



Network formation during social integration in juvenile vervet monkeys

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Understanding the development of social relationships, or the process of socialization, can provide insights into the processes by which social network structures emerge and vary across species. In this analysis, we investigated the process of network formation from a developmental perspective using data from three groups of wild vervet monkeys, *Chlorocebus pygerythrus*. We used a dynamic social network approach that allowed us to capture patterns of social change over time. Specifically, we considered the temporal dynamics of two separate interaction networks, spatial and grooming associations, and investigated these patterns between the sexes. We used these data to test predictions derived from a developmental framework on relationship formation put forward by Kohn (2019, *Animal Behaviour*, 154, 1–6). We found that females and males differed in their grooming patterns but were similar in their spatial associations. Furthermore, spatial proximity ego-networks showed seasonal patterns, whereas grooming ego-networks did not. When all relevant centrality measures were considered in concert, we found evidence to suggest that a distinctive network structure forms across the course of development, with ego-networks composed of few strong ties and many weak ties, regardless of behaviour and sex. However, these networks were not produced according to the processes described by Kohn (2019), perhaps because Kohn's framework is concerned mainly with network composition and not structure. Overall, our results provide evidence for social niche construction across development, with the formation of a core social 'bubble' of strong ties that can provide a consistent and predictable immediate social environment. More broadly, these patterns suggest that network formation is a process of ongoing adjustment to the social environment, and not an attempt to meet an optimal end goal.

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Social network analysis provides a powerful quantitative framework for measuring individual social phenotypes and social structure (Wey et al., 2013). A particular topic of interest has been the identification of the costs and benefits associated with different social network positions, and how these might link to fitness (Croft et al., 2016; Sih et al., 2009; Wey et al., 2008). Such efforts have produced evidence suggesting that the structure of networks, and individuals' position within them, can influence both adult and offspring longevity as well as offspring survival (Brent, 2015; Cheney et al., 2016; McFarland et al., 2017; Ostner & Schülke, 2018; Snyder-Mackler et al., 2020). At the same time, however, we still lack a comprehensive theory to explain how different network

structures are generated and maintained, and why network diversity varies within and between species (Ilany & Akçay, 2016).

Initial efforts to construct such a theory have been made by Ilany and Akçay (2016), who investigated whether the emergence of network structure could be explained by a process of intergenerational inheritance, where offspring acquire network connections from their parents (Ilany & Akçay, 2016). Proximally, this can be explained as a consequence of newborns staying close to their mothers, which leads them to interact initially, and primarily, with their mother's social partners (Deputte, 2000). These initial associations come to constitute the core of the developing infant's own social network (i.e. ego-network). There is evidence for this kind of network inheritance among taxa that form stable social groups and that contain multiple generations (Goldenberg et al., 2016; Ilany et al., 2021; Ward & Hart, 2003; Whitehouse & Lubin, 2005). Such patterns raise the possibility that social inheritance is a general mechanism for network maintenance among group-living

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species. However, in wild vervet monkeys, *Chlorocebus pygerythrus*, Jarrett et al. (2018) found that, although there was some evidence for network inheritance by juveniles, the adult grooming network could not be replicated by the inheritance of maternal contacts alone. This appeared to be a consequence of two factors. First, maternal networks were insufficiently stable to support the inheritance of social partners and thereby to recreate the overall network (see also Schino et al., 2004, for *Macaca*). That is, maternal network composition seemed to represent a moving target for offspring, such that matching was unavoidably imprecise. Second, simulations showed that a greater number of associations with nonmaternal contacts was needed to replicate the global network, suggesting that the formation of bonds with age cohort peers and other immatures, in addition to bonds with adults, were key to network formation, maintenance and variation over time. Functionally, it makes intuitive sense for juveniles to develop advantageous connections with peers who share a similar life expectancy and a greater probability of continued presence in the group, and not rely on contacts with older individuals alone. If this interpretation is accurate, we might anticipate that juveniles will actively structure their interactions to achieve a network containing both inherited contacts and connections formed independently of the mother.

In this regard, Kohn (2019) proposed that juvenile social relationships develop according to three temporally structured phases: exploration, pruning and consolidation. That is, as juveniles explore their social environment, their social connections go through an initial period of overproduction, followed by attrition and then consolidation. This process is argued to allow juveniles to converge on species-typical relationships first, by exploring many potential social connections in the group, and second, by responding to contingent behavioural feedback from others to guide the formation of longer-lasting relationships (Deputte, 2000). Thus, juveniles should initially explore their social environment widely and then become more selective in their choice of social partners over time (Ward & Webster, 2016). Furthermore, species sex differences have been found to appear prior to sexual maturation (Cords et al., 2010; Jarrett et al., 2018; Lonsdorf et al., 2014; Nakamichi, 1989), whereby the philopatric females have stronger social bonds than dispersing males (Andres et al., 2013; Cords et al., 2010; Frere et al., 2010; Kulik et al., 2015; Nakamichi, 1989). These early sex differences in social behaviour can be interpreted in light of the different life histories and reproductive strategies of males and females (Deputte, 2000). Therefore, Kohn's developmental steps may allow us to detect the emergence of behavioural sex differences and to track their development through time.

Kohn's (2019) mechanistic framework speaks directly to the idea of social niche construction. Social niche construction describes the way in which individuals, singly or collectively, influence the composition and dynamics of their social environments (Laland et al., 2016). While this definition of social niche construction is consistent across the literature, the definition of the 'social niche' itself varies considerably (Saltz et al., 2016). Authors have defined social niches (both explicitly and implicitly) as social groups, social environments and/or patterns of social interactions (Bergmüller & Taborsky, 2010; Flack et al., 2006; Kohn et al., 2011; Ryan, 2011) that can be stable (Kohn et al., 2011), and which exert an influence on individual's phenotype and/or fitness (Bergmüller & Taborsky, 2010; Laskowski & Bell, 2014; Montiglio et al., 2013; Ryan, 2011; Saltz et al., 2016). This imprecision is reflected in the lack of empirical attempts to characterize social niches in concrete, empirical terms (but see Kohn et al., 2011). One possible solution is to characterize a social niche using social networks. For instance, Flack et al. (2006) suggested that social niches could be represented graphically as the local connections of an individual's network

(ego-network) in multiple, overlapping social networks ('interaction networks', in Barrett et al., 2012). In other words, the different types of social interactions that characterize an individual's engagement with others constitute the components of a social niche. These components can each be represented as individual social interaction networks (Barrett et al., 2012). Here, we begin an exploration of social niche formation via an investigation of two social niche components. More specifically, we use a dynamic social network approach that allows us to capture the processes of exploration, pruning and consolidation at the individual level.

To do so, we consider the temporal dynamics of two separate interaction networks, spatial association and allogrooming, in three groups of wild vervet monkeys. Spatial association and grooming represent two key components of an individual's social niche, as both offer the means by which animals can exert control over the individuals found in their immediate vicinity. These components also provide a useful contrast, as grooming generally requires mutual attraction between partners, whereas spatial proximity can often be achieved unilaterally. In addition, we compare these patterns between the sexes, as the development of enduring social relationships should be more advantageous for females, who remain in their natal group for life, than for males, who are the migrating sex.

Regarding both spatial and grooming associations, and following Kohn (2019), we predicted that juvenile social interactions would translate into large (high network degree) and dense (high network strength) ego-networks during the exploration phase (Fig. 1a). As this phase is expected to be characterized by a lack of structure and stability in juveniles' ego-networks, we also predicted that social interactions would be distributed equally among the focal animal's partners (low skewness), and that networks should lack a consistent composition (low cosine similarity). During the pruning (Fig. 1b) and consolidation (Fig. 1c) phases, juveniles should develop and strengthen preferred social interactions. Consequently, we predicted a decline in individual ego-network size and density, followed by a stabilization of the network at this new size and strength distribution. Simultaneously, we expected social interactions to become increasingly concentrated on fewer partners that remained consistent over time. That is, we predicted an increase in skewness and cosine similarity across the developmental period, followed by a stabilization at this new level. Although we predicted that spatial and grooming associations would display the same patterns across time, we expected them to differ in magnitude in ways that would reflect the level of control an individual could exert over its associates. That is, grooming behaviour is more precisely targeted towards specific individuals, whereas spatial associations combine such active elements with more passive forms of association, where individuals demonstrate mere tolerance of others rather than choice. Consequently, we expected spatial ego-networks to be larger and more dense than grooming networks, and we predicted that spatial ego-network structure and stability would be lower than for grooming ego-networks. In addition to a test of Kohn's (2019) framework, then, our study aimed to demonstrate the general utility of social network analysis for characterizing aspects of social niche formation.

