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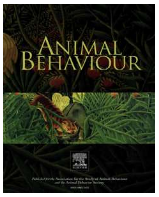

The transition to motherhood as the temporal locus of change for social network integration among wild vervet monkeys

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The birth of a first offspring represents a major change in a female mammal's social circumstances. We hypothesize that the transition to motherhood marks a significant shift in the social network dynamics of female vervet monkeys, *Chlorocebus pygerythrus*, and represents the crucial boundary between juvenile and adult patterns of engagement. To test this, we compare the grooming network structure of primiparous and multiparous females, using both direct and indirect measures of centrality. We found that, following the birth of their first infant, ego-structure of primiparous females converged with that of multiparous females and that primiparous females became more central in their grooming networks around their first birth event, as measured by eigenvector centrality. Examining shifts in the number of new social ties formed across the birth event, we found a very small increase in the formation of new strong ties, but a larger increase in the number of additional weak ties. A simulated 'knockout' analysis showed that both types of ties contributed to the observed increase in eigenvector centrality. Overall, our findings support the idea that motherhood serves as a catalyst for juveniles to transition into adult social configurations. Note, however, that although the juvenile—adult boundary marked the temporal locus of change for social integration, there was, nevertheless, a striking consistency in the stability of ego-network structure across both the juvenile period and through the motherhood transition. This structure may enhance individual flexibility in social engagement and accommodate the specific needs of females as they experience changes in status and broader demographic shifts within their groups.

Social integration describes the embeddedness of individuals within their social group (Schülke et al., 2022), and it has been shown that the nature and quality of associations with other group members have important consequences for health (Brent et al., 2011; Crockford et al., 2008; Silk et al., 2010a; Wittig et al., 2016), longevity (e.g. Brent et al., 2017; Nuñez et al., 2015) and reproductive success (McFarland et al., 2017; Schülke et al., 2010; Silk et al., 2003, 2010a). The fitness benefits of adult social integration have also been offered as a partial explanation for the long juvenile period characteristic of primates (Barrickman et al., 2008). Specifically, an extended developmental period is thought to enable juveniles to acquire the skills needed to develop and sustain valuable adult relationships (Kohn, 2019), an argument that has also been applied to other mammals and birds (Burghardt, 2005; Fantuzzo et al., 2004; Pellis & Pellis, 2013). There is evidence for shifts in developmental patterns during adolescence (Kohn et al., 2022; Kulik et al., 2015), and some authors have taken this to suggest that juveniles begin to 'behave more like adults' (Kulik et al., 2015) as they converge on species-typical relationships (Wanker et al., 1996). This view, coupled with the idea that juveniles develop adult skills that provide advantages realized in or nearer to adulthood (Cords, 2000; Rowell & Chism, 1986), implicitly assumes an optimal end point where, by the end of the juvenile period, animals have generated a network of social bonds that they can carry forward into adulthood. This view, perhaps inadvertently, fails to recognize that social integration can also be an ongoing process of continual adjustment of social relationships (Deputte, 2000), where individuals must continuously work to sustain integration over time, even after reaching adulthood (see Mason, 1976).

Our own previous work on juvenile vervet monkeys, *Chlorocebus pygerythrus*, has shown that juveniles neither fully acquire nor inherit their mothers' grooming networks as a means of replicating the adult group network (Jarrett et al., 2018; Vilette et al., 2023), nor do they simply 'start behaving like adults' (Kulik

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et al., 2015; Vilette et al., 2022). They also do not appear to strive to form long-lasting strong bonds across the duration of the developmental period, as previous empirical and theoretical work has suggested (Kohn, 2019; Silk, Alberts, & Altmann, 2006; Silk, Altmann, & Alberts, 2006; Silk et al., 2010b). Instead, they maintain their own distinctive grooming and spatial ego-network structures from a very early age (Vilette et al., 2022). For both grooming and spatial proximity, these network structures consist of a small number of strong ties and a larger number of weak ties. When investigating the subset of strong ties specifically, an individual's 'social bubble', we found that the structure and composition of spatial proximity bubbles fluctuated seasonally and were composed almost exclusively of other juveniles. In contrast, the grooming social bubble was composed of a single strong, stable tie to the juvenile's mother (Vilette et al., 2023), so, hardly a bubble at all. Consequently, juveniles did not appear to be strongly integrated into the overall adult spatial or grooming networks as they themselves reached adulthood.

