







Strong ties formation, composition and processes at play during the developmental period of juvenile vervet monkeys

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Understanding the development of social relationships can provide insights into the processes by which social network structures emerge and vary across species. Here we extend a previous analysis (Vilette et al., 2022, *Animal Behaviour*, 194, 205–223) that tested Kohn's (2019, *Animal Behaviour*, 154, 1–6) model of social relationship formation in three groups of wild juvenile vervet monkeys, *Chlorocebus pygerythrus*. This previous analysis showed that, although developmental patterns did not conform to the exploration, pruning and consolidation phases identified by Kohn (2019), juveniles formed a core of strong social ties (a social 'bubble') across development. Here, we use a novel approach to objectively extract strong ties and ask whether Kohn's (2019) phases are more appropriately evaluated with reference to the subset of strong ties that constitute social bubbles. We investigate social bubble formation and composition, as well as the role of maternal behaviour in the development of these bubbles. As before, spatial and grooming social bubbles did not develop according to Kohn's (2019) framework. On the one hand, spatial bubbles were composed mainly of juveniles and showed increased association rates for family members during the annual birth season. Juvenile grooming bubbles, on the other hand, were stable over time and restricted solely to their mothers. Resulting from this, we found that juveniles did not simply groom their closest spatial associates but distributed their grooming towards specific partners. Finally, we found that a mother's grooming ties and her offspring's grooming weak ties remained mostly different as juveniles developed. This finding supports a previous analysis on our population (Jarrett et al., 2018, *Proceedings of the Royal Society B: Biological Sciences*, 285(1876), Article 20172668), where juveniles had to develop connections with nonmaternal associates in order to replicate the overall grooming network. These results indicate that the structure and composition of social bubbles in our sample reflect both the behaviour under consideration (grooming or spatial proximity) and group demography.

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The prolonged developmental period of juvenile primates has been argued to contribute to their becoming the 'best possible adult' (Alexander, 1990; Fairbanks & Pereira, 1993). In line with this, a number of authors have suggested that juveniles use their extended developmental period to acquire the social knowledge needed to navigate their social groups, negotiate their social environments and establish and sustain fitness-enhancing social relationships (Archie et al., 2014; Bray et al., 2021; Cameron et al., 2009; Cheney et al., 2016; Deputte, 2000; Fairbanks, 2002; Feldblum et al., 2021; Frere et al., 2010; Schülke et al., 2010; Silk et al., 2003, 2009, 2010a; Stanton & Mann, 2012). In this regard, sex differences in social engagement also become relevant, given

that these have been shown to develop prior to sexual maturation (Cords et al., 2010; Jarrett et al., 2018; Kohn et al., 2011, 2013; Lonsdorf et al., 2014; Nakamichi, 1989) and vary with social structure. For example, where females are philopatric and males disperse at maturity, young females develop stronger social bonds than males (spatial and grooming associations: Kulik et al., 2015; grooming associations: Cords et al., 2010; spatial associations: Frère et al., 2010; Stumpf et al., 2009; maternal association: Andres et al., 2013; Nakamichi, 1989). Males, conversely, play more than females do (Kulik et al., 2015; Meredith, 2013).

Such findings support the idea that social relationships are established in the juvenile period and prepare animals for their sex-specific adult roles (Kulik et al., 2015; Nakamichi, 1989; Suomi, 2005), which have been seen as an attempt to build towards the optimal end goal of adulthood. More recent studies have shown,

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however, that the juvenile period may be a continuous process of social network adjustments to the prevailing social environment (Jarrett et al., 2018; Vilette et al., 2022), where the structure of the network is more relevant than the identity of the individuals who comprise the network. In other words, although social processes remain geared towards social integration into the group, they may not, at this stage at least, reflect the formation and consolidation of enduring social bonds between particular individuals. More specifically, an empirical assessment of Ilany and Akçay's (2016) model of social inheritance by Jarrett et al. (2018) found only limited evidence for the inheritance of maternal bonds in vervet monkeys, *Chlorocebus pygerythrus*; that is, there was relatively little overlap between mother and offspring grooming partners. Jarrett et al. (2018) suggested that this mismatch could be accounted for by the fact that juveniles are exposed to, and must learn to cope with, temporal shifts in maternal network structure. In other words, their findings indicated that maternal social networks present too much of a moving target for offspring to match effectively, as well as suggesting that, if they were to replicate and sustain the group level network structure over time, juveniles would need to form bonds with nonmaternal associates. This implies that the stability of mothers' networks, combined with the demography of social groups, regulates the availability of potential partners towards whom juveniles can direct their social effort. This effort will, in turn, lead to the strengthening of certain social relationships (Kohn, 2019; Schülke et al., 2010; Silk, Altmann, et al., 2006; Silk et al., 2003), and thereby to variation in the structure of both ego and global networks across time and between groups.

Social effort is known to vary across and within social relationships, leading to the notion of strong and weak ties (or relationships). Weak ties are characterized by interactions that are infrequent, while strong ties represent frequent and sustained levels of social interaction. Differentiating between social ties in this way is important because females with stronger social relationships have been shown to experience fitness-related benefits such as increased longevity (Archie et al., 2014; Silk et al., 2010b), enhanced likelihood of surviving extreme events (Lehmann et al., 2015; McFarland & Majolo, 2013), enhanced infant survival (wild baboons: Silk et al., 2003, 2009) and increased individual reproductive performance (Kulik et al., 2012; Schülke et al., 2010). By the same token, however, some studies have also shown that there are advantages to having a wide range of partners. For instance, the number of weak bonds a female possessed predicted infant 12-month survival and infant longevity in baboons (McFarland et al., 2017), while vervet monkey females that invested in grooming a wider array of partners were at lower risk of predation (Josephs et al., 2016) and less susceptible to nocturnal hypothermia (McFarland et al., 2015).

Weak and strong ties therefore characterize the two ends of the relationship spectrum, where both can deliver fitness-related benefits and where the relative merits of each are likely to be contingent on particular demographic and ecological conditions (which themselves may shift over time). This suggests that juveniles may benefit from having both strong and weak associations at their disposal. Whereas strong social ties might soften the impact of stressful interactions with novel individuals (Kohn et al., 2022), weak ties may persist because they aid in predator avoidance or thermoregulation (Josephs et al., 2016; McFarland et al., 2015; Ostner & Schülke, 2018), or they may simply be the result of social time budget limits that preclude the ability to invest high levels of effort into all potential partners. In line with this, we have found that juvenile vervet monkeys embed themselves in secure ego-network structures composed of strong ties, while retaining the benefits of broader integration in the group through the presence of weak ties (Vilette et al., 2022). As expected, sex differences emerge

early on (~8 months of age), with females putting more effort into grooming interactions and maintaining a tighter subset of strong grooming partners than males. This sex difference may have foreshadowed females' integration and acceptance into their social group, whereas males grooming patterns may be viewed as a prelude to emigration from their natal group.

The formation of these ego-network structures, however, did not conform to Kohn's (2019) proposed model of social relationship formation, whereby individuals explore their social environment forming many social connections in the group, then subsequently prune and consolidate a subset of these connections (Kohn, 2019). While Kohn's (2019) socialization framework focused more on the identity of social partners, Vilette et al.'s (2022) findings drew attention to the structure of these ego-networks themselves. That is, these ego-network structures (a core of strong ties constituting a 'social bubble' and a periphery of weaker ties) were formed early and remained moderately stable over time (Vilette et al., 2022). These structures, however, were not composed of particular network ties. One explanation for this pattern might be that the exploration, pruning and consolidation phases apply only to the formation of the social bubble composed of strong ties and not to the overall ego-network.

Here, we consider this possibility and investigate Kohn's (2019) socialization steps at the level of the social bubble alone (see Fig. 1 for a visual representation of the social bubble across these steps). We do so by isolating the subset of strong ties present within juveniles' ego-networks that comprise such bubbles. We then go onto consider the composition of social bubbles and their formation in order to investigate whether these bubbles are likely to provide social benefits to juveniles. For example, in spectacled parrotlets, *Forpus conspicillatus*, juveniles form strong relationships with siblings immediately after fledgling, which offers them a stable social position during their transition from the family group to the wider flock (Wanker et al., 1996). Kohn et al., (2022) also found similar evidence in Gouldian finches, *Erythrura gouldiae*. In vervets, we hypothesize that a social bubble of strong ties provides individuals with the chance to hone their social strategies in the context of a secure environment, as well as reducing the number of unpredictable, and potentially more risky, social encounters. That is, a stable social bubble represents a low-risk network of predictable partners that buffers juveniles from potentially stressful situations. For example, in terms of spatial proximity, an animal with a more consistent social bubble of strong spatial ties may increase protection against unfamiliar conspecific competitors (Kohn et al., 2022), while a social bubble of strong grooming ties may, for example, reduce glucocorticoid levels (Crockford et al., 2008). As socialization is heavily influenced by the availability of social partners and group composition, the specific characteristics of available group members can have a significant effect on social development (Deputte & Quris, 1997; Pereira & Leigh, 2003; Rosenblum & Coe, 1977). A social bubble is therefore likely to set the social conditions to which juveniles are exposed (Kohn et al., 2022). This raises the prospect that useful insights into the socialization process may be gained by investigating the composition and stability of social bubbles over time and how this relates to the nature of the social environment and reflects individual social preferences (Snyder-Mackler et al., 2020).

In what follows, we consider social bubble formation in male and female juvenile vervet monkeys in both the spatial and grooming domains. These provide a useful contrast, as grooming generally requires mutual attraction between partners, and therefore more active social engagement, in the effort invested and the partners targeted, whereas spatial proximity can often be achieved unilaterally, as a more passive social engagement that requires animals to be merely tolerant of each other. Our analysis comprises

three parts. The first investigates [Kohn's \(2019\)](#) socialization steps at the social bubble level. To do so, we study the spatial and grooming social bubble structures by looking at their size, the effort invested in them and the similarity in partners through time (see [Fig. 1](#) for a visual representation of our predictions). We then examine the composition of bubbles in order to assess the proportion of group members to which juveniles are exposed over their development and how varied their exposure is to both kin and nonkin adults and juveniles. Taken together, these address the question of whether social bubbles provide a stable and predictable social environment for juveniles during their development.

Finally, we consider the processes at play in the formation of social bubbles. We address two main issues. As spatial and grooming bubbles are confounded to some degree ([Henzi et al., 2013](#)), we ask how the grooming bubble compares to the spatial bubble. To do so, we determine whether juveniles develop distinct spatial and grooming bubbles that conform to [Kohn's \(2019\)](#) socialization steps. We reconsider [Jarrett et al. \(2018\)](#) and [Ilany and Akçay's \(2016\)](#) findings by investigating the similarity between the grooming partners of mothers and offspring. Based on [Jarrett et al.'s \(2018\)](#) findings, we expect maternal networks to present a moving target (i.e. to shift in composition over time) that hinders the ability of offspring to prune and consolidate strong relationships with maternal contacts and hence become part of their own social bubbles. This instability, however, may lead mothers' grooming associates to be found outside of juveniles' social bubbles (i.e. they will comprise a juvenile's weak ties). We therefore assess the extent to which a mother's grooming ties overlap with her offspring's weaker grooming ties.

METHODS

Study Population and Subjects

Data were collected between June 2014 and June 2017 from three troops of vervet monkeys occupying adjacent and overlapping home ranges in the Samara Private Game Reserve in the semi-arid Karoo biome, Eastern Cape, South Africa ([Pasternak et al., 2013](#)). The three study groups (mean \pm SD group size: PT group: = 39 \pm 8; RBM group: 49 \pm 6; RST group: 57 \pm 7) were fully habituated from 2008 for RST and RBM and from 2012 for PT. All animals were individually identifiable from natural markings. The study subjects comprised three birth cohorts from the 2013, 2014 and 2015 birth seasons. The number of juveniles, as well as the number of each sex, varied across cohorts and years (see [Table 1](#)).

Data Collection

We began data collection when all cohort members were nutritionally independent of their mothers and classified as juveniles ([Jarrett et al., 2018](#)), which corresponded to an age of approximately 7 months (\pm 1 month) for the 2013 and 2014 cohorts. Data collection began later for the 2015 cohort, at around 11 months (\pm 1 month), due to logistical reasons. Each troop was followed on foot by one or more researchers on each 10 h study day, 3–5 days a week (PT: 583 days; RBM: 601 days; RST: 613 days). We used electronic hand-held data loggers and commercial software to record data from all visible animals, using scan samples conducted every 30 min ([Young et al., 2017](#)). Each scan sample lasted 10 min, during which we collected data on each animal's activity (feeding, moving, resting and grooming) and the identity of all its neighbours within 3 m. When animals were recorded as grooming, we noted the identity of their partners. For agonistic interactions, data were collected ad libitum, with the identity of the individuals involved recorded, along with the direction of the aggression and the

outcome (winner/loser) of the encounter (i.e. methods follow [Young et al., 2017](#)).

Ethical Note

All protocols were noninvasive and adhered to the laws and guidelines of South Africa and Canada. Procedures were approved by the University of Lethbridge Animal Welfare Committee (Protocols 0702 and 1505).