METHODS

Study Population and Subjects

The data used for this study 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

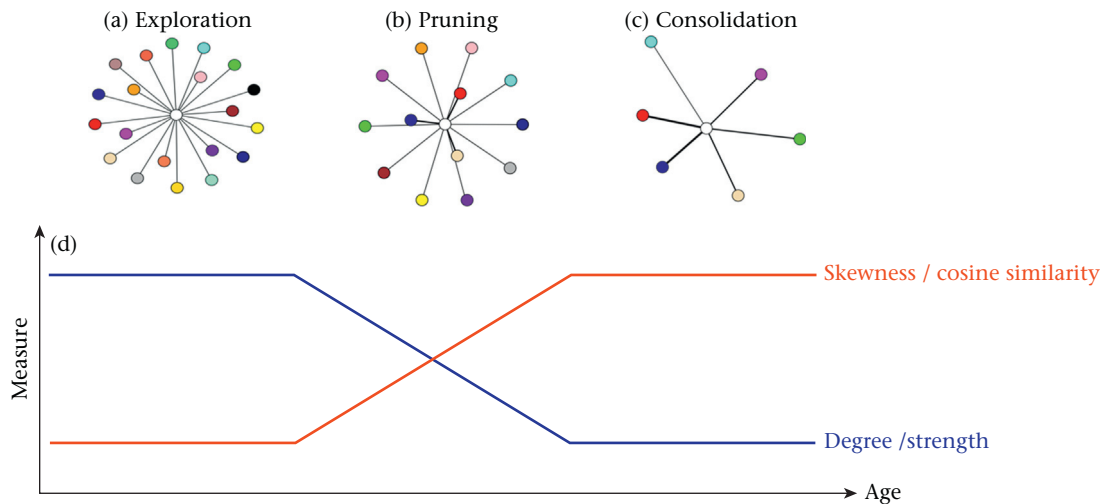


Figure 1. Kohn's (2019) phases of socialization translated into ego-networks, associated with the predictions for degree, strength, skewness and cosine similarity during juveniles' development. (a) Exploration: degree/strength are predicted to be high and skewness/cosine similarity should be low. (b)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

(Pasternak et al., 2013). The three study groups (mean \pm SD group size: PT group: 39 ± 8 ; RBM group: 49 ± 6 ; RST group: 57 ± 7) were fully habituated, and all animals were individually identifiable from natural markings. Vervets live in multimale, multifemale troops, ranging in size between five and ~75 individuals (Horrocks, 1986; Pasternak et al., 2013). The troops in our study population are much larger than the species' average (Pasternak et al., 2013). It is possible that group fission is constrained because there is a large contrast in food productivity between the acacia woodland along the river, within which the study troops inhabit, and the considerably lower productivity away from the river (Pasternak et al., 2013). On average, vervet males reach sexual maturity at 5 years of age (Horrocks, 1986), and females typically have their first infant between 3 and 5 years of age (Fairbanks & McGuire, 1984). Females are philopatric, whereas males emigrate from their natal group at sexual maturity. Thereafter, they move roughly every 2.5–3 years (Cheney et al., 1988; Henzi & Lucas, 1980), dependent upon their rank and integration into the female network (Young et al., 2019).

Vervets are seasonal breeders who give birth to a single offspring. Birth season occurs during the rainy months of the austral spring (Butynski, 1988), i.e. between October and December. The study subjects comprised three birth cohorts from the 2013, 2014 and 2015 birth seasons. The number of juveniles, as well as the representation 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

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

juveniles (Jarrett et al., 2018), which corresponded to an age of approximately 7 months (± 1 month) for the 2013 and 2014 cohorts. Data collection started later for the 2015 cohort, around 11 months (± 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 (see Young et al., 2017, for more detail). Each scan was conducted over a period of 10 min, and we collected data on each animal's activity (feeding, moving, resting and grooming) and all spatial associates 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 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 (R Core Team, 2017), both data sets were aggregated over a 60-day window that was then shifted successively by 30 days (see Appendix, Fig. A1 for sampling effort). We estimated the convergence of our measures in both the grooming and spatial proximity networks, using the 'check.windowsize' function of the 'netTS' (Bonnell & Vilette, 2020) package in R and 1000 iterations. The 'check.windowsize' function also allowed us to measure the sensitivity of this subsampling. We found high similar estimates (i.e. converged) and low variation in estimates (i.e. robust to subsampling) using a 60-day window for degree, strength and grooming cosine similarity. This means that the chosen window size was able to provide good measures. The estimates were not as robust for skewness and spatial cosine similarity, suggesting the

potential for noise in our predicted patterns. Although skewness measures showed a relatively larger amount of noise, a window size of 60 days (2 months) appeared to be a good compromise between desired temporal aggregation and noise in our estimated network measures (Supplementary Figs S1, S2). Within each window, spatial association and grooming interactions were aggregated to construct weighted, nondirected networks at the node level (i.e. ego-networks). In other words, each juvenile present within the window had an ego-network created 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 (Fuji et al., 2015) from the 'Perc' package in R. We chose this method following the training–testing procedure described in Vilette et al. (2020), and included agonistic interactions between all individuals (males, females and juveniles). 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.

Social Network Structure

To capture Kohn's (2019) phases, we extracted the following four measures of network centrality. (1) Degree, which is the sum of each node's connections. This captures the number of partners a focal subject has and indicates the extent of its connectedness to other nodes (Farine & Whitehead, 2015). (2) Strength, which is the sum of each node's connections weighted by the frequency of the interaction with other nodes. An individual with high strength is either weakly associated with many other group members and/or strongly associated with a few group members (Farine & Whitehead, 2015). (3) Skewness, which measures the extent to which the distribution of the edge weights distribution is symmetrical. Positive (right-skewed) values identify individuals that are weakly associated (low strength/weak ties) with many group members (high degree), while having strong associations (high strength/strong ties) with only a small subset (low degree). Negative (left-skewed) values indicate juveniles that are disproportionately placing effort into many partners (degree) with whom they associate very frequently (strength). A skewness of zero indicates that animals are distributing their effort equally across all partners (see Supplementary Fig. S3). To capture the distribution accurately, we calculated skewness only when the number of partners was greater than two. (4) 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, cosine similarity assesses the similarity of the edge weights between two consecutive ego-networks, with values that range between 0 and 1. An individual whose social partners (ego-network) change markedly between time t and $t + 1$ will have a low cosine similarity, whereas individuals whose social partners are similar at t and $t + 1$ will be associated with a high cosine similarity. More details on calculating cosine values are given in the Supplementary material (see Cosine Similarity Measure).

Environmental Conditions

As food availability may well contribute to the structuring of juvenile associations, we measured troop level estimates of resource availability using the normalized difference vegetation index (NDVI; Willems et al., 2009). NDVI data were collected from the moderate resolution imaging spectroradiometer (MODIS) satellite images using Google Earth Engine (Gorelick et al., 2017). The

satellites Aqua and Terra (this is the MODIS constellation) collect electromagnetic reflectance from the surface of the earth. NASA uses these two parts of the spectrum to calculate NDVI for any given point on the Earth every 16 days, so the NDVI raster is a derived bitmap image that is created from data collected by the satellite. In this study, area-weighted averages for each territory were generated for consecutive 33-day windows (16 days following 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 (see Young et al., 2019, for details of the data extraction procedures). 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 S6–S9). 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 fit to the data.

For each measure of network centrality (strength, degree, skewness) and temporal partner consistency (cosine similarity), we constructed two models: one for grooming and one for spatial associations, generating a total of eight models. For all eight models, the model structure was constant. Our data set structure consisted of repeated measures within individual, mother, cohort and troop identity, as well as sex. As such, we 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, it creates an estimate for each level of the grouping variable, but only estimates 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 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 (see Appendix, Table A1 for model structure). Apart from the number of spatial partners (i.e. spatial degree), a Poisson model was run for all our count variables (three in total). As dispersion issues are common with Poisson models, we ran an analysis of residuals from the models to detect any dispersion issues ('DHARMA' Package). We addressed dispersion issues present in our three models by running models

with a negative binomial distribution. When this approach did not remove the dispersion issue, hurdle models were run (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 ('LOO'; Vehtari et al., 2017) with the 'loo_compare' function of 'brms'. (2) We looked at the magnitude of the dispersion, from the analysis of residuals. (3) We used the posterior predictive checks. Once the model that fitted our data best was found, we compared its estimates with the estimates of our simpler original Poisson model. This was used to assess whether the influence of the dispersion issue affected our results. As this was not the case for any of our three models, we report the simpler Poisson models in the main text and provide the necessary details regarding the other models in the . As such, when considering the influence of age and sex on the number of partners, we constructed a binomial for spatial associations as the maximum number of spatial partners was known. That is, we used a binomial model (Hilbe, 2017) with troop size as the number of trials to model the number of partners. We specified a Poisson distribution for the number of grooming partners, as well as the frequency of spatial and grooming associations. Finally, for all models ran with a Poisson distribution (degree and strength), the log of the total number of observation sessions within the aggregated sample period was included as an offset in the model to account for differences in observation effort. When using the distribution of edge weights (skewness) as our response variable, we constructed a skew-normal model for spatial and grooming associations, as the response values were all positive with a skewed distribution. For both types of interaction, a zero-one inflated beta model was constructed to look at partner preference (cosine similarity), due to the presence of a large proportion of zeros. All the model summary tables are presented in the Appendix (Tables A2–A11), accompanied by Dharma nonparametric dispersion tests and posterior predictive distribution plots, when required.