These findings do not fit particularly well with the prevailing view that the juvenile period is used to develop social bonds and integrate into the adult network. Rather, our findings suggest that, in our study population at least, the juvenile period is one in which young vervets display (1) a stable ego-network structure of peers from an early age and, in the case of strong grooming ties, (2) a stable attachment figure (their mother), who forms a safe base from which to explore their social world (see Ainsworth, 1969). This suggests that, rather than juveniles forming additional and stronger bonds with older adults, they age into their adult social networks by broadening and deepening their ties to their juvenile peers across time. That is, juveniles come to replace the existing adult network, rather than becoming integrated into it.

Apropos of the latter possibility, it is apparent that the birth of a female's first offspring represents a major shift in her circumstances with respect to, among other things, energy requirements, time budget allocation, predation risk and social attractiveness. From the perspective of network integration, a new infant may offer females the opportunity to capitalize on the increased social attention they receive (Fruteau et al., 2011; Henzi & Barrett, 2002) and forge additional social relationships, and perhaps strong bonds, that potentially enable new mothers to occupy a more central position in their group's network. Thus, integration into the adult network may be triggered by the advent of motherhood, with an overt and obvious transformation of a female's social position and attractiveness. Here, then, we investigate the hypothesis that the juvenile–adult boundary constitutes the temporal locus of change for social integration. Specifically, we investigate whether the transition to motherhood provides female juveniles with the momentum needed to arrive at an adult social configuration. We focus on grooming associations, as these generally require mutual attraction, and therefore signal more active social engagement than the maintenance of spatial ties.

We begin by testing the assumption that juvenile and adult female network structures actually do differ in the manner we have previously suggested. We begin here because, up to now, we have assumed that adult female and juvenile networks do indeed vary in terms of structure, based both on our previous analyses and work on other primates. However, with respect to our own population specifically, networks have been analysed both at different time periods and across varying timescales and are not fully comparable (e.g. Henzi et al., 2013; Jarrett et al., 2018; Vilette et al., 2023). We therefore first compare juvenile and adult female ego-network structures by applying the same methodological approach used in our previous analysis of juvenile networks (see Vilette et al., 2022).

Having documented the similarities and differences between juvenile and adult females, we then go on to ask whether the transition to motherhood results in first-time mothers achieving network structures that are fully comparable to those of multiparous adult females. That is, we predicted that primiparous females' ego-network structures would come to resemble those of multiparous females following the birth of their first infant.

We then delve more deeply into the events associated with the transition to motherhood by contemplating shifts in the centrality of primiparous females' network positions. This approach allowed us to investigate social integration in a broader sense, in that we consider the role of indirect, as well as direct, relationships (Brent, 2015). We predicted that the birth of their first offspring leads primiparous females to become more central in their grooming network, and that this shift leads to greater similarity to the centrality positions observed in multiparous females.

Following this, we consider whether changes in primiparous female networks are associated with shifts in ego-network size. We do so by focusing on strong and weak social ties separately. That is, we investigate (1) whether the birth of the first offspring provides primiparous females with the impetus to expand their grooming bubble of strong ties beyond their mothers and/or (2) whether the restructuring of their social networks occurs through an increase in the number of weak grooming partners.

Finally, we use a simulated 'knockout' approach to investigate the relative importance of shifts in the formation of strong and weak ties during the transition to motherhood, and hence to social integration. By simulating the removal of all new strong and weak ties independently, we disrupt the primiparous females' ego-network structure, and so determine whether and how this changes ego-network integration within the larger group network (see e.g. Flack & Krakauer, 2006). This, in turn, offers a better understanding of the influence of direct and indirect connections on social integration. Our prediction here rests on the finding that weak ties create bridges between individual social ego-networks (Granovetter, 1973). Compared to strong ties, weak ties may therefore play a larger role in enhancing overall levels of social integration by strengthening these indirect relationships. Consequently, we predicted that the removal of newly acquired weak ties would have a greater impact on the centrality position of primiparous females compared to the removal of strong ties.