Data Extraction

Grooming and spatial data were treated separately in our analyses. Using the 'netTS' package ([Bonnell & Vilette, 2020](#)) in R version 3.5.2 (Team, 2017), both data sets were aggregated over a 60-day window that was then shifted successively by 30 days. We used this period in line with our previous analyses. However, we used the 'check.windowsize' function, specifying 1000 iterations, of the 'netTS' package to estimate the convergence of our measures in both the grooming and spatial proximity networks. The 'check.windowsize' function also allowed us to measure the sensitivity of this subsampling. With spatial associations, we found highly similar estimates (i.e. convergence) and low variation in estimates of degree and strength using a 60-day window. This means that the chosen window size was robust to subsampling and able to provide good measures. The estimates were not as robust for cosine similarity, suggesting the potential for noise in our predicted patterns. With grooming associations, degree, strength and cosine similarity showed lower estimates and higher variation. Although grooming associations showed a relatively larger amount of noise, a window size of 60 days nevertheless appeared to offer a good and usable compromise ([Supplementary Figs S1–S2](#)). Within each window, spatial association and grooming interactions were separately aggregated to construct weighted, nondirected networks at the node level (i.e. ego-networks). In other words, each juvenile present within the window had a grooming and a spatial ego-network that consisted of its direct connections. The age in days of each juvenile was registered at the start of each time block, as were the number of scans and the mean size of each troop. Applying a temporal dynamic approach allowed us to detect the points at which potential patterns emerged.

To extract ordinal ranks, we used the percolation and conductance (P&C) method ([Fujii et al., 2015](#)) from the 'Perc' package in R. We chose this method following the training–testing approach ([Vilette et al., 2020](#)), as it presented the best trade-off between the optimal amount of data required to infer reliable ranks and the ability of this method to infer reliable ranks. Therefore, we used a 4-month burn-in period, specific to each troop, and calculated ordinal ranks for each juvenile within each 60-day window, across the entire study period. We included agonistic interactions between all individuals (males, females, juveniles).

Strong ties extraction

To extract strong ties, it is common practice to select a user-determined number of social bonds ([Schülke et al., 2020](#); [Silk, Alberts, et al., 2006](#)). This approach means that all individuals are, in essence, arbitrarily allocated a certain number of strong bonds (i.e. partners with whom they interact most frequently) regardless of the actual frequency of interactions (i.e. the choices are not based on any biologically or statistically principled criteria: [Schülke et al., 2010](#); [Silk et al., 2010b](#)). Furthermore, restricting the analysis to a predetermined number of bonds eliminates the possibility of examining variability in the number of bonds formed by individuals. To address this issue, some studies have simply used higher-than-average composite sociality index (CSI) scores and

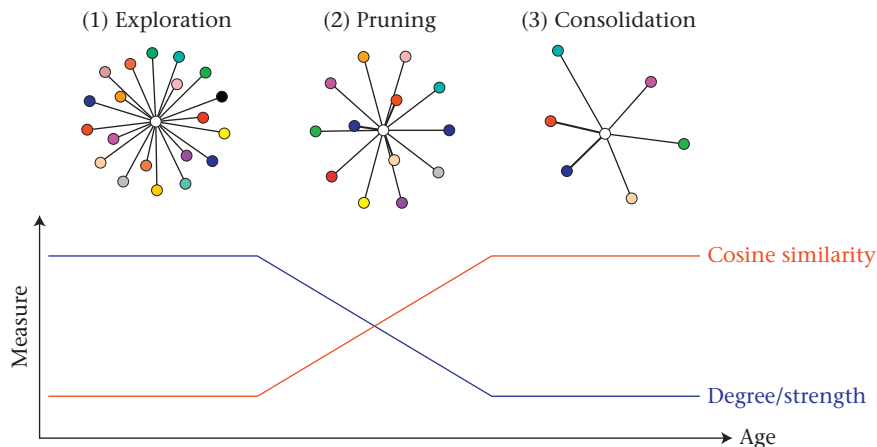


Figure 1. Kohn's (2019) phases of socialization translated into ego-networks (social bubbles), associated with the predictions for degree, strength and cosine similarity during juveniles' development. (1) Exploration: degree/strength are predicted to be high and cosine similarity should be low. (2) Pruning: degree/strength are predicted to decline and cosine similarity is predicted to increase. (3) Consolidation: degree/strength are predicted to be low and cosine similarity is predicted to be high.

lower-than-average CSI scores to identify strong and weakly bonded partners as a continuous measure (McFarland et al., 2015; Silk, Altmann, et al., 2006). Others have used several thresholds to identify a strong tie from observational data alone and counted the number of strong ties with strength above (1) the 0.9 percentile, (2) the third quartile and (3) the mean value (Schülke et al., 2022). Nevertheless, this approach also fails to consider the distribution of the data itself and, more specifically, whether a clear distinction between weak and strong ties exists (i.e. whether there is a skewed distribution). We therefore developed an algorithm to model the distribution of edge weights on the assumption that, if strong ties (relatively large edge weights) were present, then the distribution of edge weights would be skewed.

Overall, this algorithm follows the logic of a semi-supervised classification where basic information (i.e. priors about what a weak tie looks like and that strong ties should result in a skewed distribution) is used to help perform unsupervised classification. We performed two tests to assess our algorithm's accuracy. In the first, we simulated a normal distribution (i.e. no strong ties were present) and recorded how many false positives (i.e. strong ties) our function detected. The second test consisted of adding a single strong tie to a normal distribution. We then determined how many times that strong tie was detected (i.e. the number of true positives). Both tests were conducted on varying sample sizes ($N = 2-50$ interactions), with each sample size tested 10 times. These simulations helped us tune our priors and the 'min_diff' parameter to get the best results on simulated data before applying it to our real data. Using these two tests, we compared our built function to commonly used methods for the extraction of strong ties, such as counts of strong ties (strength > 0.9 percentile) and strength of strong ties (an individual's top three ties; Supplementary Figs S3–S4). As our function was more reliable than these methods in detecting strong ties, we proceeded to extract the strong ties present in our data using our model-based approach. While this algorithm performed better than measures

previously used, we should note that the algorithm requires further tuning as some flaws remain. For example, by setting our 'min_diff' parameter to 5, the algorithm is able to distinguish between strong and weak ties. However, the higher this parameter is set, the bigger the difference between a weak and strong tie must be when sample size is small (e.g. with a weight distribution of 1, 3, 15, no strong ties will be detected). This was an issue in our analysis as the sample sizes of spatial and grooming associations differed (average \pm SD interaction per individual across the study period: spatial: 33.03 ± 11.43 ; grooming: 10.87 ± 2.91). Therefore, we set the 'min_diff' parameter differently for each association type. That is, when extracting strong spatial ties, we set 'min_diff' to 5 as the sample size per individual, whereas for grooming interactions, this parameter was lowered to 2. Doing so allowed us to make the extraction of strong ties more conservative, based on the behaviour under analysis.

Within each time-aggregated window, we extracted the ego-network of each individual present, from which we assessed whether its weight distribution was skewed. Our model-based function proceeded as follows.

(1) The weight distribution was extracted for a given period, representing the total number of times the focal animal was recorded as interacting with each of its partners.

(2) We ran two models (weights ~ 1), using the 'brms' package (Bürkner, 2017), specifying a skewed-normal and a normal distribution, respectively. The priors for the mean weight (i.e. intercept) were adjusted in order to reflect the observed weak ties distribution (normal (1,2) and normal (1,1) for the skewed-normal and normal distribution, respectively) and can be tailored to what is thought to be weak ties based on prior information. We also specified priors (normal (0,10) and normal (0,1) for the skewed-normal and normal distribution, respectively) on the sigma parameter, which defines the range of weak tie values around the

Table 1
Size of cohorts at birth and at end of the study, as well as their composition

Cohort	Number of infants born	Number alive at the end of the study	Sex
2013	29	27	F = 15 M = 14
2014	30	29	F = 15 M = 15
2015	16	15	F = 8 M = 8

mean weight. Lastly, we also set a weakly informative prior with a mean of 0 and SD of 4 on the magnitude of skew in the data: i.e. alpha. To then check which distribution best fitted the extracted weight distribution, we compared the skewed-normal and normal distribution models using leave-one-out cross-validation (Vehtari et al., 2017), which computed a formal difference score between the two models, using the 'loo_compare' function of 'brms'. The presence of small sample sizes (i.e. when an individual had only one or two partners), however, meant that the information present in the weight distribution alone was inadequate, leading to a small and unreliable difference between a skewed and a normal distribution. To address this, we used a parameter ('min_diff') to indicate how much evidence we were willing to accept in the difference score, computed using the leave-one-out cross-validation, between models with a skewed and a normal distribution in ties. This min_diff parameter constrained the algorithm to select only models for which there was strong evidence of a skewed distribution. It was set to a different value, based on the studied behaviour, in order to make the selection of strong ties more conservative (see below).

(3) If a skewed distribution fit the data better, the largest weight within the distribution was classified as a strong tie. To search for the number of strong ties, we ran a model predicting weight using the classification of strong or weak ties. This model-fitting approach compared, again using loo, possible classifications of strong versus weak ties, starting with the largest weight being classified as the only strong tie, followed by the largest and second largest being strong ties, and so on. Once model comparison had identified the best model, we used that classification to define our strong and weak ties.

(4) If the normal distribution was a better fit to the focal animal's weight distribution, then no strong ties were recorded.

Using these isolated strong ties, spatial and grooming ego-networks were created for each individual, where nodes corresponded to the identity (ID) of the focal individual's partner, while edges indicated the frequency with which the two individuals interacted, as well as the nature of the interaction (spatial or grooming). From these networks, we extracted the following measures.

Social Bubble Structure

We extracted three measures to capture the size, overall social engagement and partner similarity in social bubbles. (1) Degree, which is the sum of each node's strong connections. It captures the number of strong ties a focal subject has and therefore indicates the size of a social bubble. (2) Strength, which is the sum of each node's connections weighted by the frequency of the interaction with other nodes. This measure specifies the overall effort invested in these strong ties. (3) Cosine similarity, which is used to estimate similarity in the patterning of values in two vectors (Jarrett et al., 2018; Newman, 2010; Vilette et al., 2022). Here, we used the measure to assess the similarity of the edge weights between two consecutive ego-networks, with values that range between 0 and 1. An individual whose social bubble (strong ties) changes markedly between time t and $t + 1$ will have a low cosine similarity, whereas individuals whose social bubbles are similar at t and $t + 1$ will show high cosine similarity. More details on calculating cosine values are given in the [Supplementary material \(see Cosine Similarity Measure\)](#).

Social Bubble Composition

To investigate social bubble composition, we extracted the (1) rate of association with adults, which varies between 0 and 1, and (2) rate of association with family members, composed of the

mother and any siblings, which also varies between 0 and 1. After their first birth (~3.5 years), females were considered as adults, while males were considered adults at >5 years of age.

Processes at Play: Social Bubbles Comparison

Cosine similarity is used to measure the extent to which the patterning of values in two vectors (\mathbf{a} , \mathbf{b}) is similar (Newman, 2010). Here, the measure assesses the similarity of the edge weights between two simultaneous ego-networks: the juvenile's spatial and grooming networks at time t . That is, spatial and grooming networks were compared at the individual level, within each 2-month time-aggregated window. We used cosine similarity as a multilayer network measure, where values range between 0 and 1. An individual whose strong ties to spatial and grooming partners differ markedly will have a low cosine similarity, whereas individuals whose spatial and grooming partners are similar will be associated with a high cosine similarity. We applied the same reasoning for the similarity between the mother's grooming partners and her offspring's grooming partners, where the mother's grooming ego-network and the offspring's grooming ego-network were compared at time t . When comparing the mother's grooming partners and the offspring's grooming partners, we removed the mother-offspring dyad so that the mother did not appear as the juvenile's tie and the juvenile did not appear as its mother's partner. More details on calculating cosine values are given in the [Supplementary material \(see Cosine Similarity Measure\)](#).

Environmental Conditions

As food availability contributes to the structuring of social associations (Bonnell et al., 2022), we measured troop level estimates of resource availability using the normalized difference vegetation index, NDVI (Willems et al., 2009). We generated area-weighted NDVI averages for each territory for consecutive 33-day windows (16 days post and prior to the date of each MODIS raster) by averaging all NDVI values for points falling within the territory's 95% isopleth and weighted by the troop's differential usage of its territory during that period (Young et al., 2019). NDVI scores, which range between -1 and 1 , are higher in more photosynthetically active areas and are therefore considered to indicate increased plant food availability.

Statistical Analyses

We analysed our data within a Bayesian framework, using the 'brms' package (Bürkner, 2017) in R version 3.5.2 (R Core Team, 2017). We used hierarchical generalized additive mixed models (HGAM), which allow the relationships between the explanatory variables and the response to be described by smooth curves (Pedersen et al., 2019). This approach is useful as it does not assume a fixed trend, but instead estimates a nonlinear trend without a theoretically prespecified shape. In other words, a smooth curve gives the opportunity for nonlinear trends, if any, to emerge, hence giving further freedom for the model to fit the data. We ran all models with four chains and 1000 iterations after specifying weakly informative priors (normal (0,1)). We performed prior predictive checks to ensure that these priors did not drive the patterns obtained from our predictions (see [Supplementary material](#), Prior Predictive Checks Compared to the Predicted Patterns, [Figs S5–S10](#)). Model diagnostics confirmed MCMC convergence, with all $\hat{R} < 1.1$ (Gelman & Shalizi, 2012). We used the 'posterior predictive check' ('pp_check' function) from the 'bayesplot' package (Gabry et al., 2019) to determine the quality of the model fits to the data.

Regarding the first part of our analyses, we constructed two models for each of our measures (cosine similarity, degree, strength and our two rates of association): one for grooming and one for spatial associations. This generated 10 models. For the second part of our analysis, a model was run for each of our two cosine similarity measures. For all 12 models, the model structure was constant (see [Appendix, Table A1](#) for model structure). Our data set structure consisted of repeated measures for individual, mother, cohort and troop identity, as well as for sex. We therefore let the effect of age vary by these five grouping variables, using factor smooths ([Pedersen et al., 2019](#)). We also allowed the effect of ordinal rank to vary by individual, using a factor smooth. Factor smooths implicitly incorporate group-specific intercepts. That is, they create an estimate for each level of the grouping variable but only estimate one smoothing parameter for all groups of this grouping variable. Put simply, these grouping variables deviate from the mean and hence vary in their pattern. We expected each grouping variable to vary in its ability to maintain a certain network structure as juveniles aged. Each of these interactions was added as a single smooth. We controlled for variability in environmental conditions by including NDVI as a single smooth to the model. Additionally, a single smooth for troop number was included to address variation in troop size, along with one for age, to account for developmental variation.