Given the nature of the statistical models, as well as the inclusion of interaction effects, direct interpretation of model estimates is not straightforward from a summary table. To aid interpretation, we 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 (CI) in our plots to assess whether the sexes differed meaningfully in the structure of the revealed patterns. That is, we considered whether the CIs for females and males overlapped completely (i.e. no detectable difference between the sexes) or not at all (i.e. a meaningful quantitative difference between the sexes). The raw data, plotted with the predicted patterns, are presented in the Appendix (Figs A2–A3). Model main effects are presented as summary statistics (Appendix, Tables A1–A11) for posterior means, 95% CIs, along with conditional R^2 values for each model, estimated using the 'bayes_R2' function (Gelman et al., 2019).

RESULTS

Social Network Structures

Spatial ego-network structure

Neither degree nor strength displayed the predicted pattern of high initial values followed by a decline and levelling off (Fig. 2a, b).

Instead, both sexes displayed an overall decline in the number of partners as they aged. This overall pattern was interspersed with a more dramatic drop in the number of partners at around 2.5 years of age, followed by an increase in both sexes, with males showing a more precipitous drop and greater subsequent increase than females. Predictions were estimated with a mean troop size fixed at 48 individuals, revealing that at a very young age, both sexes were spatially associated with almost the whole troop (mean degree = ~44). For strength, the general trend for both sexes was a cyclical pattern of peaks and troughs that aligned with the annual birth season, with higher strength during the birth season, accompanied by an overall and constant decrease (Fig. 2b). Despite the general similarity in the pattern shown, female strength values were higher than those of males throughout the developmental period. As might be expected, given these results, neither skewness nor cosine similarity showed the predicted increase over time. Instead, both sexes displayed fluctuating positive skewness values across birth seasons (Fig. 2c), with a more nuanced increase for the third birth season. During the second birth season, females displayed much higher skewness values than males. Spatial cosine similarity values declined over time for both sexes, with the deceleration being more pronounced for males (Fig. 2d). Nevertheless, both sexes sustained high cosine values overall. Lastly, this overall decrease was interspersed with a slight increase in cosine similarity values during the second birth season.

Grooming network structure

Again, observed patterns did not support our predictions. Rather, the mean number of grooming partners steadily increased over time for both sexes. The increase was, however, slower for males, with the result that divergence between the sexes also increased over time (Fig. 3a). There was an increase in grooming strength observed in females, before settling down following the first birth season. A peak in strength was then observed between the second and third birth season. This overall increase in strength was not mirrored by males, where strength declined with age (Fig. 3b). Yet, the same peak was observed, to a lesser magnitude, between the second and third birth season. The sexes thus displayed meaningfully different patterns in their grooming associations. With respect to skewness, females showed a fluctuating positive pattern over time, which reached a somewhat bumpy plateau between ~1.5 and 2.5 years of age, followed by a decrease (Fig. 3c). This pattern was mirrored by males, although at a distinctively lower level. In the case of cosine similarity in grooming, both sexes began with high mean cosine values, followed by a consistent decline in partner similarity as they grew older (Fig. 3d), with the decrease being somewhat more pronounced for males.

DISCUSSION

Taken together, our results did not show convincing evidence for the developmental patterns of social engagement predicted by Kohn (2019). That is, for both spatial proximity and grooming networks, the high initial observed values of degree and strength were not followed by a period of consistent decline that eventually reached a plateau, representing the formation of a stable network comprising a subset of similar contacts.

If we consider spatial proximity first, we found that, for both sexes, although it underwent an overall decline, degree nevertheless remained high across development, and did so despite a dramatic drop observed around the 2.5-year mark. In the case of strength, both sexes showed a striking cyclical pattern corresponding to the annual birth season, with an overall decline in strength across time. We also did not find the patterns expected for skewness and cosine similarity. Instead, values for both skewness

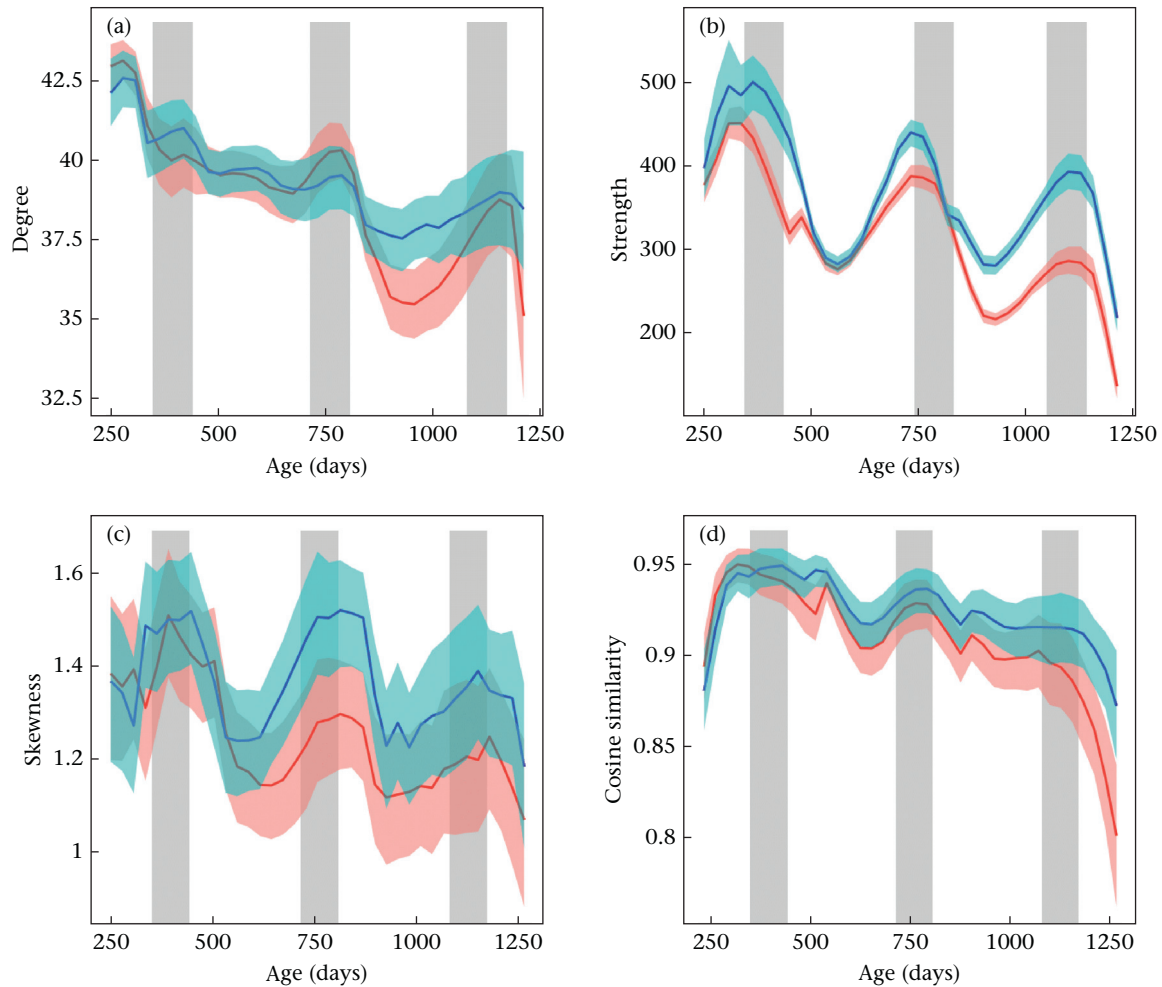


Figure 2. Variation in the (a) degree (b) strength (c) skewness and (d) cosine similarity of spatial associations by age and sex for juvenile vervets. The red and blue lines show the global smooth for the average male and female, respectively, with upper and lower 95% credible intervals (bands). Grey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

and cosine similarity were high initially and remained so over time. However, this is not to suggest there was no variation at all. In the case of skewness, there was again evidence for a cyclical pattern corresponding to each birth season, but at a lower magnitude during the third. For cosine similarity, although we found a decline over time, the magnitude of this shift was small, and values remained high across the entire period.

