	1
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	

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

	Parameter	Estimate	P-value	Relative importance
	Maternal relatedness			1
	0.5(mother)	1.863	< 0.0001	
	0.25(siblings)	1.240	< 0.0001	
	0.0625(cousins)	1.005	0.015	
Nearest	Rank T	-0.314	0.034	0.94
neighbour	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
Five-meter	Age s	-0.052	0.351	0.85
perimeter	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

Table 5 Predictors of social attention in juveniles from combined group models, without the proximity variable and without adult males. Significant predictors are displayed in bold, for the selected best models (ΔAICc<4). *s: 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 d	-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	

Figures captions

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

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

Fig. 2a,b Interaction between sex of the focal juveniles (named Observer) and rank of the target on social attention. Social attention as measured by average of number of looks at others across 10 focal bouts per juvenile. Target rank: 0.05= (0, 0.1]; 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** With target adult males removed.

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

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: c.) and the 3yo focal juveniles (b. and d.).

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

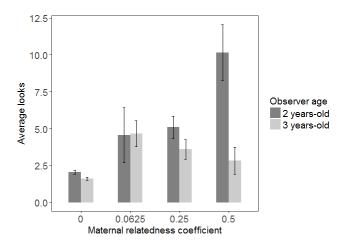
d Lowest level of social attention in the 3yo juveniles: Jun, a male from NH (social rank: 0.445).

We used Gephi 0.9.2 (Bastian et al., 2009; https://gephi.org/) to do these figures.

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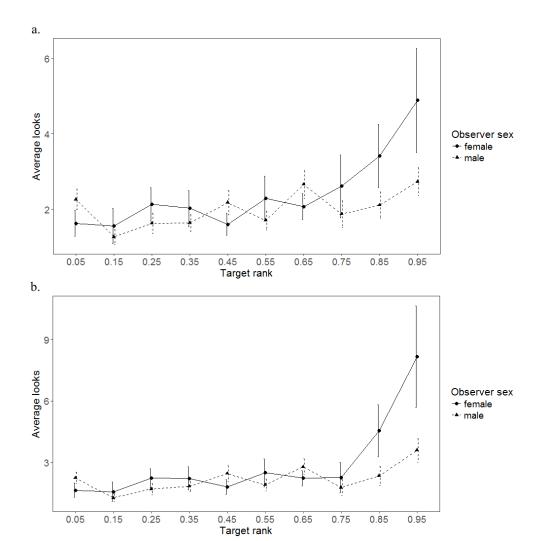
724 <u>Figures</u>