Continuous variables were scaled and mean-centred. For the count variables (i.e. spatial/grooming degree and strength), a Poisson model was run, with the log of the total number of observation sessions (i.e. scan samples) within the aggregated sample period included as an offset variable to account for differences in observation effort. As dispersion issues are common with Poisson models, we ran an analysis of residuals from the models using the 'DHARMA' package ([Hartig, 2020](#)). We addressed identified dispersion issues by running models with a negative binomial distribution. When this did not remove the dispersion issue, we ran hurdle models ([Hilbe, 2017](#)). To determine which model to report in the main text, we used three approaches in concert. (1) Models were compared using leave-one-out cross-validation with the 'loo_compare' function of 'brms'. (2) We assessed the magnitude of the dispersion from the analysis of residuals. (3) We used the posterior predictive checks. We then compared the estimates of the best models with the estimates of our simpler, original Poisson models. This was used to determine whether the influence of the dispersion issue affected our results. With our grooming/spatial degree and spatial strength models, the dispersion issue was influential, hence we report the results from the negative binomial models in the main text for these three variables. With respect to our grooming strength model, dispersion was not influential, and we therefore report the simpler Poisson models in the main text while providing the necessary details regarding the other model in the [Supplementary material \(Figs S17–S20\)](#).

When our response variables were the rates of association with adults and with family members and responses varied between 0 and 1, we constructed zero-one-inflated beta models for spatial and grooming associations. We also used a zero-one-inflated beta model when we looked at spatial and grooming partner similarity, as well as when we investigated the similarity between grooming and spatial strong partners. A zero-one-inflated beta model was also run when comparing ties of the mother's grooming ego-networks with those of her offspring. All the model summary tables are presented in the [Appendix \(Tables A2–A14\)](#), accompanied by Dharma nonparametric dispersion tests and posterior predictive distribution plots, as required.

Given the nature of the statistical models, as well as the inclusion of interaction effects, using a summary table on its own to interpret model estimates is not straightforward. We therefore

generated whole model predictions, using the 'fitted()' function from the 'brms' package to extract the fitted values of our models. Variables that were not of direct interest were fixed to their mean (e.g. troop size, NDVI, rank), while predictions were made for the variables of interest (i.e. age and sex). These predictions were then used to construct predictive posterior plots with the 'ggplot2' package ([Wickham, 2009](#)). These plots allowed us to see how males and females differed in their response to the average effect of our response variables. Given their interpretative familiarity, we specified the 95% credible intervals (CIs) in our plots to guide our assessment of whether the sexes differed meaningfully in the structure of the revealed patterns. Model main effects are presented as summary statistics ([Appendix, Table A2–A14](#)) for posterior means, 95% CIs and conditional R^2 values for each model, estimated using the 'bayes_R2' function ([Gelman et al., 2019](#)).

RESULTS

Social Bubble Ego-network Structure

Spatial structure

As they aged, both sexes displayed a general decline in the number of partners within their spatial social bubble ([Fig. 2a](#)). There were, nevertheless, fluctuations, with slight temporary increases that aligned with each annual birth season. There were no sustained sex differences. Although more pronounced, the same overall pattern was observed for mean strength ([Fig. 2b](#)). Finally, for both sexes, the observed pattern in the similarity of spatial partners present within juveniles' social bubbles was one of overall stability, although values were quite low. There was, however, a peak that aligned with the first birth season ([Fig. 2c](#)).

Grooming structure

With respect to the number of grooming partners (degree) in their social bubble ([Fig. 3a](#)), both sexes showed a pattern of stable, but low values, with increasing uncertainty in the estimates of the mean over time. In contrast, mean strength declined over time, although birth season seemed to exert a clear effect in one year ([Fig. 3b](#)). Finally, both sexes displayed a consistent pattern of very high values in the similarity of their grooming partners within their social bubble over time ([Fig. 3c](#)).

Social Bubble Composition

Spatial bubbles

For spatial association with adults over time, both sexes displayed a pattern of stable, but low, association over time ([Fig. 4a](#)). With respect to the rate of spatial association with kin, the general trend, for both sexes, was a cyclical pattern of peaks and troughs that aligned with the annual birth season, with rates increasing during the birth season ([Fig. 4b](#)).

Grooming bubbles

Both sexes displayed consistent and high levels of grooming association rates with adults ([Fig. 5a](#)) and family members ([Fig. 5b](#)) over time, with association rates with adults being slightly higher than with family members.

Processes at Play: Social Bubble Comparison

Spatial versus grooming bubbles

Although spatial grooming cosine similarity was generally low, there was a slight increase over time for females, whereas the general trend for males was a pattern of slightly fluctuating low values ([Fig. 6](#)).

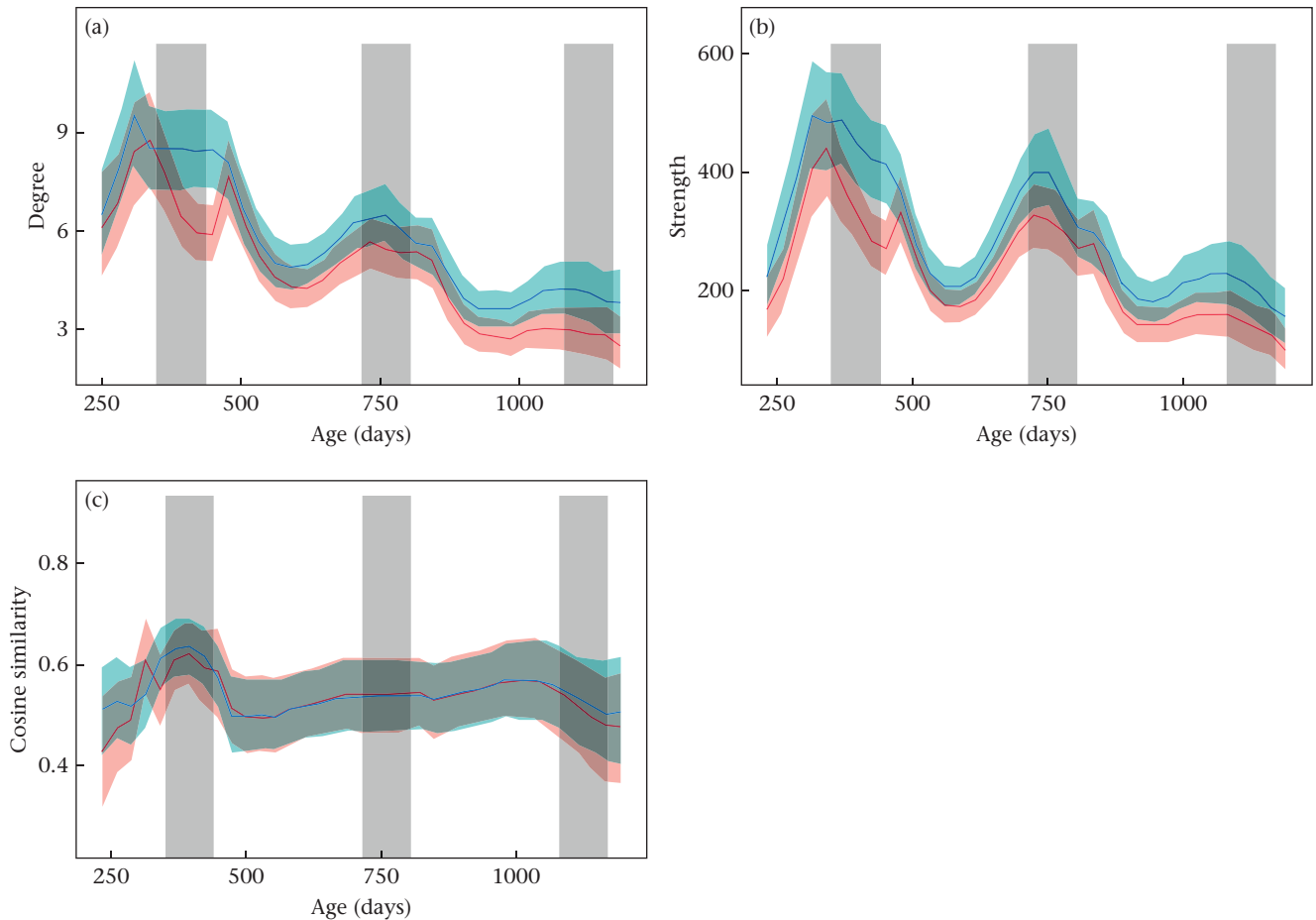


Figure 2. Variation in the (a) degree (b) strength and (c) cosine similarity of spatial associations by age and sex for juvenile vervets. The blue and red lines show the global smooth for the average female and male, respectively, with upper and lower 95% credible intervals (bands). Grey areas delimit the average annual birth season. Predictions were estimated with mean troop size fixed at 48 individuals.

Comparison between the mother's grooming partners and those of her offspring

The similarity between mothers' grooming ties and juvenile females' weak ties showed a slight overall decline through time. Although at a lower level, this pattern was mirrored by juvenile males, with a more pronounced deceleration (Fig. 7). For both sexes, the overall decrease was interspersed with an increase in cosine similarity values during the first birth season, followed by a plateau.

DISCUSSION

We found that neither the structure of spatial proximity bubbles nor the structure of grooming bubbles developed according to Kohn's (2019) socialization steps. In the case of spatial bubbles, these showed an overall decline in degree with age (Fig. 2a), interspersed with two increases during the birth season. Strength displayed the same pattern, although this was more pronounced and of greater magnitude (Fig. 2b). Cosine similarity was low and stable over time for both sexes (Fig. 2c). Taken together, these results suggest that, for both sexes, juveniles' spatial bubbles became more concentrated, in terms of size and social engagement, focusing on fewer partners with whom they associated more strongly, although the identity of these partners differed. While the patterns displayed did not follow Kohn's (2019) socialization phases precisely, there was some resemblance, given that juveniles

narrowed and strengthened certain social relationships. An important distinction here, however, is that Kohn's (2019) framework was couched in terms of who comprised the network (i.e. that exploration, pruning and consolidation were conducted with respect to particular individuals), whereas in our case, juveniles did not appear to go through a process of pruning and consolidation with respect to particular individual partners; rather, they seemed to prune and consolidate the social bubble structure itself.

Similarly, patterns of grooming social bubble structure did not conform to Kohn's (2019) framework. Instead, the number of grooming partners (degree) remained low and stable across development, while the overall effort invested in grooming (strength) decreased (Fig. 3a, b). For both sexes, similarity in grooming partners remained high and stable over time (Fig. 3c). Here, it is relevant to also consider composition, as we found that rates of grooming with adults and family members (Fig. 5a, b) remained high and constant over time for both sexes. Taken together, this indicates that juveniles have small but stable grooming bubbles, composed almost exclusively of adults and family members or, more precisely, of a single family member: their mother. Our longitudinal analysis thus confirms previous work on cross-sectional samples (Silk, Alberts, et al., 2006; Silk, Altmann, et al., 2006).

Across time, juveniles sustained a single and consistent unique strong tie with their mothers but did not maintain their initial high grooming frequency. Focusing on female juveniles, we suspect that

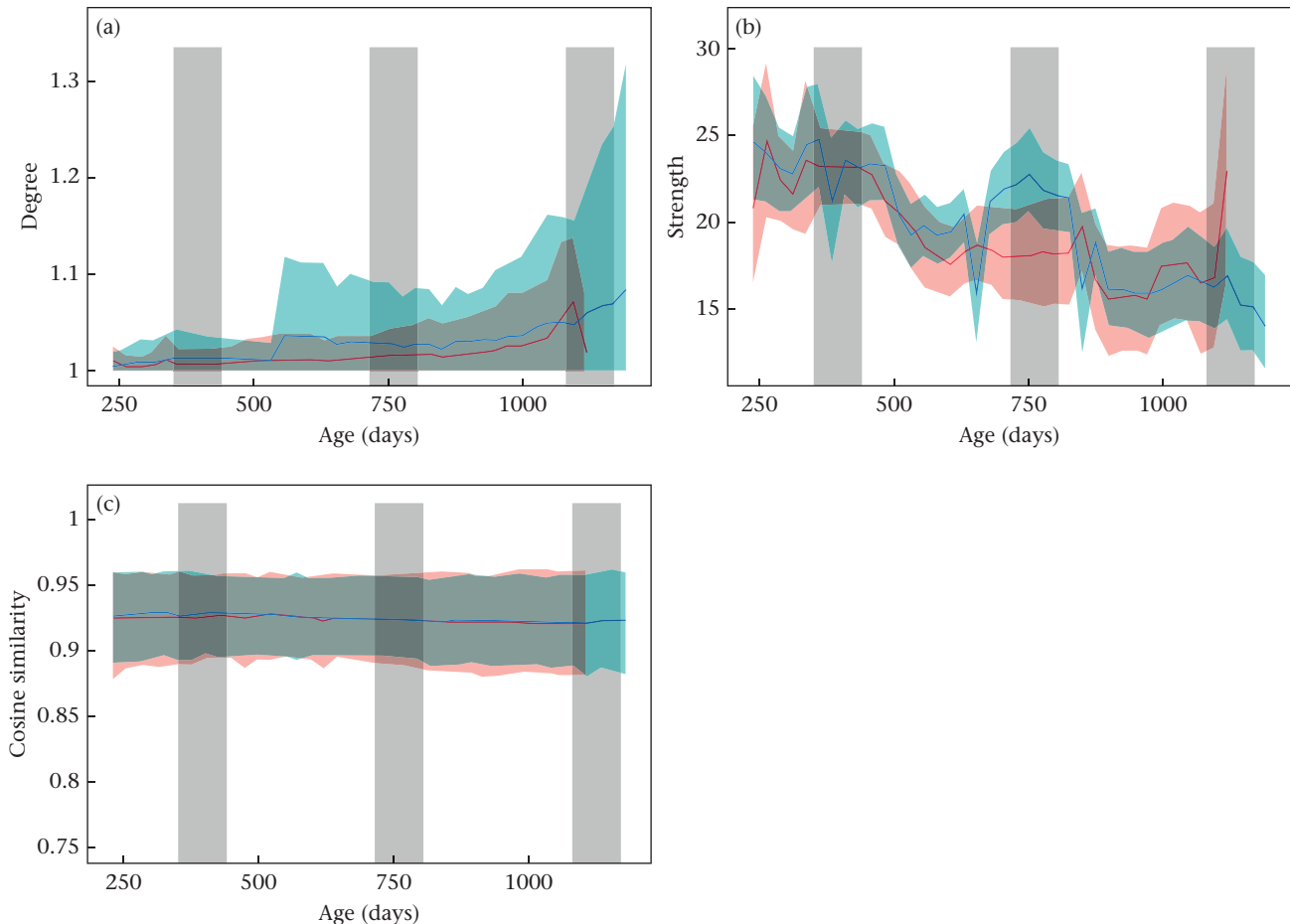


Figure 3. Variation in the (a) degree (b) strength and (c) cosine similarity of grooming associations by age and sex for juvenile vervets. The blue and red lines show the global smooth for the average female and male, respectively, with upper and lower 95% credible intervals (bands). Grey areas delimit the average annual birth season. Predictions were estimated with mean troop size fixed at 46 individuals.