In social network terms, these results suggest that, for both sexes, spatial ego-networks became smaller and also diminished in density (i.e. juveniles were less frequently in proximity to other individuals). The skewness measure suggested that these ego-networks were composed of numerous weak ties and a few strong ones, with the strong ties remaining similar through time (which accounts for the sustained high cosine values). In other words, individuals were not distributing their effort equally. This finding comes as a surprise for two reasons. First, we initially assumed that individuals would find it harder to structure their spatial interactions consistently. Second, given the observed seasonal variations in the frequency of interactions, we would have expected to observe a loss of structure at some point (i.e. the distribution no longer being positively skewed). This suggests that the arrival of a new cohort of newborns into the group led to changes in size, composition and dynamics of the group, to which juvenile interactions were sensitive. Previous work has shown that

attraction to newborns may promote close spatial associations with mothers (Silk, 1999, 2009; Silk et al., 2003), leading spatial social structure topologies to become more centralized. This is indeed what we observed with spatial associations, where the upward shifts in strength during the birth season (Fig. 2b) combined with the positive fluctuations in skewness (Fig. 3c) suggest that these associations become centred on a subset of individuals at this time (i.e. the surplus of effort put on fewer strong ties increases the contrast between weak and very strong ties, leading to an increase in skewness). Future studies might helpfully investigate whether the birth of a new infant draws juveniles back to their mothers and her associates, and also how strength and skewness relate to each other. In other words, it would be useful to address whether the increase in frequency of associations leads juveniles to focus more tightly on a subset of their partners (increase in skewness) or whether is it the change in their ego-network structure (high skewness) that allows them to then increase their association frequency.

If we now turn to grooming patterns, although we also found distinctive patterns across time, once again these did not conform to Kohn's (2019) developmental model. We found that juvenile females were characterized by low degree at the beginning of the study period, followed by a consistent increase in the number of partners (from around five partners at the beginning of the period

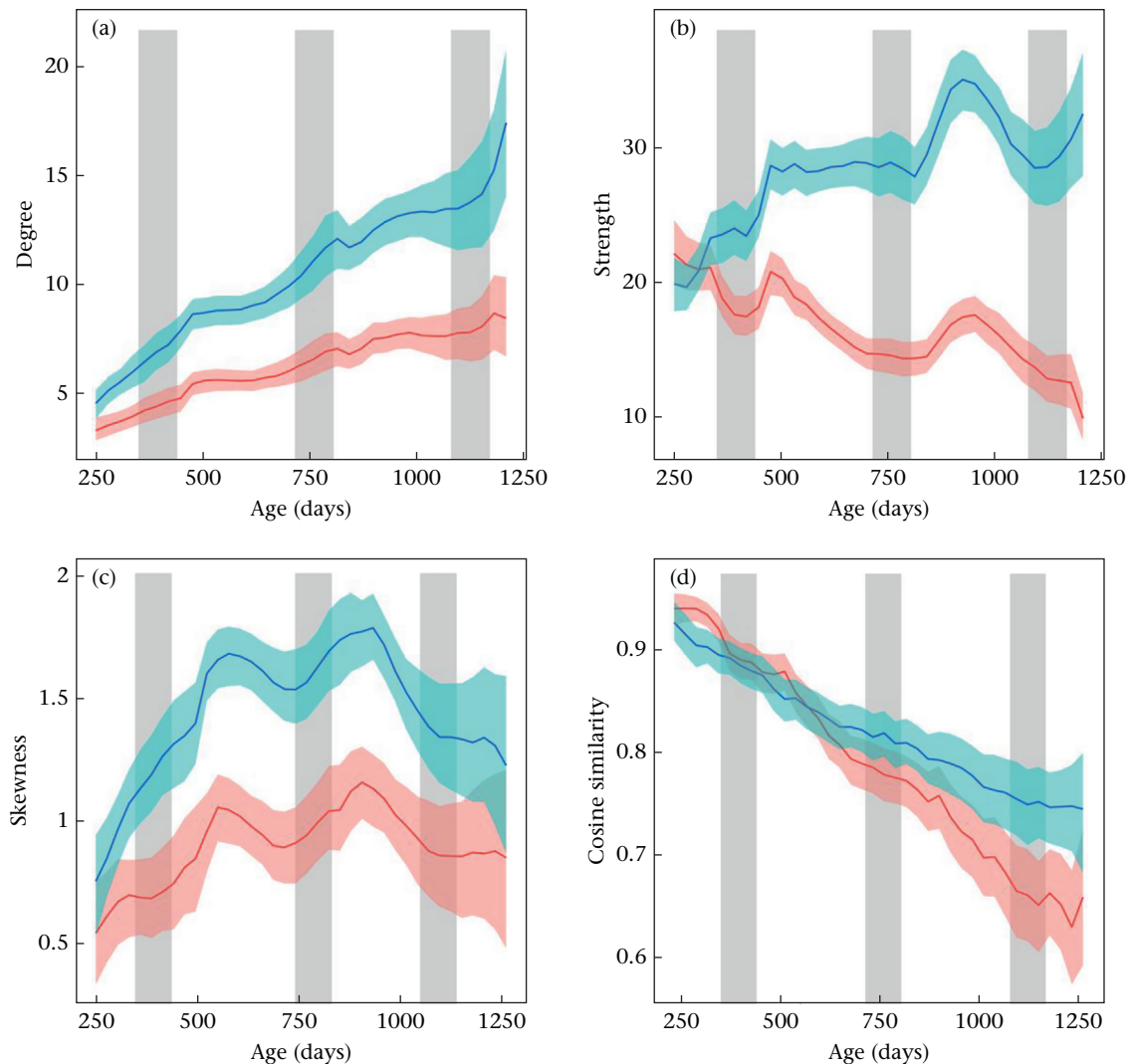


Figure 3. Variation in (a) degree (b) strength (c) skewness and (d) cosine of grooming associations by age and sex for juvenile vervets. The red and blue lines show the global smooth for the average male and female, respectively, with upper and lower 95% credible intervals (bands). Grey areas delimit the average annual birth season. Predictions were calculated with a mean troop size fixed at 49 individuals.

up to 15 partners at the end) and their frequency of interaction over time. This raises issues concerning time budget constraints and social coordination. Among cercopithecines, adult females can groom across the entire female cohort (i.e. the total number of females in the group) as long as this cohort remains below some threshold size (e.g. seven for female mountain baboons, *Papio cynocephalus ursinus*; Henzi et al., 1997; five to six for vervet monkeys; Henzi et al., 2013). Above this level, grooming cliques become smaller due to problems that arise with respect to social coordination. As such, the large grooming cliques acquired by juvenile females seem anomalous. However, the increase in grooming partners was also accompanied by an increase in positive skewness values until 2.5 years of age. This suggests that the average female frequently groomed a small subset of partners (strong ties), while the remainder of her partners were groomed infrequently (weak ties). Furthermore, throughout the first 2.5 years, the contrast between weak and strong ties increased, suggesting that juvenile females were not forced to reduce or cap the number of partners in their grooming cliques, but instead underwent a shift in how they distributed their grooming within their networks as degree increased. Around 2.5 years of age, however, a

decrease in skewness was observed, although values remained positive. This decrease was accompanied by an increase in degree, which suggests that the contrast between strong and weak ties became less stark. That is, some compromises may take place on strong partners, rather than on the number of partners, where juveniles invest less in their strong ties. Therefore, it would be interesting to further investigate how degree and skewness respond in relation to variation in troop size.

In contrast to the female pattern, males showed a much shallower rise in degree over time, along with a decrease in the frequency of interactions (Fig. 3a, b). Males also showed generally high skewness values, with an increase across the first 2.5 years, while their values were nevertheless consistently lower than those for females (Fig. 3c). Thus, although male ego-networks showed the same structure of weak and strong ties, this was not as pronounced as it was for females. Males were, however, similar to females with respect to cosine estimates, again showing a constant decline in partner similarity over time (Fig. 3d). Taken together, these patterns suggest that males were less strongly integrated into grooming networks than females (Fig. 3a, b), a pattern also found in previous studies (Blaszczuk, 2018; Cords et al., 2010; Jarrett et al., 2018). This

sex difference may arise because males migrate at sexual maturity and are less likely to invest in the development of enduring social relationships.