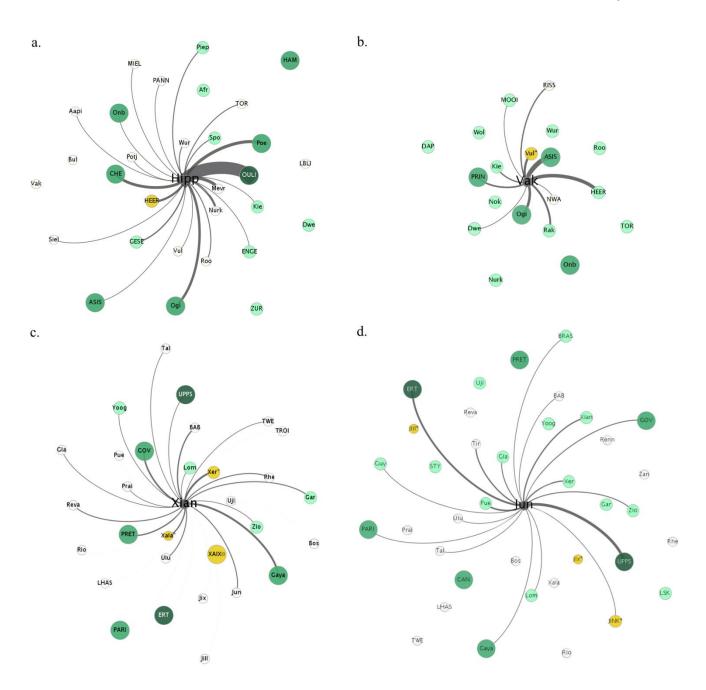
726 Fig. 1

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729 Fig. 2a,b



732 Fig. 3a,b,c,d

Supplementary material

Table 1 Dominance ranks given according to Elo-ratings in AK group, study period from 01/05/2015 (May) to 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
Gele	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
Gho	2	m	0.800	0.793	0.793	0.793	0.794
Hib	4	m	0.766	X	X	x	0.766
Hwa	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	<i>≠</i>
Inkw	1	f	0.633	0.655	0.655	0.620	0.640
Ubu	3	m	0.600	0.620	0.620	0.586	0.606
FUD	>6	m	0.566	0.551	0.724	0.724	<i>≠</i>
Unw	2	m	0.533	0.586	0.517	0.482	0.529
Hey	2	m	0.500	0.310	0.310	0.275	0.348
NKOS	>6	f	0.466	0.517	0.482	0.689	<i>≠</i>
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	<i>≠</i>
Ilon	1	f	0.333	0.379	0.379	0.344	0.382
Nyo	2	m	0.300	0.275	0.241	0.206	0.255
Hol	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
Idwa	3	m	0.200	0.241	0.275	0.241	0.239
Hlo	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
	2	m	0.066	0.034	0.068	0.034	0.05
Mvu	4	m	0.033	X	X	X	0.033
Mun	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

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

			For					
Name	Age	Sex	March	For April	For May	For June	For July	Rank
			month					
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
СНЕ	>6	m	0.928	0.926	0.906	0.930	0.948	0.927
Ogi	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
Onb	2	m	0.837	0.860	0.809	0.804	0.692	0.800
Poe	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
Piep	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	#
Spo	3	m	0.465	0.465	0.642	0.634	0.666	0.574
<u>Hipp</u>	2	f	0.534	0.511	0.5	0.536	0.589	0.534
Nok	3	m	0.441	0.441	0.452	0.121	0.179	0.326
Akk	3	m	0.418	0.418	0.428	0.439	0.564	0.453
Siel	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
Alsi	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
Nurk	2	f	0.116	0.232	0.309	0.195	0.230	0.216
Wur	2	m	0.093	0.093	0.023	0	0	0.041
Vul	2	m	0.069	0.069	0.095	0.170	0.205	0.121
<u>Vak</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
22.2172			0.250	020				

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

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
Gaya	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	<i>≠</i>
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	<i>≠</i>
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	<i>≠</i>
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
Gar	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
Zio	3	m	0.659	0.681	0.651	0.666	0.809	0.693
Xer	3	m	0.636	0.659	0.627	0.595	0.500	0.603
<u>Xian</u>	2	f	0.613	0.636	0.604	0.642	0.476	0.594
Lom	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
Pue	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>Jun</u>	3	m	0.454	0.454	0.441	0.452	0.428	0.445
Zan	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

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
8 9 10 11 12 13	Ratio age of target Rank of target Age of observer * Maternal relatedness Age of target * Sex of observer Age of target * Ratio age of target Sex of observer * Rank of target

Component of models	df	ΔAICc	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

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

Component of models	df	ΔAICc	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

Table 6 Best models selected to explain the variance of the proximity variables: the nearest neighbour's identity 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

Component of models	df	ΔAICc	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

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

Component of models	df	ΔAICc	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

Table 7 Best models selected to explain the variance of number of looks in table 5 in the main text (without 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

Component of models	df	ΔAICc	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
1/2/3/45/6/7/9	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

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

Parameter	Estimate	P-value	Relative importance	Best models
				$(\Delta AICc < 4)$
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

Table 9 Best models selected to explain the variance of number of looks in table 8 of the supplementary material, 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

Component of models	df	ΔAICc	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