reducing grooming investment in this strong tie enabled them to invest in ties outside of their grooming bubble, as demonstrated by the increase both in grooming frequency and in the number of grooming partners shown in our previous analyses (i.e. female juveniles increased their number of grooming partners from 5 to ~15 individuals over the developmental period: Vilette et al., 2022). For males, in contrast, both our current and previous analyses suggest they were less engaged and more scattered in terms of their grooming effort and overall number of grooming partners: males showed only a small increase from five to seven partners and engaged in less grooming over time (Vilette et al., 2022). By reducing overall grooming investment, males may increase the time available to engage in other kinds of social behaviour (e.g. locomotor or social play), which may be more beneficial to their development in other respects. Alternatively, it may be that juveniles are too young to impose their partner preferences on other group members. That is, the mother may control the frequency of grooming interactions with offspring, and changes in effort therefore reflect the mother's shift in focus to other individuals, including younger siblings. If this is the case, then the changes observed over time in juvenile grooming effort would occur passively and therefore not represent active decision making on the part of juveniles.

Although our analysis did not provide support for Kohn's (2019) framework in structural terms, the possibility remains that we have focused on the wrong timescale, or it may be that Kohn's (2019)

phases recur, at least to some degree, each time a change in size and composition occurs within the social group. That is, group level changes may disrupt networks and so relaunch the network formation process; this would align with our suggestion that social integration is a process of ongoing continual adjustment (Vilette et al., 2022). As such, Kohn's (2019) model may be valid across shorter timescales, where the socialization phases occur as individuals receive real-time feedback from their daily interactions. That is, the phases of socialization may happen at the social interaction level rather than at the level of the overall social relationship.

As expected, juveniles associated with more spatial partners (Figs 2–3a) and showed lower partner stability (Fig. 2c) than they did with their grooming partners (Fig. 3c). While this aligns with the idea that juveniles have different interaction styles (passive versus active) across different contexts, a more focused and stable grooming bubble may also provide juveniles with the safety needed to explore their social environment and learn how to navigate it effectively and at low risk. In other words, by having a stable and predictable grooming partner to whom it is possible to return for protection when needed, juveniles may be able to spatially associate more freely with other partners and, in this way, begin to build their own ego-networks of weak and strong ties. Supporting this view is our finding that, despite the size of spatial bubbles offering immatures the opportunity to develop additional strong grooming ties, they apparently did not do so, and grooming bubbles remained small and consistent over time. Indeed, the mother remained the

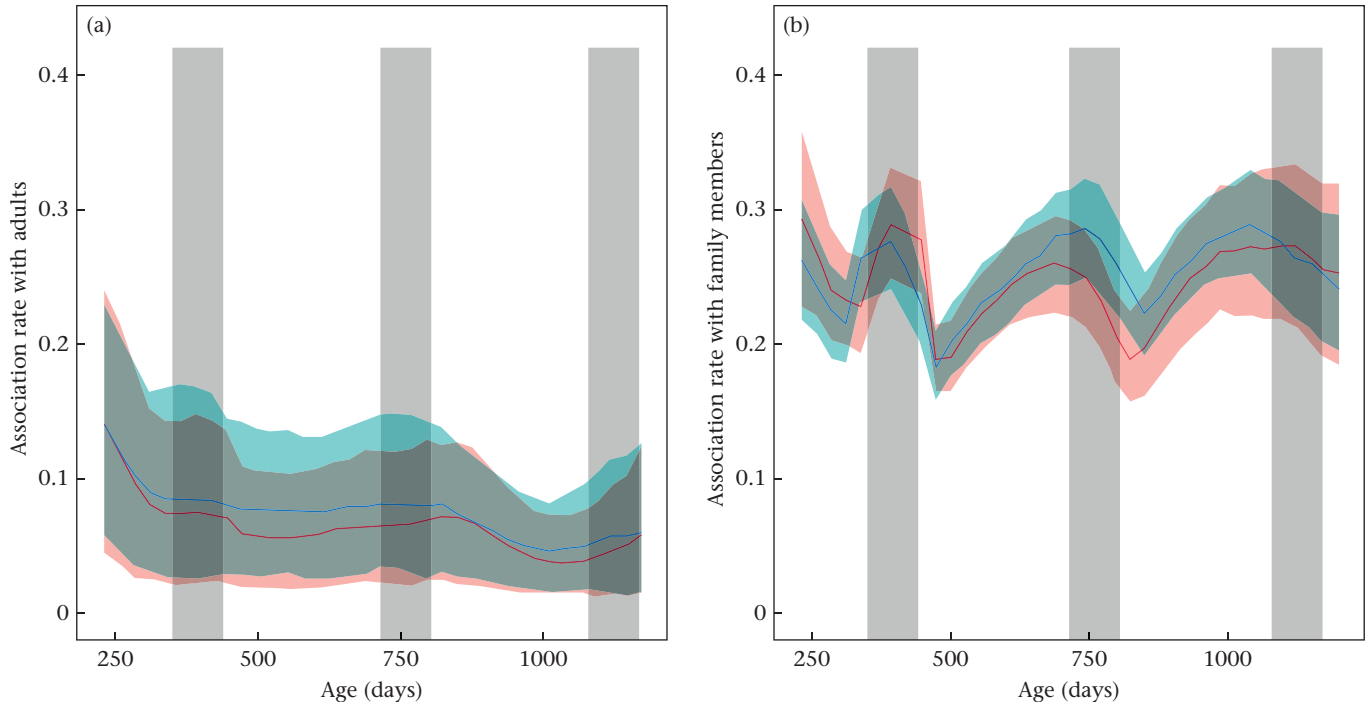


Figure 4. Variation in the (a) rate of spatial associations with adults and (b) rate of spatial associations with family members by age and sex for juvenile vervets. The blue and red lines show the global smooth for the average female and male, respectively, with upper and lower 95% credible intervals (bands). Grey areas delimit the average annual birth season.

only strong tie across the entire developmental period covered by our sample, a finding that does not fit particularly well with the notion that juveniles use their developmental period to develop social bonds and integrate into the adult network. Rather, it speaks directly to the importance of having a secure base for attachment

during the social development of immatures (Bowlby et al., 1989); the grooming bubble we identify can just as easily be referred to as the juveniles' primary attachment figure.

If we now turn to the composition of spatial social bubbles, we found that, for both sexes, young vervets mostly associated with

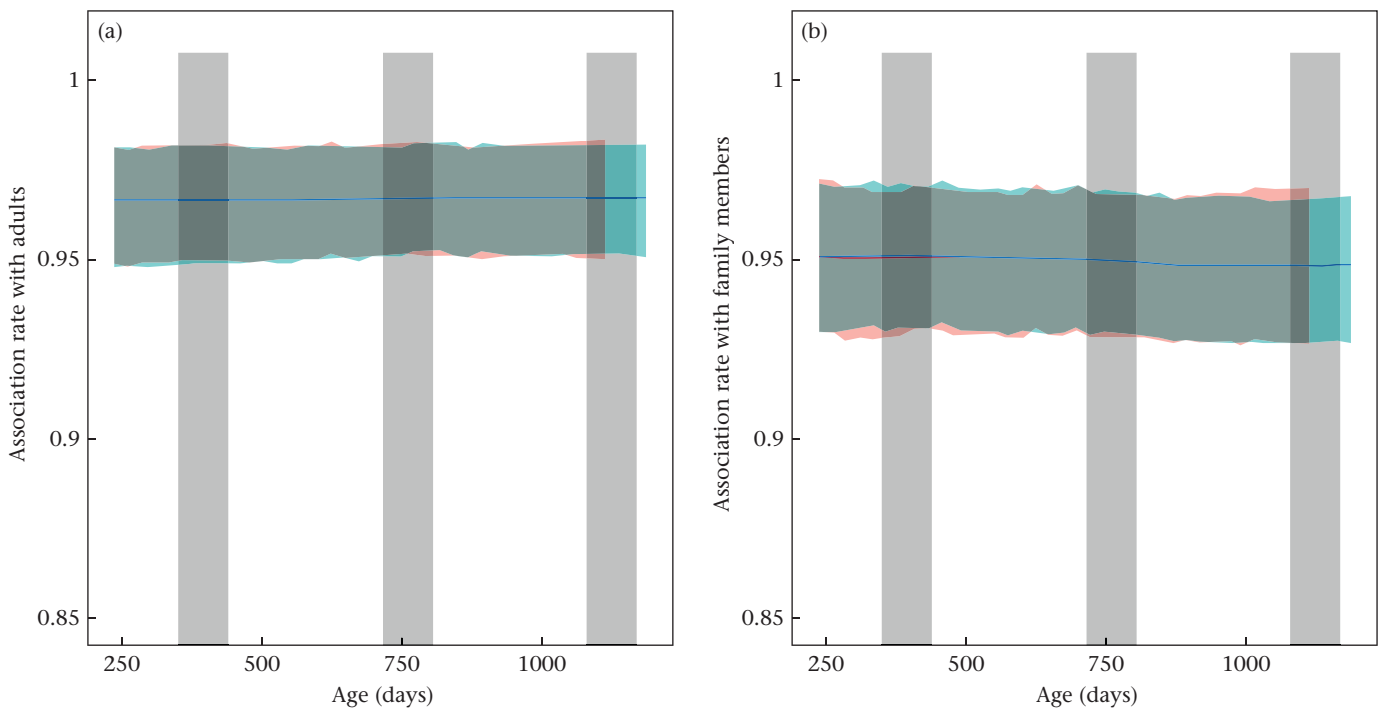


Figure 5. Variation in the (a) rate of grooming associations with adults and (b) rate of grooming associations with family members by age and sex for juvenile vervets. The blue and red lines show the global smooth for the average female and male, respectively, with upper and lower 95% credible intervals (bands). Grey areas delimit the average annual birth season.

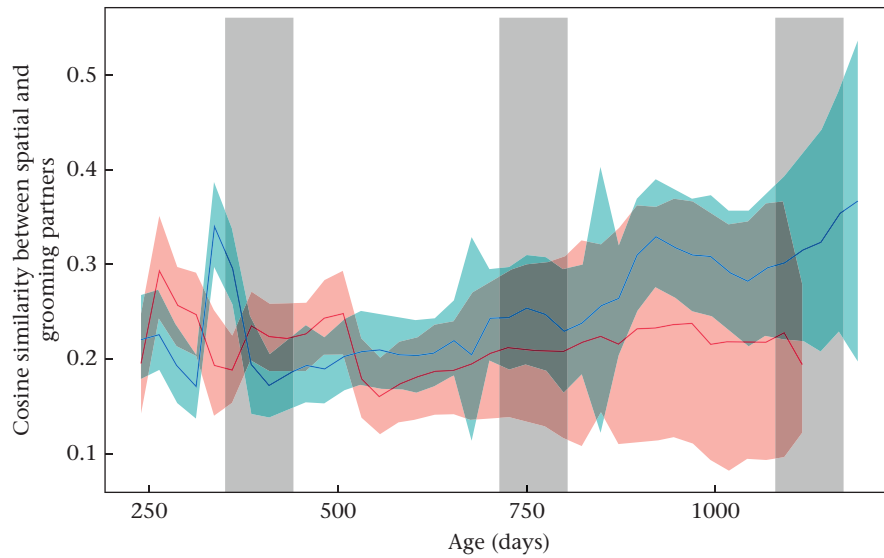


Figure 6. Variation in mean cosine similarity between spatial and grooming partners by age and sex for juvenile vervets. The blue and red lines show the global smooth for the average female and male, respectively, with upper and lower 95% credible intervals (bands). Grey areas delimit the average annual birth season.

other juveniles. We also found that the rate of spatial association with family members fluctuated, manifesting a cyclical pattern of peaks that aligned with the annual birth season (Fig. 4a, b). Overall, the absence of association with adults suggests that the structuring of spatial interactions is unlikely to be the consequence of spatial association patterns being passively mediated by kinship (i.e. the mother). In other words, and importantly, juveniles appear to be building their own spatial network structures rather than integrating into existing adult networks. Associating with other immatures in this way may enable juveniles to engage in various forms of social play and/or engage with partners that have broadly similar time budgets. As suggested previously, this may allow juveniles to build the peer relationships that will comprise their adult networks when they reach maturity (Jarrett et al., 2018).