Although we have treated spatial proximity and grooming as two separate components of the animals' social niche, examining these patterns in concert can help our understanding of the process by which juveniles build their niches. First and foremost, spatial proximity ego-networks showed seasonal patterns, whereas grooming ego-networks did not. As predicted, juveniles associated more frequently with spatial partners than with grooming partners (Figs 2, 3b) and they associated with more spatial partners (Figs 2, 3a) than they did grooming partners. One possible interpretation, then, is that juveniles have different interaction styles (passive versus active) across behavioural contexts. It may be that, for juveniles, regulating who is within 3 m of them may be challenging. A grooming interaction, in contrast, involves two willing partners, allowing a more active, controlled choice of association, in terms of the effort invested and the partners targeted. Against our predictions, however, spatial proximity associations showed higher partner stability and revealed ego-networks composed of many weak ties and few strong ties. One possible explanation here is that spatial ego-networks may be less robust to large-scale changes at the level of the group, such as the arrival of the birth season, where the sudden influx of multiple newborns may lead juveniles to be in proximity to others more frequently due to the increased attention received by their mothers and new siblings. In contrast, grooming interactions are less likely to be affected by such large-scale shifts in group dynamics because juveniles can control partner choice. However, they may be more likely to respond to smaller-scale, more continuous fluctuations, such as shifts in time budget demands with increasing troop size. Indeed, adult patterns of grooming in our population respond to contingent ecological and demographic conditions in just this way (Henzi et al., 2013; Young et al., 2019).

Although our patterns did not resemble those predicted by Kohn (2019), a common pattern was observed in the structure of the networks (i.e. social niche components) for both sexes. This finding, we believe, allows us to explain why Kohn's (2019) model apparently does not describe social integration in our population. Our data suggest that individuals' ego-networks are composed of many weak ties and few strong ties. While the focus of many network studies often falls on the identity and traits of the individuals (the 'who') that comprise an ego-network, we suggest that, in this case, it is the structure of the network itself that is of developmental relevance (the 'how'). Kohn's (2019) model is largely focused on the 'who', where the third and final step is based on the establishment of preferred relationships. What our findings suggest is that juveniles are also building a network of a particular structure, as well as establishing preferred relationships. We interpret the formation of this subset of strong ties as a way to create a more secure social space for an individual, which we can characterize as a 'social bubble'. Having found this additional 'level' of structure, it raises the possibility that, by considering the overall ego-network, we have focused on the wrong level, and that it is within the layer of strong ties that Kohn's (2019) proposed phases operate. Taking a closer look at social bubble formation and composition over time is therefore warranted, as it seems likely that this sets the social conditions to which juveniles are exposed (see Kohn et al., 2022). For example, in terms of spatial proximity, an animal that is broadly spatially integrated, with numerous weak ties, may ensure enhanced protection against predators, while a more consistent social bubble of strong ties may guarantee protection against potential conspecific competitors. In a grooming setting, infrequent grooming partners may translate into more opportunistic grooming that serves immediate goals (Barrett & Henzi, 2006), while a

social bubble of frequent grooming ties, perhaps with kin, may serve other fitness-related goals (Josephs et al., 2016; Silk et al., 2006). Therefore, our findings point to the necessity of better understanding the relative role of strong and weak ties in predicting primate fitness, as suggested in other recent work (Ellis et al., 2019; Ostner & Schülke, 2018; Schülke et al., 2022).

Finally, another component likely to have had an impact on our observed patterns is the chosen timescale. Kohn did not explicitly consider temporal dynamics and did not give details of the period over which these phases were believed to occur, and many possible timescales are possible, from days to weeks to, as we have considered here, years. With regard to social integration in our population, questions about its duration and whether individuals all integrate at the same pace remain unanswered. It is possible that Kohn's (2019) three phases may, in concert, operate over a shorter timescale than we considered here. It is also possible that each phase may have its own particular duration and that this may vary individually. For example, in species where juveniles can explore their social group without being socially at risk (e.g. where there is no infanticide), it may be that the exploration phase takes longer than the other two phases. In addition, as relationships in a social group represent a dynamic negotiation between dyads in response to ecological factors and other aspect of group dynamics, it is also possible that Kohn's (2019) phases may recur, at least to some degree, each time the social group undergoes a change in size and composition. That is, such changes may disrupt and relaunch the network formation process, resulting in a series of network formation cycles, rather than a singular, clean, linear progression. Investigating individual variation may therefore help us understand the pace at which juveniles integrate into the group, and hence the appropriate time frame needed to cover the entire process of integration.

Overall, consideration of developmental social dynamics has allowed us to get a more detailed appreciation of how social networks and social niches are constructed over time. One obvious point to make is that both spatial proximity and grooming patterns did not reveal any shift, either gradual or sudden, that marked the end of the juvenile period and the emergence of an adult pattern. This contrasted with gross sex differences in patterning, where a clear differentiation between male and female social engagement became increasingly apparent. This suggests that the former pattern does not simply reflect a methodological failure to detect a pattern that was, in fact, there. Consequently, our findings do not indicate any kind of 'social revolution' occurring at a key point in development as suggested for other species (Kulik et al., 2015), whereby a typical juvenile form of engagement is discarded in order to commence the daily business of adulthood. The early and distinct behavioural sex differences found in our population also suggest that the migrating males and philopatric females may adopt different social strategies as soon as they become independent of their mothers and do not arise as a result of sexual maturity. It seems much more likely that, as we have seen, there are no large-scale shifts in social engagement, but rather continuous, multiple, small adjustments that result in the formation of a beneficial network structure. Thus, ongoing social dynamics may promote only short-term stability that can be expected to shift over time, and juveniles form the network structures that serve them best for the time being (i.e. they are not engaging in suboptimal patterns of engagement as part of the process of working towards a more beneficial end goal). That is, being able to coordinate activities and sustain proximity with specific partners calls for individuals to be able to flexibly adjust to temporal shifts in their social network structure throughout the developmental period. Hence, it seems reasonable to consider the possibility that social integration, in general, may be a process of ongoing continual adjustment

achieved through social niche construction among highly social species. In turn, social niche construction offers a mechanism by which individuals can form the network structures that best serve their needs given the ecological and social conditions they face. Here, social niche construction apparently enables young animals to embed themselves in more secure ego-network structures (social bubbles), while retaining the benefits of broader integration in the group through the presence of weak social ties (McFarland et al., 2017).

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. All authors approved the final version of the manuscript.

Data Availability

Data will be made available on request.

Declaration of Interest

We declare there were no conflicts 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.2022.10.006>.

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Appendix



Figure A1. Variation in the average number of scans per window, by troop.