METHODS

Study Population and Subjects

Data were collected between April 2013 and November 2018 from three troops of wild vervet monkeys occupying adjacent and overlapping home ranges in the Samara Private Game Reserve in the semiarid Karoo biome, Eastern Cape, South Africa (Pasternak et al., 2013). The study period ended 5 y after the 2013 cohort was born, that is, in December 2018. As such, we extracted data on the juvenile and adult females across 5 y. We chose to cover a 5-year time period as, on average, vervet males reach sexual maturity at 5 y of age (Horrocks, 1986), and females typically have their first infant between 3 and 5 years of age (Fairbanks & McGuire, 1984). Since we followed the 2013, 2014 and 2015 cohorts, the 5-year time period covered as much of the juvenile period as possible for these three cohorts. The three study groups, RST (mean ± SD group size: 57 ± 7), RBM (49 ± 6) and PT (39 ± 8), have been fully habituated since 2008 (RST and RBM) and 2012 (PT). Ages were known within 1 day for all offspring born during the study period. All animals were individually identifiable from natural markings.

Table 1
Number of primiparous and multiparous females across the studied years

	2013	2014	2015	2016	2017	2018	Number/ status
Number of primiparous females	15	8	2	1	2	9	37
Number of multiparous females	30	38	39	29	25	27	188
Total number of females	45	46	41	30	27	36	225

Data Collection

Each troop was followed on foot by one or more researchers on each 10 h study day, for 3–5 days per week per troop (RBM: 601 days; RST: 613 days; PT: 583 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 its nearest female, male and juvenile neighbours. 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.

For each female present within our sample, the dates of her first and all successive births were recorded. In this analysis, only females who had a live birth during the study period were considered. The number of primiparous and multiparous females across the study period are given in Table 1. We anticipate no systematic differences between primiparous and multiparous females regarding pregnancy-related factors, such as food acquisition or body size, that could potentially influence their social behaviour, independent of any birth-related effects.

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

For our analyses, we used the 'netTS' package (Bonnell & Vilette, 2020) in R version 3.5.2 (R Core Team, 2017). Based on our previous analyses (Vilette et al., 2022, 2023), our grooming data sets were aggregated over a 60-day window that was then shifted successively by 30 days.

Within each time window, grooming interactions were aggregated to construct weighted, nondirected ego-networks at the individual level, from which our measures were extracted. Simultaneously, the number of scans was registered at the start of each time block, as was the mean size of each troop.

For grooming network structure comparison, calendar date from the start of the year was converted into number of days and extracted at the start of each time aggregation. For ease of comparison, we aligned the start date with that from our previous analysis on juveniles (Vilette et al., 2022), which was 1 June 2014. When comparing primiparous and multiparous females' ego-network structures and maternal social integration, as well as primiparous females' network size, data were extracted from 6 months prior to the birth event up until 6 months following it. A female was considered as primiparous if she had not previously given birth, and multiparous otherwise.

To extract individual ratings, we used the Elo-rating method and the 'EloRating' package (Albers & de Vries, 2001; Neumann et al., 2011) in R. We chose this method based on the training–testing approach described in Vilette et al. (2020), as it presented the best trade-off between the amount of data required to infer reliable ranks, the method's ability to infer reliable ranks and computational efficiency. We used a 5-month burn-in period, specific to each troop, and extracted ratings for each juvenile by the end of each 60-day window, across the entire study period. We included agonistic interactions between all individuals (males, females, juveniles).

Grooming Ego-network Structure Comparisons

To compare the adult grooming network structure to juvenile networks, and primiparous/multiparous females' structures, we extracted the same four measures used to capture juveniles' grooming ego-network structure (see Vilette et al., 2022).

(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 relatively equally across all partners (see Supplementary Fig. S1). To capture the distribution accurately, we calculated skewness only when the number of partners was greater than two.

(4) 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, 2023). 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 ego-networks change markedly between time t and $t + 1$ will have a low cosine similarity, whereas those whose ego-networks are similar at t and $t + 1$ will show high cosine similarity. For more details on calculating cosine values, see Supplementary material (Cosine Similarity Measure).

Social Integration in Primiparous and Multiparous

Eigenvector centrality values take the entire network into account, such that nodes may obtain a high centrality by being connected to many low-centrality nodes or by being connected to a smaller number of high-centrality nodes (Bonacich, 2007). We extracted undirected eigenvector centrality, which is a combined measure of the individual's direct and indirect associations. This is useful as it indicates an individual's centrality within the entire network.