Although we treated spatial proximity and grooming as two separate bubbles, it would be beneficial in future analyses to

explore their composition in concert. This will help us understand how strong maternal connections are initially formed and maintained. That is, as already noted, an active behaviour, such as grooming, may be more easily controlled by the mother compared to a more passive outcome, like spatial association. Investigating the direction of grooming interactions, as well as who maintains spatial associations, would allow us to draw a clearer picture as to how stable connections with mothers, and possibly other family members, come about. For example, in free-ranging rhesus monkeys, *Macaca mulatta*, Berman (1988) found that mothers appeared to seek more proximity with their infants when they were in larger groups, and that their infants tended to form social networks that were more highly focused on kin (see also Berman et al., 1997). While our analysis controlled for group size, investigating the impact of troop size variation might well provide further details regarding the social processes behind the observed patterns.

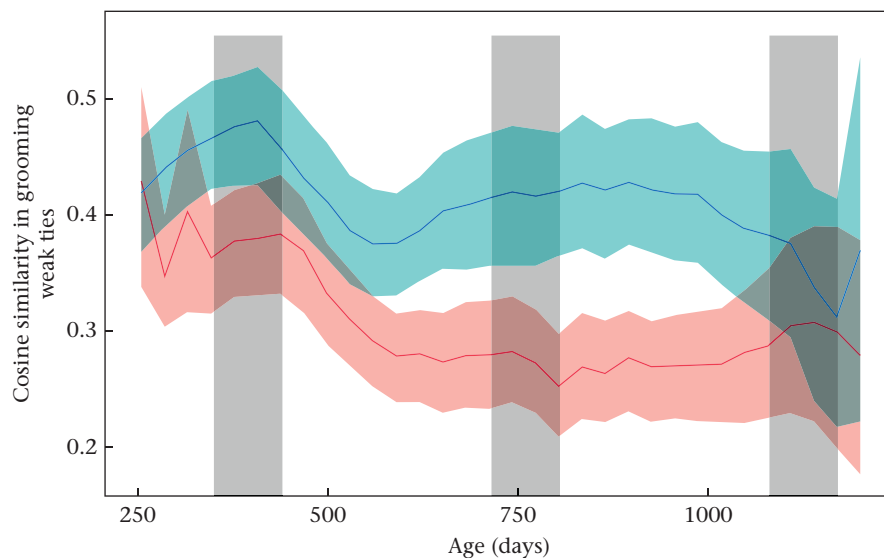


Figure 7. Variation in mean cosine similarity between mothers' grooming ties and their offsprings' grooming ties by age and sex for juvenile vervets. The blue and red lines show the global smooth for the average female and male, respectively, with upper and lower 95% credible intervals (bands). Grey areas delimit the average annual birth season.

When we compared the structure and composition of spatial proximity and grooming bubbles in concert in our current analyses, the clearest contrast between them, in addition to size, was seasonal variation: spatial bubbles revealed clear seasonal patterns, whereas grooming bubbles did not. The observed sensitivity to changes in group composition for spatial behaviour was also seen in our earlier analysis (Vilette et al., 2022), which did not distinguish between weak and strong ties. Focusing on the birth season, the upward shifts in association rate with family members, combined with positive fluctuations in strength and degree, suggest that juvenile spatial bubble structure is sensitive to the arrival of infants. Here, the increase in the number of strong ties and the effort placed into them are reflected in an increase in the association rate with family members. Again, whether these seasonal fluctuations result from an active or passive process remains to be determined. We can hypothesize that increases in bubble size and social effort result from an active process whereby juveniles seek proximity to specific individuals. Indeed, juveniles' ability to respond flexibly to changes in spatial social dynamics may help them to sustain a more robust grooming bubble structure (i.e. their social connection to their mothers). Alternatively, it is possible that such patterns are the passive consequence of the social group becoming less dispersed during the birth season, leading juveniles to be in closer proximity to one another and hence more spatially engaged. With regard to the increase in rates of association with family members, previous work has shown that attraction to newborns promotes close spatial associations with mothers (Fairbanks, 1990; Johnson et al., 1980; Silk, 1999; Silk et al., 2003, 2009); an attraction that could also result from an active or a passive process. If we extend our timeline a little and speculate on the process by which juveniles begin to expand their grooming bubble, the seasonal patterns we observe raise the possibility that the incorporation of additional strong ties into female juveniles' network (i.e. those beyond the mother) may well be tied to juveniles' reaching sexual maturity and the birth of their first offspring. That is, females may capitalize on the increased social attention that attends the birth of an infant to forge additional bonds with both peers and adult females. In this view, juvenile social behaviour does not reflect an attempt to integrate into the adult network (and a 'rehearsal' for adulthood), but instead reflects a specific juvenile strategy that serves a juvenile's current need. This could help explain why juveniles sustained only a single strong tie with their mothers over the entire 3-year period covered by our sample. Integration into, and formation of, an adult network then occurs at the point at which the females themselves achieve adulthood, and so require a more extensive network of strong ties that helps buffer and protect the female and her offspring.

Considering the potential processes at play in the formation of social bubbles, the similarity in spatial and grooming bubbles remained consistently low over the juvenile period (Fig. 6). This was not surprising, given that we observed a spatial bubble made of nonrelated juveniles (Fig. 4a, b) and a grooming bubble composed only of the juvenile's mother (Fig. 5a, b). This corroborates Henzi et al.'s (2013) observation that adult vervet monkey females do not simply groom their spatial associates but distribute their grooming more actively towards specific partners. Future analyses might well consider whether the grooming bubble shapes the structure of the spatial bubble, or vice versa. Given the size and composition of juveniles' grooming bubbles, our question about the similarity of ties between a mother's grooming partners and those of her offspring boils down to investigating whether juveniles acquire the same partners as their mothers among their weak ties alone. We found that juveniles showed a slight overall decrease in similarity (Fig. 7); that is, contrary to our predictions, juveniles' weak ties were mostly

different to their mother's grooming partners. Our original stance was that maternal grooming networks would be too unstable for juveniles to share similar partners within their strong ties. However, we predicted that the social inheritance process may allow for juveniles to interact with their mother's partners at some level, even if these relationships are not consolidated in the sense that Kohn (2019) intended (i.e. a mother's grooming partners being part of her offspring's weak ties). Although mothers' grooming partners were, to a small extent, part of juveniles' weak ties, our finding supports the idea that, to replicate the overall grooming network, juveniles would have to associate with a greater number of nonmaternal contacts (Jarrett et al., 2018). Compared to juvenile males, juvenile females showed a higher similarity in grooming partners with their mother. Maintaining close proximity to mothers may promote the connection to various grooming partners, which could, in a later stage, facilitate the development of enduring social relationships for females. Lastly, although no sex differences were found within strong ties, some emerged when focusing on juveniles' weak ties and their similarity with their mothers' grooming ties. Considering that previous findings (Vilette et al., 2022) showed behavioural sex differences within the juveniles' grooming ego-networks (i.e. composed of weak and strong ties), it suggests that sex behavioural differences may emerge within juveniles' grooming weak ties. This would reinforce the idea that the value of sociability may also lie in the formation of a more extended social network (McFarland et al., 2017), and not just in a small number of strong and consistent social relationships (Silk et al., 2003, 2009; 2010a; 2010b).

Author Contributions

C.V. contributed to the study concept/design, data collection, data analysis and drafting the manuscript. S.P.H. and L.B. contributed to funding acquisition, supervision and the drafting and critical revision of the manuscript. T.B. contributed to data analysis, supervision and helped draft the manuscript. D.M. contributed to data extraction. All authors approved the final version of the manuscript.

Data Availability

All code and data used to generate this paper are available at: github.com/ChloeVilette/Strong_ties_analysis.

Declaration of Interest

The authors declare there was no conflict of interest.

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at <https://doi.org/10.1016/j.anbehav.2023.05.003>.