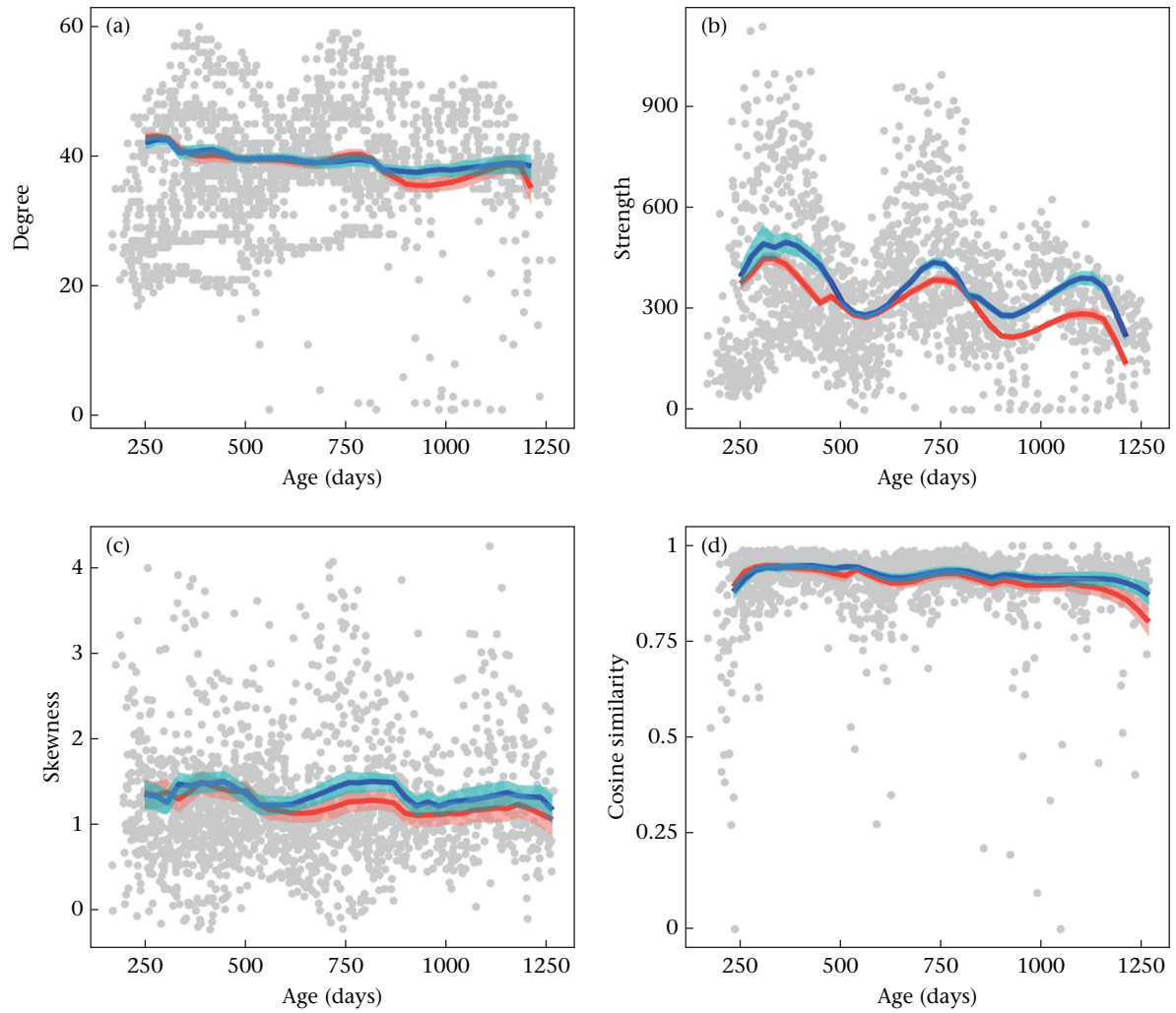


Figure A2. Variation in the (a) degree (b) strength (c) skewness and (d) cosine similarity of spatial associations by age and sex for juvenile vervets. The red and blue lines show the global smooth for the average male and female, respectively, with upper and lower 95% credible intervals (bands). The grey dots show the raw data. Predictions were estimated with mean troop size fixed at 48 individuals.

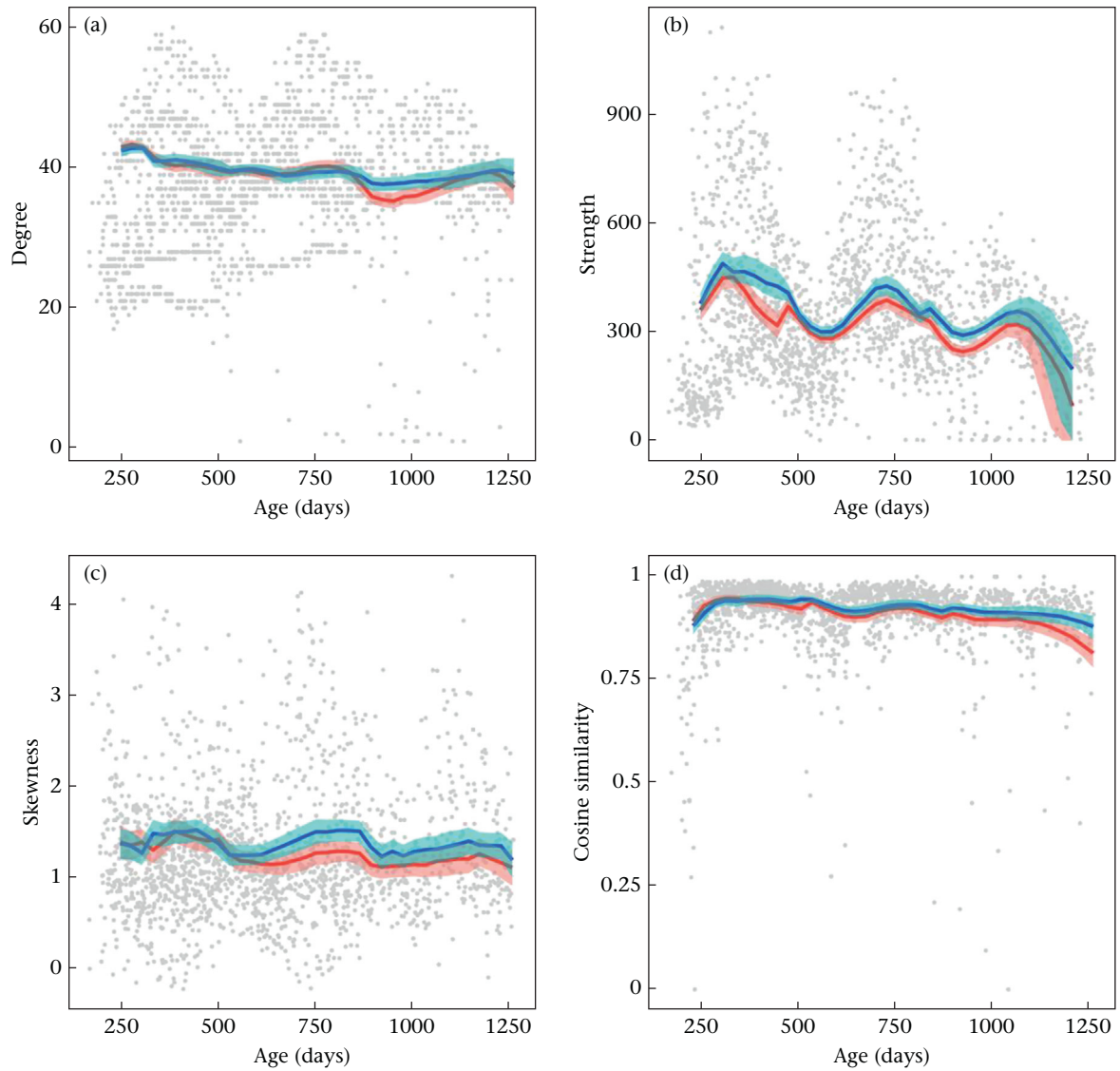


Figure A3. Variation in the (a) degree (b) strength (c) skewness and (d) cosine similarity of grooming associations by age and sex for juvenile vervets. The red and blue lines show the global smooth for the average male and female, respectively, with upper and lower 95% credible intervals (bands). The grey dots show the raw data. Predictions were estimated with mean troop size fixed at 49 individuals.

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	Degree	Age Scan.nb NDVI	Age by juvenile ID Age by cohort ID Age by sex Age by troop ID Age by mother ID Rank by ID	Binomial
	Strength	Age NDVI Troop.nb	Same as above	Poisson
	Skewness	Age Scan.nb NDVI Troop.nb	Same as above	Skew-normal
	Cosine similarity	Age Scan.nb NDVI Troop.nb	Same as above	Zero-one-inflated beta
Grooming	Degree	Age NDVI Troop.nb	Same as above	Poisson
	Strength	Age NDVI Troop.nb	Same as above	Poisson
	Skewness	Age Scan.nb NDVI Troop.nb	Same as above	Skew-normal
	Cosine similarity	Age Scan.nb NDVI Troop.nb	Same as above	Zero-one-inflated beta

All independent variables and interactions had a smooth term around them. All continuous predictor variables were mean-centred and standardized by two standard deviations to allow for effect size comparisons across continuous and dichotomous variables (Gelman, 2008).

Table A2

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

Effect	Parameter	Estimate	Estimate error	Lower 95% CI	Upper 95% CI
Population level effects	Intercept	1.60	0.50	0.51	2.50
	s(age)	-0.35	0.90	-2.09	1.30
	s(scan.nb)	0.88	0.80	-0.74	2.40
	s(NDVI)	-0.15	0.57	-1.50	0.88
Smooth terms	sds(age)	0.84	0.70	0.03	2.53
	sds(age ID1)	0.85	0.10	0.64	1.03
	sds(age ID2)	0.43	0.32	0.02	1.18
	sds(age cohort1)	1.86	0.38	1.27	2.75
	sds(age cohort2)	2.05	1.82	0.07	6.67
	sds(age troop1)	1.68	0.30	1.19	2.37
	sds(age troop2)	3.72	1.91	1.52	8.65
	sds(age mumID1)	0.26	0.18	0.01	0.64
	sds(age mumID2)	1.47	0.74	0.18	2.94
	sds(scan.nb)	2.18	0.63	1.25	3.65
	sds(age sex1)	0.32	0.21	0.01	0.79
	sds(age sex2)	1.28	1.41	0.04	5.39
	sds(NDVI)	0.40	0.44	0.01	1.67
	sds(rank ID1)	0.52	0.07	0.40	0.66
	sds(rank ID2)	0.40	0.30	0.02	1.14
		Estimate	Estimate error	Q2.5	Q97.5
		R ² marginal	0.91	0.00	0.90