Ties Extraction

To extract females' strong grooming ties, we made use of a previously developed algorithm (see Vilette et al., 2023), which models the distribution of edge weights on the assumption that, if strong ties (relatively large edge weights) are present, then the distribution of edge weights will be skewed (see Supplementary material, Strong Tie Function; for details of how the function was built and tested, see Vilette et al., 2023). The ‘min_diff’ parameter was adjusted based on the number of interactions within each time-aggregated window. If it exceeded 10, ‘min_diff’ was set to 3; otherwise, it was set to 1. Within each time-aggregated window, we extracted the ego-network of each individual present, from which we assessed whether its weight distribution was skewed. If the weight distribution was skewed, strong ties that fell outside the range expected from a normal distribution of weak ties were extracted. Weights that remained within the range were extracted as weak ties.

Using these isolated weak/strong ties, networks were then 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. We then extracted network degree to assess the size of an individual’s grooming ‘bubble’ (Vilette et al., 2023), as well as the number of weak ties. The degree measure 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). When females had no strong ties, degree took the value of zero.

Knockout Analysis

In our study, the knockout procedure was conducted between two distinct time periods denoted as time t and time $t + 1$, representing different stages of social integration. The first time period t was the reference period, as social integration had not yet occurred. The second time period $t + 1$ corresponded to the moment where social integration had taken place and had reached its peak. We systematically removed specific nodes from the ego-networks of primiparous females, thereby examining the resulting effects on their social integration. That is, all newly identified strong ties at time $t + 1$ were simultaneously removed, along with their corresponding social associations, and a new measure of eigenvector centrality was inferred. This process was then iterated for all identified weak ties, and for all identified ties (i.e. weak and strong ties combined) added at time $t + 1$.

Concretely, two ego-networks were extracted: one capturing the reference period t, which corresponded to the 2 months prior to the birth event, and another ego-network encapsulating social integration at $t + 1$, which occurred between the first and third month following birth. A comparison of these two ego-networks allowed identification of nodes representing new strong/weak ties in the ego-network after integration at time $t + 1$. Subsequently, all newly established strong and/or weak ties were removed, and new eigenvector centrality values were inferred for these two modified networks (i.e. the ones with removed new strong and weak ties, respectively). These new eigenvector centrality values enabled us to determine the level of a primiparous female’s social integration had she not established these new strong and/or weak ties.

Environmental Conditions

As food availability contributes to the structuring of associations (Bonnell et al., 2022), we measured troop level estimates of resource availability using the normalized difference vegetation index (NDVI; Willems et al., 2009). Area-weighted NDVI averages for each group’s territory were generated 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 estimates a nonlinear trend without a theoretically prespecified shape, enabling nonlinear trends, if present, to emerge. We ran all models with four chains and 2000 iterations after specifying weakly informative priors (normal (0,1)). Model diagnostics confirmed Markov chain Monte Carlo (MCMC) convergence, with all $\widehat{R} < 1.1$ (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.

All model summary tables of this study are presented in the Appendix (Tables A1–A18), accompanied by DHARMa nonparametric dispersion tests and posterior predictive distribution plots, as required (Supplementary Figs S6–S33). All model structures are available at: github.com/ChloeVilette/Parity_status_analysis/README.md.

Grooming Ego-network Structure Comparisons

Juvenile and adult females

We constructed a model for each of our measures of adult female network structure (i.e. degree, strength, skewness and cosine similarity). This generated four models, whose structure was kept constant. Models for juveniles and adults did, however, differ in their variable of interest. Age was the variable used to explain the juveniles' measures (i.e. their social development as they aged), whereas time (i.e. number of days) was used in the adult model as a way to trace potential variability in adult females' measures. We did this as age was not available for all adults. With both juvenile and adult models, we expected female network structure to change based on the variable of interest and individual identity. As such, we let the effect of age for juveniles and time (i.e. number of days) for adults vary by this grouping variable. We used factor smooths for this interaction as a way to implicitly incorporate group-specific splines (Pedersen et al., 2019). That is, factor smooths create a spline for the grouping variable but only estimate one smoothing parameter for all groups of the given grouping variable (i.e. individual identity). With both juvenile and adult models, we controlled for variability in environmental conditions by including NDVI, the effect of ordinal rank and variation in troop size, as well as social temporal variation by including scan number. Each of these variables were added as a single smooth in the model. We also entered troop identity as group level effect, using a single smooth, and in the juvenile model, we further added cohort identity as another group level effect, also using a single smooth. Lastly, to account for the cyclical nature of seasonal influences in the adult model, we included day of year, using a cyclic cubic regression spline.