References

- Alexander, R. D. (1990). *How did humans evolve? Reflections on the uniquely unique species*. University of Michigan Museum of Zoology. <https://deepblue.lib.umich.edu/handle/2027.42/57178>.
- Andres, D., Clutton-Brock, T. H., Kruuk, L. E. B., Pemberton, J. M., Stopher, K. V., & Ruckstuhl, K. E. (2013). Sex differences in the consequences of maternal loss in a long-lived mammal, the red deer (*Cervus elaphus*). *Behavioral Ecology and Sociobiology*, 67(8), 1249–1258. <https://doi.org/10.1007/s00265-013-1552-3>
- Archie, E. A., Tung, J., Clark, M., Altmann, J., & Alberts, S. C. (2014). Social affiliation matters: Both same-sex and opposite-sex relationships predict survival in wild female baboons. *Proceedings of the Royal Society B: Biological Sciences*, 281(1793), Article 20141261. <https://doi.org/10.1098/rspb.2014.1261>
- Berman, C. M. (1988). Demography and mother-infant relationships: Implications for group structure. In J. E. Fa, & C. H. Southwick (Eds.), *Ecology and behavior of food-enhanced primate groups* (pp. 269–296). Alan R. Liss.
- Berman, C. M., Rasmussen, K. L. R., & Suomi, S. J. (1997). Group size, infant development and social networks in free-ranging rhesus monkeys. *Animal Behaviour*, 53(2), 405–421.
- Bonnell, T. R., Henzi, S. P., & Barrett, L. (2022). Using network synchrony to identify drivers of social dynamics. *Proceedings of the Royal Society B: Biological Sciences*, 289(1977), Article 20220537. <https://doi.org/10.1098/rspb.2022.0537>
- Bonnell, T. R., & Vilette, C. (2020). Constructing and analysing time-aggregated networks: The role of bootstrapping, permutation and simulation. *Methods in Ecology and Evolution*, 12(1), 114–126. <https://doi.org/10.1111/2041-210X.13351>
- Bowlby, J., May, D. S., & Solomon, M. (1989). *Attachment theory*. Lifespan Learning Institute.
- Bray, J., Murray, C. M., Gilby, I. C., & Stanton, M. A. (2021). Immature male chimpanzees' (*Pan troglodytes schweinfurthii*) social relationships with adult males, but not peers, persist into adulthood. *International Journal of Primatology*, 42, 701–721. <https://doi.org/10.1007/s10764-021-00235-1>
- Bürkner, P.-C. (2017). brms: An R package for Bayesian multilevel models using Stan. *Journal of Statistical Software*, 80(1), 1–28.
- Cameron, E. Z., Setsaas, T. H., & Linklater, W. L. (2009). Social bonds between unrelated females increase reproductive success in feral horses. *Proceedings of the National Academy of Sciences of the United States of America*, 106(33), 13850–13853. <https://www.pnas.org/doi/full/10.1073/pnas.0900639106>
- Cheney, D. L., Silk, J. B., & Seyfarth, R. M. (2016). Network connections, dyadic bonds and fitness in wild female baboons. *Royal Society Open Science*, 3(7), Article 160255. <https://doi.org/10.1098/rsos.160255>
- Cords, M., Sheehan, M. J., & Ekernas, L. S. (2010). Sex and age differences in juvenile social priorities in female philopatric, nondespotic blue monkeys. *American Journal of Primatology*, 72, 193–205. <https://doi.org/10.1002/ajp.20768>
- Crockford, C., Wittig, R. M., Whitten, P. L., Seyfarth, R. M., & Cheney, D. L. (2008). Social stressors and coping mechanisms in wild female baboons (*Papio hamadryas ursinus*). *Hormones and Behavior*, 53(1), 254–265. <https://doi.org/10.1016/j.yhbeh.2007.10.007>
- Deputte, B. L. (2000). Primate socialization revisited: Theoretical and practical issues in social ontogeny. *Advances in the Study of Behavior*, 29, 99–157. <https://www.sciencedirect.com/science/article/pii/S0065345408601047>
- Deputte, B. L., & Quris, R. (1997). Socialization processes in primates: Use of multivariate analyses. II. Influence of sex on social development of captive rhesus monkeys. *Behavioural Processes*, 40(1), 85–96.
- Fairbanks, L. A. (1990). Reciprocal benefits of allomothering for female vervet monkeys. *Animal Behaviour*, 40(3), 553–562. <https://www.sciencedirect.com/science/article/pii/S0003347205805366>
- Fairbanks, L. A. (2002). Juvenile vervet monkeys: Establishing relationships and practicing skills for the future. In M. E. Pereira, & L. A. Fairbanks (Eds.), *Juvenile primates: Life history, development and behavior* (pp. 211–227). University of Chicago Press.
- Fairbanks, L. A., & Pereira, M. E. (Eds.). (1993). *Juvenile primates: Life history, development, and behavior*. University of Chicago Press.
- Feldblum, J. T., Krupenye, C., Bray, J., Pusey, A. E., & Gilby, I. C. (2021). Social bonds provide multiple pathways to reproductive success in wild male chimpanzees. *iScience*, 24(8), Article 102864. <https://www.sciencedirect.com/science/article/pii/S2589004221008324>
- Frere, C. H., Krützen, M., Mann, J., Watson-Capps, J. J., Tsai, Y. J., Patterson, E. M., Connor, R., Bejder, L., & Sherwin, W. B. (2010). Home range overlap, matrilineal and biparental kinship drive female associations in bottlenose dolphins. *Animal Behaviour*, 80(3), 481–486. <https://doi.org/10.1016/j.anbehav.2010.06.007>
- Fujii, K., Jin, J., Shev, A., Beisner, B., McCowan, B., & Fushing, H. (2015). Perc: Using percolation and conductance to find information flow certainty in a directed network (R package Version 0.1.3) <https://CRAN.R-project.org/package=Perc>
- Gabry, J., Simpson, D., Vehtari, A., Betancourt, M., & Gelman, A. (2019). Visualization in Bayesian workflow. *Journal of the Royal Statistical Society: Series A*, 182(2), 389–402.
- Gelman, A., Goodrich, B., Gabry, J., & Vehtari, A. (2019). R-squared for Bayesian regression models. *American Statistician*, 73(3), 307–309. <https://doi.org/10.1080/00031305.2018.1549100>
- Gelman, A., & Shalizi, C. R. (2012). Philosophy and the practice of Bayesian statistics. *British Journal of Mathematical and Statistical Psychology*, 66(1), 8–38. <https://doi.org/10.1111/j.2044-8317.2011.02037.x>
- Hartig, F. (2020). DHARMA: Residual diagnostics for hierarchical (multi-level/mixed) regression models (R package Version 0.3. 3.0) <https://CRAN.R-project.org/package=DHARMA>
- Henzi, S. P., Forshaw, N., Boner, R., Barrett, L., & Lusseau, D. (2013). Scalar social dynamics in female vervet monkey cohorts. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368, Article 20120351. <https://doi.org/10.1098/rstb.2012.0351>
- Hilbe, J. M. (2017). The statistical analysis of count data/El análisis estadístico de los datos de recuento. *Cultura y Educación*, 29(3), 409–460. <https://doi.org/10.1080/11356405.2017.1368162>
- Ilany, A., & Akçay, E. (2016). Social inheritance can explain the structure of animal social networks. *Nature Communications*, 7, Article 146. <https://doi.org/10.1038/ncomms12084>
- Jarrett, J. D., Bonnell, T. R., Young, C., Barrett, L., & Henzi, S. P. (2018). Network integration and limits to social inheritance in vervet monkeys. *Proceedings of the Royal Society B: Biological Sciences*, 285(1876), Article 20172668. <https://doi.org/10.1098/rspb.2017.2668>
- Johnson, C., Koerner, C., Estrin, M., & Duos, D. (1980). Alloparental care and kinship in captive social groups of vervet monkeys (*Cercopithecus aethiops sabaues*). *Primates*, 21(3), 406–415. <https://link.springer.com/article/10.1007/BF02390469>
- Josephs, N., Bonnell, T., Dostie, M., Barrett, L., & Henzi, S. P. (2016). Working the crowd: Sociable vervets benefit by reducing exposure to risk. *Behavioral Ecology*, 27(4), 988–994. <https://doi.org/10.1093/beheco/arw003>
- Kohn, G. M. (2019). How social systems persist: Learning to build a social network in an uncertain world. *Animal Behaviour*, 154, 1–6. <https://doi.org/10.1016/j.anbehav.2019.06.006>
- Kohn, G. M., King, A. P., Dohme, R., Meredith, G. R., & West, M. J. (2013). Robust autumn social attributes predict spring courtship skills in juvenile female brown-headed cowbirds, *Molothrus ater*. *Animal Behaviour*, 85(4), 727–732. <https://doi.org/10.1016/j.anbehav.2013.01.009>
- Kohn, G. M., King, A. P., Scherschel, L. L., & West, M. J. (2011). Social niches and sex assortment: Uncovering the developmental ecology of brown-headed cowbirds, *Molothrus ater*. *Animal Behaviour*, 82, 1015–1022. <https://doi.org/10.1016/j.anbehav.2011.07.035>
- Kohn, G. M., Nugent, M. R., & Dail, X. (2022). Juvenile Gouldian finches (*Erythrura gouldiae*) form sibling subgroups during social integration. *Developmental Psychobiology*, 64(4), Article e22262. <https://doi.org/10.1002/dev.22262>
- Kulik, L., Amici, F., Langos, D., & Widdig, A. (2015). Sex differences in the development of social relationships in rhesus macaques (*Macaca mulatta*). *International Journal of Primatology*, 36, 353–376. <https://doi.org/10.1007/s10764-015-9826-4>
- Kulik, L., Muniz, L., Mundry, R., & Widdig, A. (2012). Patterns of interventions and the effect of coalitions and sociality on male fitness. *Molecular Ecology*, 21(3), 699–714.
- Lehmann, J., Majolo, B., & McFarland, R. (2015). The effects of social network position on the survival of wild Barbary macaques, *Macaca sylvanus*. *Behavioral Ecology*, 27, 20–28. <https://doi.org/10.1093/beheco/arv169>
- Lonsdorf, E. V., Markham, A. C., Heintz, M. R., Anderson, K. E., Ciuk, D. J., Goodall, J., & Murray, C. M. (2014). Sex differences in wild chimpanzee behavior emerge during infancy. *PLoS One*, 9, Article 99099. <https://doi.org/10.1371/journal.pone.0099099>
- McFarland, R., Fuller, A., Hetem, R. S., Mitchell, D., Maloney, S. K., Henzi, S. P., & Barrett, L. (2015). Social integration confers thermal benefits in a gregarious primate. *Journal of Animal Ecology*, 84, 871–878. <https://doi.org/10.1111/1365-2656.12329>
- McFarland, R., & Majolo, B. (2013). Coping with the cold: Predictors of survival in wild Barbary macaques, *Macaca sylvanus*. *Biology Letters*, 9(4), Article 20130428. <https://doi.org/10.1098/rsbl.2013.0428>
- McFarland, R., Murphy, D., Lusseau, D., Henzi, S. P., Parker, J. L., Pollet, T. V., & Barrett, L. (2017). The 'strength of weak ties' among female baboons: Fitness-related benefits of social bonds. *Animal Behaviour*, 126, 101–106. <https://doi.org/10.1016/j.anbehav.2017.02.002>
- Meredith, S. L. (2013). Identifying proximate and ultimate causation in the development of primate sex-typed social behavior. In K. B. H. Clancy, K. Hinde, & J. N. Rutherford (Eds.), *Building babies* (pp. 411–433). Springer. https://doi.org/10.1007/978-1-4614-4060-4_18
- Nakamichi, M. (1989). Sex differences in social development during the first 4 years in a free-ranging group of Japanese monkeys, *Macaca fuscata*. *Animal Behaviour*, 38(5), 737–748. <https://www.sciencedirect.com/science/article/pii/S000334728980106X>
- Newman, M. (2010). *Networks: An introduction*. Oxford University Press. <https://doi.org/10.1093/acprof:oso/9780199206650.001.0001>
- Ostner, J., & Schülke, O. (2018). Linking sociality to fitness in primates: A call for mechanisms. *Advances in the Study of Behavior*, 50, 127–175. <https://doi.org/10.1016/bs.asb.2017.12.001>
- Pasternak, G., Kienzle, S., Barrett, L., Henzi, P., Brown, L. R., & Fuller, A. (2013). Population ecology of vervet monkeys in a high latitude, semi-arid riparian woodland. *Koedoe: African Protected Area Conservation and Science*, 55(1), 1–9.
- Pedersen, E. J., Miller, D. L., Simpson, G. L., & Ross, N. (2019). Hierarchical generalized additive models in ecology: An introduction with mgcv. *PeerJ*, 7, Article e6876. <https://doi.org/10.7717/peerj.6876>
- Pereira, M. E., & Leigh, S. R. (2003). Modes of primate development. In P. M. Kappeler, & M. E. Pereira (Eds.), *Primate life histories and socioecology* (pp. 149–176). University of Chicago Press.
- Rosenblum, L. A., & Coe, C. L. (1977). The influence of social structure on squirrel monkey socialization. In F. E. Poirier, & S. Chevalier-Skolnikoff (Eds.), *Primate bio-social development* (pp. 479–500). Garland.

- Schülke, O., Anzà, S., Crockford, C., De Moor, D., Deschner, T., Fichtel, C., Gogarten, J. F., Kappeler, P. M., Manin, V., Müller-Klein, N., Prox, L., Sadoughi, B., Tountou, S., Wittig, R. M., & Ostner, J. (2022). Quantifying within-group variation in sociality: Covariation among metrics and patterns across primate groups and species. *Behavioral Ecology and Sociobiology*, 76(4), Article 50. <https://doi.org/10.1007/s00265-022-03133-5>
- Schülke, O., Bhagavatula, J., Vigilant, L., & Ostner, J. (2010). Social bonds enhance reproductive success in male macaques. *Current Biology*, 20(24), 2207–2210. <https://doi.org/10.1016/j.cub.2010.10.058>
- Schülke, O., Dumdey, N., & Ostner, J. (2020). Selective attention for affiliative and agonistic interactions of dominants and close affiliates in macaques. *Scientific Reports*, 10, Article 5962. <https://doi.org/10.1038/s41598-020-62772-8>
- Silk, J. B. (1999). Why are infants so attractive to others? The form and function of infant handling in bonnet macaques. *Animal Behaviour*, 57(5), 1021–1032. <https://www.sciencedirect.com/science/article/pii/S000334729891065X>
- Silk, J. B., Alberts, S. C., & Altmann, J. (2003). Social bonds of female baboons enhance infant survival. *Science*, 302, 1231–1234. <https://doi.org/10.1126/science.1088580>
- Silk, J. B., Alberts, S. C., & Altmann, J. (2006). Social relationships among adult female baboons (*Papio cynocephalus*) II. Variation in the quality and stability of social bonds. *Behavioral Ecology and Sociobiology*, 61, 197–204. <https://doi.org/10.1007/s00265-006-0250-9>
- Silk, J. B., Altmann, J., & Alberts, S. C. (2006). Social relationships among adult female baboons (*Papio cynocephalus*) I. Variation in the strength of social bonds. *Behavioral Ecology and Sociobiology*, 61, 183–195. <https://doi.org/10.1007/s00265-006-0249-2>
- Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., Wittig, R. M., Seyfarth, R. M., & Cheney, D. L. (2009). The benefits of social capital: Close social bonds among female baboons enhance offspring survival. *Proceedings of the Royal Society B: Biological Sciences*, 276(1670), 3099–3104. <https://doi.org/10.1098/rspb.2009.0681>
- Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., Wittig, R. M., Seyfarth, R. M., & Cheney, D. L. (2010a). Strong and consistent social bonds enhance the longevity of female baboons. *Current Biology*, 20(15), 1359–1361. <https://doi.org/10.1016/j.cub.2010.05.067>
- Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., Wittig, R. M., Seyfarth, R. M., & Cheney, D. L. (2010b). Female chacma baboons form strong, equitable, and enduring social bonds. *Behavioral Ecology and Sociobiology*, 64, 1733–1747. <https://doi.org/10.1007/s00265-010-0986-0>
- Snyder-Mackler, N., Burger, J. R., Gaydosh, L., Belsky, D. W., Noppert, G. A., Campos, F. A., Bartolomucci, A., Yang, Y. C., Aiello, A. E., O'Rand, A., Harris, K. M., Shively, C. A., Alberts, S. C., & Tung, J. (2020). Social determinants of health and survival in humans and other animals. *Science*, 368(6493), Article eaax9553. <https://doi.org/10.1126/science.aax9553>
- Stanton, M. A., & Mann, J. (2012). Early social networks predict survival in wild bottlenose dolphins. *PLoS One*, 7(10), Article e47508. <https://doi.org/10.1371/journal.pone.0047508>
- Stumpf, R. M., Emery Thompson, M., Muller, M. N., & Wrangham, R. W. (2009). The context of female dispersal in Kanyawara chimpanzees. *Behaviour*, 146(4–5), 629–656. <https://doi.org/10.1163/156853909X413853>
- Suomi, S. J. (2005). Mother–infant attachment, peer relationships, and the development of social networks in rhesus monkeys. *Human Development*, 48, 67–79. <https://doi.org/10.1159/000083216>
- Vehtari, A., Gelman, A., & Gabry, J. (2017). Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Statistics and Computing*, 27(5), 1413–1432. <https://doi.org/10.1007/s11222-016-9696-4>
- Vilette, C., Bonnell, T., Dostie, M. J., Henzi, S. P., & Barrett, L. (2022). Network formation during social integration in juvenile vervet monkeys. *Animal Behaviour*, 194, 205–223. <https://doi.org/10.1016/j.anbehav.2022.10.006>
- Vilette, C., Bonnell, T., Henzi, S. P., & Barrett, L. (2020). Comparing dominance hierarchy methods using a data-splitting approach with real-world data. *Behavioral Ecology*, 31(6), 1379–1390. <https://doi.org/10.1093/beheco/araa095>
- Wanker, R., Bernate, L. C., & Franck, D. (1996). Socialization of spectacled parrotlets *Forpus conspicillatus*: The role of parents, crèches and sibling groups in nature. *Journal für Ornithologie*, 137(4), 447–461. <https://link.springer.com/article/10.1007/BF01661101>
- Wickham, H. (2009). *ggplot: Using the grammar of graphics with R*. Springer-Verlag.
- Willems, E. P., Barton, R. A., & Hill, R. A. (2009). Remotely sensed productivity, regional home range selection, and local range use by an omnivorous primate. *Behavioral Ecology*, 20(5), 985–992. <https://doi.org/10.1093/beheco/arp087>
- Young, C., Bonnell, T. R., Brown, L. R., Dostie, M. J., Ganswindt, A., Kienzle, S., McFarland, R., Henzi, S. P., & Barrett, L. (2019). Climate induced stress and mortality in vervet monkeys. *Royal Society Open Science*, 6(11), Article 191078. <https://doi.org/10.1098/rsos.191078>
- Young, C., McFarland, R., Barrett, L., & Henzi, S. P. (2017). Formidable females and the power trajectories of socially integrated male vervet monkeys. *Animal Behaviour*, 125, 61–67. <https://doi.org/10.1016/j.anbehav.2017.01.006>

Appendix

Table A1

Summary of the model parameters used in hierarchical generalized additive models (HGAMs) to assess the influence of age and sex factors and our response variables

Interaction type	Response variable	Fixed effects	Interactions	Distribution
Spatial proximity	Cosine similarity	Age	Age by juvenile ID	Zero-one-inflated beta
		Scan.nb	Age by cohort ID	
		NDVI	Age by sex	
		Troop.nb	Age by troop ID	
			Age by mother ID	
Grooming	Degree	Same as above	Rank by ID	Negative binomial
	Strength	Same as above		Negative binomial
	Association rate with adults	Same as above		Zero-one-inflated beta
	Association rate with family members	Same as above		Zero-one-inflated beta
	Cosine similarity	Age	Age by juvenile ID	Zero-one-inflated beta
Spatial/Grooming comparison	Cosine similarity	Scan.nb	Age by cohort ID	Zero-one-inflated beta
		NDVI	Age by sex	
		Troop.nb	Age by troop ID	
			Age by mother ID	
			Rank by ID	
Mother/Offspring comparison	Cosine similarity	Degree	Same as above	Negative binomial
		Strength	Same as above	Hurdle Poisson
		Association rate with adults	Same as above	Zero-one-inflated beta
		Association rate with family members	Same as above	Zero-one-inflated beta
			Same as above	Zero-one-inflated beta

ID = identity; nb = number; NDVI = normalized difference vegetation index.