CI = credible interval; s() = spline; sds() = spline 'wiggleness' (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 Poisson distribution

Effect	Parameter	Estimate	Estimate error	Lower 95% CI	Upper 95% CI
Population level effects	Intercept	-4.04	0.43	-4.92	-3.18
	s(age)	1.27	0.80	-0.42	2.69
	s(NDVI)	0.14	0.55	-1.02	1.18
	s(troop.nb)	-0.42	0.54	-1.58	0.53
Smooth terms	sds(age)	0.55	0.52	0.02	1.96
	sds(age ID1)	0.43	0.09	0.24	0.58
	sds(age ID2)	0.54	0.34	0.03	1.24
	sds(age cohort1)	0.74	0.22	0.40	1.22
	sds(age cohort2)	1.61	1.38	0.06	5.29
	sds(age troop1)	0.18	0.11	0.01	0.42
	sds(age troop2)	1.91	1.28	0.51	5.27
	sds(age mumID1)	0.18	0.11	0.01	0.41
	sds(age mumID2)	0.83	0.36	0.13	1.54
	sds(age sex1)	0.18	0.11	0.01	0.44
	sds(age sex2)	3.27	2.13	1.08	8.80
	sds(NDVI)	0.39	0.25	0.07	1.02
	sds(troop.nb)	0.41	0.35	0.02	1.31
	sds(rank ID1)	0.06	0.04	0.00	0.16
	sds(rank ID2)	0.48	0.31	0.02	1.15
		Estimate	Estimate error	Q2.5	Q97.5
		R ² marginal	0.76	0.01	0.74

CI = credible interval; s() = spline; sds() = spline 'wiggleness' (spline variance parameter).

Table A4

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	-4.32	0.45	-5.22	-3.39
	s(age)	1.62	0.89	-0.15	3.35
	s(NDVI)	0.01	0.56	-1.14	1.11
	s(troop.nb)	-0.25	0.54	-1.39	0.80
Smooth terms	sds(age)	1.15	0.72	0.12	2.85
	sds(age ID1)	0.62	0.10	0.41	0.81
	sds(age ID2)	0.57	0.38	0.03	1.42
	sds(age cohort1)	0.57	0.31	0.07	1.23
	sds(age cohort2)	1.16	1.21	0.03	4.38
	sds(age troop1)	0.28	0.18	0.02	0.72
	sds(age troop2)	2.23	1.39	0.59	5.95
	sds(age mumID1)	0.28	0.16	0.01	0.59
	sds(age mumID2)	1.13	0.47	0.14	2.02
	sds(age sex1)	0.18	0.17	0.01	0.60
	sds(age sex2)	3.67	2.09	1.33	9.56
	sds(NDVI)	0.40	0.26	0.08	1.08
	sds(troop.nb)	0.50	0.44	0.02	1.67
	sds(rank ID1)	0.07	0.05	0.00	0.20
	sds(rank ID2)	0.52	0.35	0.02	1.31
Family-specific parameters	Shape	405.62	143.81	199.78	737.86
		Estimate	Estimate error	Q2.5	Q97.5
	R ² marginal	0.77	0.01	0.75	0.79

CI = credible interval; s() = spline; sds() = spline 'wiggleness' (spline variance parameter).

Table A5

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

Effect	Parameter	Estimate	Estimate error	Lower 95% CI	Upper 95% CI	
Population level effects	Intercept	0.45	0.71	-0.82	1.95	
	s(age)	1.32	0.36	0.67	2.05	
	s(NDVI)	2.10	0.27	1.59	2.68	
	s(troop.nb)	0.45	0.71	-0.82	1.95	
	sds(age)	14.12	3.54	8.59	22.12	
Smooth terms	sds(age ID1)	1.47	0.09	1.32	1.68	
	sds(age ID2)	0.81	0.50	0.08	1.81	
	sds(age cohort1)	6.63	1.71	3.77	10.56	
	sds(age cohort2)	9.07	6.52	0.36	25.34	
	sds(age troop1)	3.01	0.93	1.75	5.95	
	sds(age troop2)	1.37	1.29	0.05	4.61	
	sds(age mumID1)	1.81	0.18	1.51	2.23	
	sds(age mumID2)	1.94	0.49	1.05	2.91	
	sds(age sex1)	0.16	0.13	0.00	0.48	
	sds(age sex2)	2.58	2.60	0.27	9.46	
	sds(NDVI)	0.93	0.25	0.57	1.49	
	sds(troop.nb)	0.63	0.19	0.35	1.08	
	sds(rank ID1)	0.54	0.04	0.47	0.62	
	sds(rank ID2)	0.88	0.54	0.05	2.05	
		Estimate	Estimate error	Q2.5	Q97.5	
		R ² marginal	0.98	0.00	0.97	0.98

CI = credible interval; s() = spline; sds() = spline 'wiggleness' (spline variance parameter).

Table A6

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	0.00	0.43	-0.81	1.00	
	hu_Intercept	-0.66	2.35	-6.38	3.00	
	s(age)	0.49	0.83	-1.20	2.10	
	s(NDVI)	0.36	0.57	-0.78	1.51	
	s(troop.nb)	1.05	0.57	0.06	2.23	
	hu s(age)	188.33	189.10	9.69	715.22	
	hu s(NDVI)	144.92	147.50	10.70	607.41	
	hu s(troop.nb)	49.73	67.92	-12.62	263.74	
	sds(age)	3.85	1.30	1.79	6.77	
	sds(age ID1)	0.66	0.07	0.53	0.81	
Smooth terms	sds(age ID2)	0.32	0.24	0.01	0.89	
	sds(age cohort1)	0.72	0.30	0.30	1.45	
	sds(age cohort2)	2.21	1.81	0.11	6.98	
	sds(age troop1)	0.71	0.20	0.41	1.22	
	sds(age troop2)	3.09	1.74	1.05	7.20	
	sds(age mumID1)	0.68	0.09	0.50	0.85	
	sds(age mumID2)	2.99	0.69	1.78	4.40	
	sds(age sex1)	0.11	0.10	0.00	0.35	
	sds(age sex2)	1.75	1.54	0.11	5.78	
	sds(NDVI)	1.07	0.40	0.48	2.00	
	sds(troop.nb)	0.54	0.35	0.14	1.44	
	sds(rank ID1)	0.07	0.04	0.00	0.17	
	sds(rank ID2)	0.28	0.21	0.01	0.75	
	sds(hu_age)	2.75	2.95	0.10	9.89	
	sds(hu_age ID1)	4.23	6.82	0.10	18.41	
	sds(hu_age ID2)	3.01	3.74	0.10	11.65	
	sds(hu_age cohort1)	2.73	3.49	0.08	9.95	
	sds(hu_age cohort2)	272.29	396.11	0.22	1303.94	
	sds(hu_age troop1)	2.56	2.53	0.09	9.31	
	sds(hu_age troop2)	2.79	3.72	0.07	10.57	
	sds(hu_age mumID1)	4.57	7.40	0.11	21.37	
	sds(hu_age mumID2)	3.12	5.03	0.09	12.44	
	sds(hu_age sex1)	2.76	3.02	0.07	10.87	
	sds(hu_age sex2)	111.10	259.84	0.14	862.71	
	sds(hu_NDVI)	2.63	2.76	0.10	8.89	
	sds(hu_troop.nb)	2.64	2.97	0.10	9.45	
	sds(hu_rank ID1)	3.36	3.86	0.08	13.60	
	sds(hu_rank ID2)	3.05	3.72	0.08	12.17	
	Family-specific parameters	Shape	44.83	2.78	39.71	50.50
			Estimate	Estimate error	Q2.5	Q97.5
	R ² marginal	0.93	0.00	0.92	0.94	

CI = credible interval; s() = spline; sds() = spline 'wiggleness' (spline variance parameter). Estimates are on the logit scale for the hurdle portion of the model (hu; probability of application).