All continuous variables were scaled and mean-centred. We ran Poisson models for count variables (i.e. degree and strength). As dispersion issues are common with Poisson models, we assessed model residuals with the 'DHARMa' Package (Hartig, 2020). No dispersion issues were detected. Therefore, we report Poisson models for our count variables with both juvenile and adult models. We modelled skewness using a skew-normal distribution. Values of the cosine similarity model varied between 0 and 1 for juveniles, and we therefore specified a zero-one-inflated beta model. Lastly, a zero-inflated beta model was used as no adult females had cosine similarity values of one.

Primiparous and multiparous females

Here again we constructed four model for each of our measures of adult female network centrality (i.e. degree, strength, skewness and cosine similarity) and kept its structure constant. Our data set structure consisted of repeated measures for individual and troop identities, maternal parity, as well as the year that females gave birth. We let the effect of time vary by individual and maternal parity, using factor smooths (Pedersen et al., 2019). Troop identity and year were included as random intercepts. A single smooth was added for each interaction/variable. We controlled for variability in environmental conditions by including NDVI, as well as the effect of ordinal rank, both as a single smooth in the model. Lastly, a single smooth for troop member number was included to address variation in troop size, along with one for scan number, to account for sampling effort.

All continuous variables were scaled and mean-centred. For degree and strength (our count variables), a Poisson model was run. With these Poisson models, the same procedure as above was followed (i.e. dispersion issue check). We addressed identified dispersion issues by running our models with a negative binomial distribution. When this did not resolve the issue, we ran hurdle models (Hilbe, 2017). To determine the best model, 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 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 respect to our degree and strength models, 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 S18–S25). We used a skew-normal distribution to model our skewness variable. Lastly, a beta model was specified for cosine similarity as values fell within the [0, 1] interval.

Female social integration and primiparous female network structure

We constructed a model for each of our measures (i.e. eigenvector centrality and degree for strong and weak ties). This generated three models, and the same model structure was used as the one for comparing primiparous and multiparous females' structures.

All continuous variables were scaled and mean-centred. When our response variable was eigenvector centrality, values varied between 0 and 1. We hence constructed a zero-one-inflated beta model. For degree, our count variable on weak and strong ties, a Poisson model was run. For both models (weak and strong ties), we report the simpler Poisson models in the main text as no dispersion issues were detected (see Supplementary Figs S29–S32).

Knockout Analysis

We determined whether the addition of ties influenced primiparous females' levels of social integration. Our response variable was composed of four different types of eigenvector centrality values inferred at time $t + 1$: (1) the original eigenvector inferred on unaltered ego-networks and the eigenvector extracted from altered ego-networks where (2) the new strong ties, (3) the new weak ties and (4) both new strong and weak ties had been removed, respectively. We let the effect of maternal parity (primiparous/multiparous) vary by the type of eigenvector values (i.e. original, removed new strong, new weak or both new strong and weak ties). We included the initial eigenvector centrality value based on the full ego-network at time t, troop size and scan number as statistical controls for the possible effects of variation in social conditions (i.e. network density and size) and sampling effort, respectively. We included NDVI to control for variability in environmental conditions, as well as ordinal ranks to control for its the effect. Finally, we entered troop and individual identity, as well as the year that females gave birth, as group level effects. All continuous variables were scaled and mean-centred. As our response variable varied between 0 and 1, we constructed a zero-one-inflated beta model.