Table A2

Summary statistics of a Bayesian hierarchical generalized additive mixed model (HGAM) for the number of partners (degree) in spatial associations, using a negative binomial distribution

Effect	Parameter	Estimate	Estimate error	Lower 95% CI	Upper 95% CI
Population level effects	Intercept	−4.49	0.47	−5.42	−3.56
	s(age)	0.55	0.99	−1.30	2.46
	s(NDVI)	0.41	0.67	−0.81	1.79
	s(troop.nb)	0.02	0.83	−1.64	1.61
	sds(age)	2.04	1.42	0.14	5.39
Smooth terms	sds(age ID1)	1.21	0.14	0.94	1.47
	sds(age ID2)	1.04	0.70	0.06	2.53
	sds(age cohort1)	1.97	0.50	1.17	3.15
	sds(age cohort2)	2.15	1.78	0.08	6.58
	sds(age troop1)	0.93	0.27	0.50	1.52
	sds(age troop2)	1.14	1.13	0.03	4.23
	sds(age mumID1)	0.41	0.26	0.03	0.93
	sds(age mumID2)	1.64	0.77	0.11	3.09
	sds(age sex1)	0.20	0.17	0.01	0.64
	sds(age sex2)	2.54	1.82	0.41	7.77
	sds(NDVI)	0.57	0.52	0.02	1.96
	sds(troop.nb)	1.82	0.70	0.72	3.48
	sds(rank ID1)	0.13	0.09	0.00	0.33
	sds(rank ID2)	1.03	0.67	0.04	2.43
	Family-specific parameters	Shape	273.51	128.23	109.83
		Estimate	Estimate error	Q2.5	Q97.5
R^2 marginal		0.75	0.01	0.73	0.77

CI = credible interval; NDVI = normalized difference vegetation index; nb = number; ID = identity; mum = mother; s() = spline. Smooth-term sds() = spline 'wiggliness' (spline variance parameter).

Table A3

Summary statistics of a Bayesian hierarchical generalized additive mixed model (HGAM) for the number of partners (degree) in grooming associations, using a negative binomial distribution

Effect	Parameter	Estimate	Estimate error	Lower 95% CI	Upper 95% CI
Population level effects	Intercept	−12.67	1.50	−16.18	−10.04
	s(age)	0.07	0.98	−1.81	1.94
	s(NDVI)	0.18	0.97	−1.68	2.03
	s(troop.nb)	−0.13	0.95	−1.98	1.67
	sds(age)	1.73	1.61	0.06	5.63
Smooth terms	sds(age ID1)	2.61	1.95	0.12	7.08
	sds(age ID2)	2.92	2.87	0.12	10.69
	sds(age cohort1)	2.33	1.88	0.09	7.07
	sds(age cohort2)	3.97	5.17	0.11	15.99
	sds(age troop1)	2.20	1.83	0.09	6.63
	sds(age troop2)	2.37	2.49	0.07	8.47
	sds(age mumID1)	2.57	1.99	0.14	7.55
	sds(age mumID2)	2.95	2.99	0.10	11.03
	sds(age sex1)	1.58	1.39	0.07	5.29
	sds(age sex2)	2.75	2.94	0.10	10.79
	sds(NDVI)	1.71	1.53	0.08	5.37
	sds(troop.nb)	1.51	1.46	0.05	4.95
	sds(rank ID1)	2.28	1.69	0.08	6.26
	sds(rank ID2)	2.94	2.90	0.09	11.15
	Family-specific parameters	Shape	25.62	42.81	0.38
		Estimate	Estimate error	Q2.5	Q97.5
R^2 marginal		0.38	0.18	0.06	0.67

CI = credible interval; NDVI = normalized difference vegetation index; nb = number; ID = identity; mum = mother; s() = spline. Smooth-term sds() = spline 'wiggliness' (spline variance parameter).

Table A4

Summary statistics of a Bayesian hierarchical generalized additive mixed hurdle model (HGAM) for the frequency of interactions (strength) in spatial associations, using a negative binomial distribution

Effect	Parameter	Estimate	Estimate error	Lower 95% CI	Upper 95% CI	
Population level effects	Intercept	-0.60	0.57	-1.70	0.55	
	hu_Intercept	0.42	0.94	-1.41	2.21	
	s(age)	0.30	0.70	-0.95	1.78	
	s(NDVI)	0.67	0.75	-0.78	2.20	
	s(troop.nb)	-0.60	0.57	-1.70	0.55	
Smooth terms	sds(age)	4.22	2.28	0.56	9.37	
	sds(age ID1)	1.46	0.18	1.13	1.82	
	sds(age ID2)	0.97	0.66	0.04	2.44	
	sds(age cohort1)	2.64	0.69	1.52	4.21	
	sds(age cohort2)	2.39	2.05	0.09	7.68	
	sds(age troop1)	1.22	0.34	0.69	1.99	
	sds(age troop2)	1.52	1.39	0.07	5.09	
	sds(age mumID1)	0.53	0.30	0.03	1.09	
	sds(age mumID2)	2.00	0.78	0.15	3.41	
	sds(age sex1)	0.21	0.20	0.01	0.74	
	sds(age sex2)	2.59	1.88	0.48	7.37	
	sds(NDVI)	0.53	0.53	0.02	1.94	
	sds(troop.nb)	0.87	0.53	0.22	2.22	
	sds(rank ID1)	0.15	0.11	0.01	0.40	
	sds(rank ID2)	0.94	0.65	0.03	2.43	
	Family-specific parameters	Shape	3.51	0.18	3.18	3.85
		R² marginal	Estimate	Estimate error	Q2.5	Q97.5
		0.77	0.01	0.74	0.79	

CI = credible interval; hu = hurdle; NDVI = normalized difference vegetation index; nb = number; ID = identity; mum = mother; s() = spline. Smooth-term sds() = spline 'wiggleness' (spline variance parameter).

Table A5

Summary statistics of a Bayesian hierarchical generalized additive mixed hurdle model (HGAM) for the frequency of interactions (strength) in grooming, using a Poisson distribution

Effect	Parameter	Estimate	Estimate error	Lower 95% CI	Upper 95% CI
Population level effects	Intercept	-2.86	0.27	-3.39	-2.28
	s(age)	-0.31	0.72	-1.74	1.14
	s(NDVI)	-0.03	0.43	-0.93	0.86
	s(troop.nb)	-0.09	0.53	-1.02	1.22
	Smooth terms	sds(age)	0.43	0.40	0.01
sds(age ID1)		0.89	0.09	0.71	1.08
sds(age ID2)		0.47	0.33	0.02	1.22
sds(age cohort1)		0.62	0.21	0.28	1.07
sds(age cohort2)		1.15	1.20	0.04	4.39
sds(age troop1)		0.30	0.20	0.01	0.74
sds(age troop2)		1.65	1.22	0.18	4.91
sds(age mumID1)		0.21	0.16	0.01	0.59
sds(age mumID2)		0.44	0.33	0.01	1.21
sds(age sex1)		0.15	0.12	0.00	0.44
sds(age sex2)		1.25	1.48	0.03	5.07
sds(NDVI)		0.22	0.21	0.01	0.85
sds(troop.nb)		0.31	0.33	0.01	1.21
sds(rank ID1)		0.12	0.08	0.01	0.29
sds(rank ID2)		0.42	0.31	0.01	1.16
R² marginal		Estimate	Estimate error	Q2.5	Q97.5
			0.79	0.01	0.76

CI = credible interval; NDVI = normalized difference vegetation index; nb = number; ID = identity; mum = mother; s() = spline. Smooth-term sds() = spline 'wiggleness' (spline variance parameter).

Table A6

Summary statistics of a Bayesian hierarchical generalized additive mixed model (HGAM) for the frequency of interactions (strength) in grooming associations, using a negative binomial distribution

Effect	Parameter	Estimate	Estimate error	Lower 95% CI	Upper 95% CI
Population level effects	Intercept	−3.49	0.35	−4.18	−2.77
	s(age)	−0.46	0.85	−2.04	1.19
	s(NDVI)	−0.36	0.58	−1.41	0.93
	s(troop.nb)	−0.10	0.56	−1.14	1.16
	sds(age)	0.58	0.55	0.03	1.97
Smooth terms	sds(age ID1)	1.49	0.15	1.19	1.77
	sds(age ID2)	0.66	0.50	0.02	1.85
	sds(age cohort1)	0.90	0.32	0.31	1.61
	sds(age cohort2)	1.51	1.33	0.05	5.09
	sds(age troop1)	0.53	0.31	0.03	1.17
	sds(age troop2)	2.63	1.54	0.56	6.56
	sds(age mumID1)	0.33	0.25	0.02	0.95
	sds(age mumID2)	0.71	0.51	0.03	1.88
	sds(age sex1)	0.22	0.18	0.01	0.68
	sds(age sex2)	1.38	1.43	0.04	5.21
	sds(NDVI)	0.30	0.30	0.01	1.11
	sds(troop.nb)	0.29	0.30	0.01	1.03
	sds(rank ID1)	0.22	0.14	0.01	0.50
	sds(rank ID2)	0.62	0.47	0.02	1.73
	Family-specific parameters	Shape	45.66	19.26	23.59
		Estimate	Estimate error	Q2.5	Q97.5
R^2 marginal		0.78	0.02	0.73	0.82

CI = credible interval; NDVI = normalized difference vegetation index; nb = number; ID = identity; mum = mother; s() = spline. Smooth-term sds() = spline 'wiggleness' (spline variance parameter).

Table A7

Summary statistics of a Bayesian hierarchical generalized additive mixed model (HGAM) for the spatial association rate with adults, using a zero-one-inflated beta distribution

Effect	Parameter	Estimate	Estimate error	Lower 95% CI	Upper 95% CI
Population level effects	Intercept	−1.52	0.29	−2.05	−0.90
	s(age)	−0.35	0.96	−2.23	1.48
	s(scan.nb)	−0.82	0.69	−1.99	0.77
	s(NDVI)	−0.41	0.87	−2.14	1.29
	s(troop.nb)	0.09	0.59	−1.07	1.29
Smooth terms	sds(age)	0.94	0.82	0.04	3.08
	sds(age ID1)	1.76	0.45	0.77	2.57
	sds(age ID2)	2.23	1.37	0.12	5.00
	sds(age cohort1)	2.71	0.63	1.65	4.18
	sds(age cohort2)	3.16	2.29	0.19	8.84
	sds(age troop1)	0.41	0.33	0.02	1.24
	sds(age troop2)	1.54	1.37	0.07	5.17
	sds(age mumID1)	1.17	0.61	0.08	2.32
	sds(age mumID2)	2.29	1.36	0.09	5.04
	sds(scan.nb)	0.38	0.44	0.01	1.59
	sds(age sex1)	0.85	0.62	0.04	2.26
	sds(age sex2)	1.72	1.64	0.07	6.23
	sds(NDVI)	2.04	1.14	0.41	4.69
	sds(troop.nb)	0.31	0.35	0.01	1.26
	sds(rank ID1)	0.49	0.29	0.02	1.08
sds(rank ID2)	2.61	1.72	0.10	6.06	
Family-specific parameters	Phi	40.46	4.28	32.50	49.40
	Zoi	0.67	0.01	0.64	0.69
	Coi	0.02	0.00	0.01	0.03
		Estimate	Estimate error	Q2.5	Q97.5
	R^2 marginal	0.12	0.04	0.06	0.22

CI = credible interval; nb = number; NDVI = normalized difference vegetation index; ID = identity; mum = mother; s() = spline. Smooth-term sds() = spline 'wiggleness' (spline variance parameter).

Table A8

Summary statistics of a Bayesian hierarchical generalized additive mixed model (HGAM) for the grooming association rate with adults, using a zero-one-inflated beta distribution

Effect	Parameter	Estimate	Estimate error	Lower 95% CI	Upper 95% CI
Population level effects	Intercept	0.81	1.54	-2.10	3.93
	s(age)	0.01	0.98	-1.93	1.90
	s(scan.nb)	0.13	0.96	-1.82	2.01
	s(NDVI)	-0.02	1.00	-2.01	1.99
	s(troop.nb)	0.08	1.01	-1.91	2.09
Smooth terms	sds(age)	2.37	2.24	0.10	7.86
	sds(age ID1)	1.96	1.75	0.07	6.21
	sds(age ID2)	2.44	2.38	0.09	8.51
	sds(age cohort1)	2.02	1.83	0.08	6.81
	sds(age cohort2)	2.57	2.47	0.10	8.95
	sds(age troop1)	2.03	1.85	0.08	6.54
	sds(age troop2)	2.67	2.80	0.09	9.86
	sds(age mumID1)	1.94	1.68	0.10	6.21
	sds(age mumID2)	2.42	2.50	0.05	9.00
	sds(scan.nb)	1.87	1.82	0.06	6.38
	sds(age sex1)	2.03	1.91	0.03	7.16
	sds(age sex2)	2.59	2.57	0.07	9.00
	sds(NDVI)	2.09	1.82	0.09	6.72
	sds(troop.nb)	2.01	1.81	0.08	6.78
	sds(rank ID1)	1.90	1.61	0.09	5.97
	sds(rank ID2)	2.50	2.42	0.09	8.60
	Family-specific parameters	Phi	42.40	54.90	2.30
Zoi		0.99	0.00	0.98	1.00
Coi		0.97	0.01	0.95	0.98
Estimate		Estimate error	Q2.5	Q97.5	
R^2 marginal	0.00	0.00	0.00	0.00	

CI = credible interval; nb = number; NDVI = normalized difference vegetation index; ID = identity; mum = mother; s() = spline. Smooth-term sds() = spline 'wiggleness' (spline variance parameter).