Table A7

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

Effect	Parameter	Estimate	Estimate error	Lower 95% CI	Upper 95% CI
Population level effects	Intercept	-2.86	0.47	-3.73	-1.86
	s(age)	-0.10	0.72	-1.53	1.31
	s(NDVI)	-0.23	0.56	-1.18	1.01
Smooth terms	s(troop.nb)	0.47	0.52	-0.38	1.63
	sds(age)	0.44	0.41	0.02	1.49
	sds(age ID1)	1.28	0.10	1.07	1.45
	sds(age ID2)	0.71	0.50	0.04	1.85
	sds(age cohort1)	0.61	0.23	0.24	1.15
	sds(age cohort2)	1.30	1.24	0.04	4.47
	sds(age troop1)	0.50	0.14	0.25	0.81
	sds(age troop2)	2.47	1.85	0.57	6.66
	sds(age mumID1)	0.42	0.23	0.03	0.83
	sds(age mumID2)	2.06	0.72	0.38	3.49
	sds(age sex1)	0.32	0.15	0.06	0.66
	sds(age sex2)	3.07	2.13	0.88	8.73
	sds(NDVI)	0.43	0.29	0.08	1.16
	sds(troop.nb)	0.41	0.37	0.03	1.44
	sds(rank ID1)	0.14	0.07	0.01	0.27
	sds(rank ID2)	0.64	0.47	0.03	1.76
		Estimate	Estimate error	Q2.5	Q97.5
	R ² marginal	0.88	0.00	0.87	0.88

CI = credible interval; s() = spline; sds() = spline 'wiggleness' (spline variance parameter).

Table A8

Summary statistics of a Bayesian hierarchical generalized additive mixed model (HGAM) for the distribution of edge weights (skewness) in spatial associations, using a skew-normal distribution

Effect	Parameter	Estimate	Estimate error	Lower 95% CI	Upper 95% CI
Population level effects	Intercept	1.49	0.26	0.94	2.05
	s(age)	-0.10	0.76	-1.58	1.39
	s(scan.nb)	-0.06	0.53	-1.25	0.94
	s(NDVI)	-0.90	0.79	-2.37	0.73
	s(troop.nb)	-0.07	0.64	-1.44	1.07
Smooth terms	sds(age)	0.47	0.42	0.02	1.57
	sds(age ID1)	1.26	0.10	1.08	1.46
	sds(age ID2)	0.62	0.44	0.03	1.63
	sds(age cohort1)	0.97	0.27	0.54	1.60
	sds(age cohort2)	1.51	1.35	0.05	5.00
	sds(age troop1)	0.36	0.15	0.07	0.68
	sds(age troop2)	0.87	0.90	0.03	3.25
	sds(age mumID1)	0.27	0.19	0.01	0.67
	sds(age mumID2)	1.78	0.47	0.82	2.70
	sds(scan.nb)	0.48	0.39	0.03	1.46
	sds(age sex1)	0.18	0.13	0.01	0.52
	sds(age sex2)	1.32	1.41	0.04	5.08
	sds(NDVI)	1.33	0.56	0.61	2.72
	sds(troop.nb)	0.71	0.45	0.16	1.86
	sds(rank ID1)	0.18	0.10	0.01	0.37
sds(rank ID2)	0.63	0.46	0.02	1.68	
Family-specific parameters	Sigma	0.41	0.01	0.39	0.43
	Alpha	5.25	1.04	3.67	7.73
		Estimate	Estimate error	Q2.5	Q97.5
	R ² marginal	0.60	0.02	0.57	0.63

CI = credible interval; s() = spline; sds() = spline 'wiggleness' (spline variance parameter).

Table A9

Summary statistics of a Bayesian hierarchical generalized additive mixed model (HGAM) for the distribution of edge weights (skewness) in grooming associations, using a skew-normal distribution

Effect	Parameter	Estimate	Estimate error	Lower 95% CI	Upper 95% CI	
Population level effects	Intercept	1.01	0.43	0.14	1.86	
	s(age)	0.67	0.80	-0.95	2.19	
	s(scan.nb)	0.78	0.76	-0.96	1.93	
	s(NDVI)	-0.44	0.53	-1.46	0.71	
	s(troop.nb)	-0.05	0.45	-1.05	0.78	
Smooth terms	sds(age)	0.85	0.66	0.04	2.56	
	sds(age ID1)	0.96	0.11	0.74	1.18	
	sds(age ID2)	0.48	0.33	0.02	1.22	
	sds(age cohort1)	0.58	0.31	0.06	1.23	
	sds(age cohort2)	1.42	1.26	0.06	4.69	
	sds(age troop1)	0.26	0.20	0.01	0.73	
	sds(age troop2)	0.91	0.94	0.03	3.56	
	sds(age mumID1)	0.23	0.15	0.01	0.55	
	sds(age mumID2)	0.46	0.34	0.01	1.25	
	sds(scan.nb)	0.43	0.37	0.02	1.37	
	sds(age sex1)	0.40	0.25	0.04	0.97	
	sds(age sex2)	2.93	2.06	0.71	8.58	
	sds(NDVI)	0.32	0.28	0.01	1.05	
	sds(troop.nb)	0.23	0.24	0.01	0.86	
	sds(rank ID1)	0.14	0.10	0.01	0.36	
	sds(rank ID2)	0.42	0.31	0.01	1.15	
	Family-specific parameters	Sigma	0.49	0.01	0.46	0.51
		Alpha	-0.03	0.58	-1.06	1.03
		R² marginal	Estimate	Estimate error	Q2.5	Q97.5
	0.52	0.02	0.49	0.56		

CI = credible interval; s() = spline; sds() = spline 'wiggleness' (spline variance parameter).

Table A10

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	2.43	0.55	1.29	3.44	
	s(age)	0.53	0.93	-1.21	2.34	
	s(scan.nb)	1.60	0.85	-0.11	3.26	
	s(NDVI)	-0.46	0.88	-2.23	1.26	
	s(troop.nb)	-0.27	0.74	-1.31	1.44	
Smooth terms	sds(age)	4.09	1.74	1.24	7.99	
	sds(age ID1)	0.63	0.08	0.46	0.79	
	sds(age ID2)	0.58	0.38	0.03	1.39	
	sds(age cohort1)	1.74	0.57	0.82	3.03	
	sds(age cohort2)	4.59	2.70	0.78	11.43	
	sds(age troop1)	0.47	0.21	0.11	0.95	
	sds(age troop2)	1.05	1.01	0.04	3.64	
	sds(age mumID1)	0.17	0.12	0.01	0.45	
	sds(age mumID2)	0.66	0.43	0.04	1.61	
	sds(scan.nb)	2.09	0.69	1.06	3.79	
	sds(age sex1)	0.49	0.28	0.08	1.16	
	sds(age sex2)	2.21	1.99	0.26	7.22	
	sds(NDVI)	2.08	0.79	0.95	3.88	
	sds(troop.nb)	0.47	0.57	0.01	2.16	
	sds(rank ID1)	0.73	0.10	0.53	0.94	
	sds(rank ID2)	0.49	0.35	0.02	1.31	
	Family-specific parameters	Phi	52.81	2.44	48.28	57.87
		Zoi	0.00	0.00	0.00	0.01
		Coi	0.67	0.18	0.30	0.95
	R² marginal	Estimate	Estimate error	Q2.5	Q97.5	
	0.53	0.02	0.49	0.58		

CI = credible interval; s() = spline; sds() = spline 'wiggleness' (spline variance parameter).

Table A11

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	1.90	0.31	1.27	2.56	
	s(age)	-1.09	0.96	-2.91	0.85	
	s(scan.nb)	1.64	0.58	0.23	2.55	
	s(NDVI)	0.23	0.58	-0.83	1.46	
	s(troop.nb)	-0.09	0.72	-1.34	1.45	
Smooth terms	sds(age)	1.00	0.62	0.11	2.49	
	sds(age ID1)	1.43	0.20	1.04	1.83	
	sds(age ID2)	0.82	0.61	0.04	2.32	
	sds(age cohort1)	0.38	0.30	0.01	1.09	
	sds(age cohort2)	1.24	1.26	0.04	4.53	
	sds(age troop1)	0.57	0.34	0.03	1.31	
	sds(age troop2)	1.46	1.31	0.06	4.75	
	sds(age mumID1)	0.60	0.33	0.02	1.19	
	sds(age mumID2)	2.74	0.77	0.97	4.20	
	sds(scan.nb)	0.31	0.38	0.01	1.29	
	sds(age sex1)	0.44	0.24	0.05	0.96	
	sds(age sex2)	1.50	1.53	0.06	5.43	
	sds(NDVI)	0.38	0.38	0.01	1.36	
	sds(troop.nb)	0.83	0.91	0.02	3.49	
	sds(rank ID1)	0.47	0.20	0.05	0.83	
	sds(rank ID2)	0.84	0.59	0.04	2.26	
	Family-specific parameters	Phi	9.99	0.46	9.12	10.93
		Zoi	0.03	0.00	0.02	0.03
		Coi	0.71	0.07	0.57	0.83
		R² marginal	Estimate	Estimate error	Q2.5	Q97.5
	0.43	0.02	0.40	0.46		

CI = credible interval; s() = spline; sds() = spline 'wiggleness' (spline variance parameter).