Table A9

Summary statistics of a Bayesian hierarchical generalized additive mixed model (HGAM) for the spatial association rate with family members, using a zero-one-inflated beta distribution

Effect	Parameter	Estimate	Estimate error	Lower 95% CI	Upper 95% CI
Population level effects	Intercept	-0.69	0.50	-1.60	0.37
	s(age)	-0.64	0.94	-2.47	1.18
	s(scan.nb)	-1.03	0.81	-2.40	0.85
	s(NDVI)	-0.61	1.00	-2.57	1.33
	s(troop.nb)	-0.18	0.85	-1.86	1.51
Smooth terms	sds(age)	1.67	1.52	0.07	5.80
	sds(age ID1)	1.45	0.25	0.95	1.92
	sds(age ID2)	0.70	0.53	0.03	1.94
	sds(age cohort1)	2.62	0.66	1.52	4.15
	sds(age cohort2)	2.52	2.19	0.14	8.01
	sds(age troop1)	0.36	0.26	0.02	0.98
	sds(age troop2)	1.34	1.23	0.06	4.54
	sds(age mumID1)	0.70	0.37	0.04	1.37
	sds(age mumID2)	1.92	0.81	0.25	3.45
	sds(scan.nb)	0.56	0.47	0.03	1.73
	sds(age sex1)	0.67	0.46	0.03	1.74
	sds(age sex2)	1.81	1.82	0.05	6.38
	sds(NDVI)	3.01	1.27	0.91	5.86
	sds(troop.nb)	1.58	1.02	0.06	3.79
	sds(rank ID1)	0.25	0.17	0.01	0.61
	sds(rank ID2)	0.66	0.50	0.03	1.85
	Family-specific parameters	Phi	20.24	1.45	17.45
Zoi		0.43	0.01	0.41	0.46
Coi		0.15	0.01	0.12	0.18
Estimate		Estimate error	Q2.5	Q97.5	
R^2 marginal	0.16	0.01	0.13	0.18	

CI = credible interval; nb = number; NDVI = normalized difference vegetation index; ID = identity; mum = mother; s() = spline. Smooth-term sds() = spline 'wiggleness' (spline variance parameter).

Table A10

Summary statistics of a Bayesian hierarchical generalized additive mixed model (HGAM) for the grooming association rate with family members, using a zero-one-inflated beta distribution

Effect	Parameter	Estimate	Estimate error	Lower 95% CI	Upper 95% CI
Population level effects	Intercept	0.33	1.09	−1.81	2.53
	s(age)	−0.05	0.99	−1.99	1.91
	s(scan.nb)	−0.23	1.00	−2.12	1.71
	s(NDVI)	−0.02	1.02	−2.00	1.90
	s(troop.nb)	−0.05	0.96	−1.89	1.77
Smooth terms	sds(age)	1.92	1.69	0.08	6.19
	sds(age ID1)	1.55	1.31	0.07	4.89
	sds(age ID2)	2.37	2.31	0.07	8.17
	sds(age cohort1)	1.80	1.51	0.08	5.60
	sds(age cohort2)	2.72	2.91	0.10	10.45
	sds(age troop1)	1.70	1.42	0.05	5.22
	sds(age troop2)	2.33	2.09	0.10	7.88
	sds(age mumID1)	1.60	1.32	0.05	4.99
	sds(age mumID2)	2.42	2.45	0.06	8.27
	sds(scan.nb)	1.49	1.29	0.08	4.69
	sds(age sex1)	1.57	1.37	0.07	5.01
	sds(age sex2)	2.36	2.36	0.06	8.25
	sds(NDVI)	1.50	1.35	0.07	4.97
	sds(troop.nb)	1.45	1.30	0.06	4.70
	sds(rank ID1)	1.13	0.99	0.05	3.68
	sds(rank ID2)	2.29	2.16	0.07	8.19
	Family-specific parameters	Phi	61.10	60.59	6.49
Zoi		0.98	0.01	0.97	0.99
Coi		0.96	0.01	0.94	0.97
Estimate		Estimate error	Q2.5	Q97.5	
R^2 marginal	0.00	0.00	0.00	0.00	

CI = credible interval; nb = number; NDVI = normalized difference vegetation index; ID = identity; mum = mother; s() = spline. Smooth-term sds() = spline 'wiggleness' (spline variance parameter).

Table A11

Summary statistics of a Bayesian hierarchical generalized additive mixed model (HGAM) for the similarity in spatial partners (cosine), using a zero-one-inflated beta distribution

Effect	Parameter	Estimate	Estimate error	Lower 95% CI	Upper 95% CI
Population level effects	Intercept	0.30	0.48	−0.63	1.27
	s(age)	−0.03	0.93	−1.85	1.85
	s(scan.nb)	0.80	0.91	−0.92	2.60
	s(NDVI)	0.43	0.98	−1.48	2.40
	s(troop.nb)	−0.69	0.98	−2.44	1.23
Smooth terms	sds(age)	0.67	0.62	0.02	2.26
	sds(age ID1)	0.73	0.17	0.38	1.06
	sds(age ID2)	0.92	0.60	0.05	2.25
	sds(age cohort1)	0.68	0.48	0.04	1.82
	sds(age cohort2)	3.91	2.46	0.42	10.20
	sds(age troop1)	1.58	0.46	0.72	2.55
	sds(age troop2)	1.91	1.61	0.09	6.01
	sds(age mumID1)	0.20	0.15	0.01	0.53
	sds(age mumID2)	1.16	0.63	0.08	2.38
	sds(scan.nb)	2.73	1.10	1.10	5.19
	sds(age sex1)	0.26	0.21	0.01	0.82
	sds(age sex2)	1.33	1.39	0.04	4.82
	sds(NDVI)	3.18	1.27	1.30	6.27
	sds(troop.nb)	3.91	2.37	0.09	8.88
	sds(rank ID1)	0.25	0.17	0.01	0.63
	sds(rank ID2)	0.84	0.57	0.04	2.09
	Family-specific parameters	Phi	4.53	0.23	4.10
Zoi		0.14	0.01	0.12	0.16
Coi		0.04	0.01	0.01	0.07
Estimate		Estimate error	Q2.5	Q97.5	
R^2 marginal	0.14	0.02	0.11	0.17	

CI = credible interval; nb = number; NDVI = normalized difference vegetation index; ID = identity; mum = mother; s() = spline. Smooth-term sds() = spline 'wiggleness' (spline variance parameter).

Table A12

Summary statistics of a Bayesian hierarchical generalized additive mixed model (HGAM) for the similarity in grooming partners (cosine), using a zero-one-inflated beta distribution

Effect	Parameter	Estimate	Estimate error	Lower 95% CI	Upper 95% CI
Population level effects	Intercept	1.48	1.17	−0.85	3.86
	s(age)	−0.02	0.99	−1.90	1.79
	s(scan.nb)	−0.12	0.98	−1.99	1.78
	s(NDVI)	0.03	0.90	−1.69	1.81
	s(troop.nb)	0.11	1.01	−1.90	2.04
Smooth terms	sds(age)	1.90	1.77	0.04	6.08
	sds(age ID1)	2.24	1.97	0.06	7.97
	sds(age ID2)	2.84	2.69	0.08	9.98
	sds(age cohort1)	1.95	1.68	0.06	6.27
	sds(age cohort2)	2.64	3.03	0.09	9.00
	sds(age troop1)	2.06	1.70	0.07	6.21
	sds(age troop2)	2.67	2.68	0.11	9.50
	sds(age mumID1)	2.00	1.64	0.08	5.75
	sds(age mumID2)	2.83	2.77	0.14	10.35
	sds(scan.nb)	1.94	1.70	0.07	5.86
	sds(age sex1)	1.61	1.39	0.07	5.14
	sds(age sex2)	2.63	2.55	0.11	9.18
	sds(NDVI)	1.66	1.41	0.06	5.02
	sds(troop.nb)	1.49	1.43	0.04	5.21
	sds(rank ID1)	1.68	1.44	0.07	5.17
	sds(rank ID2)	2.82	2.95	0.08	10.42
	Family-specific parameters	Phi	61.88	68.03	6.75
Zoi		0.95	0.01	0.92	0.97
Coi		0.94	0.02	0.90	0.96
R² marginal		Estimate	Estimate error	Q2.5	Q97.5
	0.00	0.00	0.00	0.01	

CI = credible interval; nb = number; NDVI = normalized difference vegetation index; ID = identity; mum = mother; s() = spline. Smooth-term sds() = spline 'wiggleness' (spline variance parameter).

Table A13

Summary statistics of a Bayesian hierarchical generalized additive mixed model (HGAM) for the similarity between spatial and grooming partners (cosine), using a zero-one-inflated beta distribution

Effect	Parameter	Estimate	Estimate error	Lower 95% CI	Upper 95% CI
Population level effects	Intercept	−0.81	0.58	−1.96	0.40
	s(age)	−0.02	1.00	−1.95	2.01
	s(scan.nb)	−0.38	0.99	−2.23	1.56
	s(NDVI)	−0.22	0.81	−1.93	1.34
	s(troop.nb)	−0.90	0.72	−2.21	0.67
Smooth terms	sds(age)	1.36	1.23	0.04	4.67
	sds(age ID1)	1.85	0.46	0.67	2.57
	sds(age ID2)	1.41	1.01	0.06	3.66
	sds(age cohort1)	2.76	0.67	1.62	4.24
	sds(age cohort2)	2.91	2.54	0.10	9.55
	sds(age troop1)	0.88	0.58	0.05	2.19
	sds(age troop2)	1.69	1.48	0.06	5.24
	sds(age mumID1)	1.01	0.58	0.06	2.16
	sds(age mumID2)	1.64	1.09	0.08	3.94
	sds(scan.nb)	1.45	0.90	0.30	3.71
	sds(age sex1)	0.52	0.44	0.02	1.62
	sds(age sex2)	1.66	1.71	0.06	6.29
	sds(NDVI)	0.77	0.77	0.02	2.46
	sds(troop.nb)	0.36	0.35	0.01	1.28
	sds(rank ID1)	0.24	0.18	0.01	0.67
	sds(rank ID2)	1.32	0.97	0.06	3.59
	Family-specific Parameters	Phi	37.71	4.92	28.86
Zoi		0.37	0.02	0.33	0.42
Coi		0.07	0.02	0.04	0.11
R² marginal		Estimate	Estimate error	Q2.5	Q97.5
	0.27	0.02	0.23	0.32	

CI = credible interval; nb = number; NDVI = normalized difference vegetation index; ID = identity; mum = mother; s() = spline. Smooth-term sds() = spline 'wiggleness' (spline variance parameter).

Table A14

Summary statistics of a Bayesian hierarchical generalized additive mixed model (HGAM) for the similarity between a mother's grooming partners and her offspring's weak grooming partners (cosine), using a zero-one-inflated beta distribution

Effect	Parameter	Estimate	Estimate error	Lower 95% CI	Upper 95% CI	
Population level effects	Intercept	1.59	0.25	1.09	2.12	
	s(age)	0.18	0.76	-1.44	1.62	
	s(scan.nb)	-0.37	0.69	-1.86	0.85	
	s(NDVI)	-0.07	0.63	-1.63	0.97	
	s(troop.nb)	0.80	0.73	-0.72	2.14	
Smooth terms	sds(age)	0.48	0.45	0.02	1.68	
	sds(age ID1)	0.23	0.16	0.01	0.61	
	sds(age ID2)	0.41	0.31	0.01	1.20	
	sds(age cohort1)	0.59	0.31	0.07	1.24	
	sds(age cohort2)	1.08	1.06	0.03	3.84	
	sds(age troop1)	0.37	0.24	0.02	0.92	
	sds(age troop2)	1.16	1.16	0.04	4.07	
	sds(age mumID1)	0.35	0.19	0.03	0.69	
	sds(age mumID2)	1.05	0.51	0.09	2.03	
	sds(scan.nb)	0.52	0.47	0.01	1.77	
	sds(age sex1)	0.17	0.15	0.01	0.57	
	sds(age sex2)	0.98	1.00	0.02	3.72	
	sds(NDVI)	0.32	0.32	0.01	1.17	
	sds(troop.nb)	0.61	0.36	0.18	1.53	
	sds(rank ID1)	0.20	0.14	0.01	0.50	
	sds(rank ID2)	0.38	0.30	0.01	1.12	
	Family-specific parameters	Phi	6.84	0.30	6.28	7.44
		Zoi	0.01	0.00	0.01	0.02
		Coi	0.47	0.12	0.24	0.70
Estimate		Estimate error	Q2.5	Q97.5		
R^2 marginal		0.15	0.02	0.12	0.19	

CI = credible interval; nb = number; NDVI = normalized difference vegetation index; ID = identity; mum = mother; s() = spline. Smooth-term sds() = spline 'wiggleness' (spline variance parameter).