Finally, given the nature of all our statistical models, and the inclusion of interaction effects, using a summary table on its own to interpret model estimates is not sufficient. We therefore generated model predictions, using the 'fitted()' function from the 'brms' package to extract the mean expected 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. time and parity status). These predictions were then used to construct predictive posterior plots with the 'ggplot2' package (Wickham, 2009). When investigating the adult female grooming network structure, predictions were made to capture the variability seen in adult females over the entire study period. We used the predictions of juveniles' grooming patterns (Vilette et al., 2022) to assess whether their patterns became more similar to adults' average estimates as they aged. When investigating females' social integration, the prediction plot allowed us to see how primiparous and multiparous mothers differed in their response to the average effect of our response variable. Lastly, to compare the effect of adding weak or strong ties on the primiparous females' integration, we used a dot plot with error bars inferred using the 95% credible intervals. Model main effects are presented as summary statistics (see Appendix, Tables A1–A18) 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

Grooming Network Structure Comparisons

Juvenile and adult females

Overall, the average number of grooming partners increased over time for female juveniles (Fig. 1a), with three peaks occurring approximately every 500 days. By the end of the study period, female juveniles had acquired a similar number of grooming partners (~17 partners) as the average adult female. Grooming strength exhibited a similar trend, with an increase in grooming frequency over time, and the same pattern of regularly occurring peaks (Fig. 1b). The effort invested in grooming (~45 interactions), however, was much lower than the average grooming effort displayed by adult females (~85 interactions). With respect to skewness, female juveniles showed an asymptotic pattern of positive values (Fig. 1c), reaching a plateau around ~1.5 years of age. Overall, female

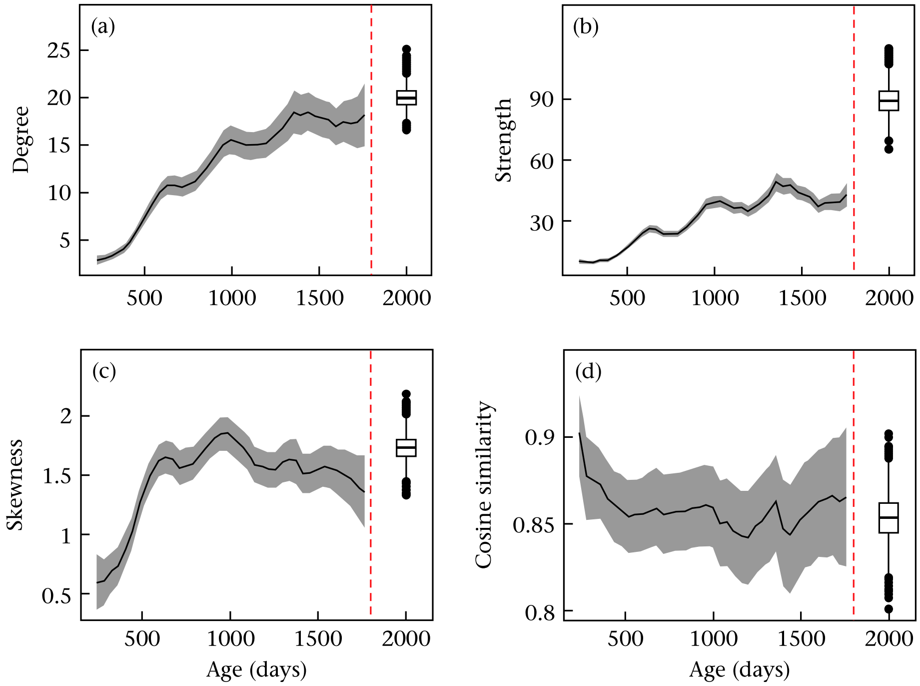

Figure 1. On the left side of the red dashed line: variation in (a) degree (b) strength (c) skewness and (d) cosine similarity of grooming associations by age for female juvenile vervets. The black line shows the global smooth for the average juvenile female with upper and lower 95% credible intervals (grey bands). Predictions for female juveniles were calculated with a mean troop size fixed at 49 individuals. On the right side of the red dashed line: box plots indicating the median values and percentiles of the variables (a) degree (b) strength (c) skewness and (d) cosine similarity of grooming associations for the average adult female vervet over the entire study period.

juveniles displayed a similar skewness value (~1.5) to the average adult female. In the case of cosine similarity, female juveniles began with high mean cosine values in partner similarity, which declined before stabilizing as they grew older (Fig. 1d). By the end of the study period, female juveniles' cosine values were high and comparable to those of adult females (~0.86).

Primiparous and multiparous females network measures

Primiparous females displayed a steady increase in the mean number of grooming partners leading up to, and across, the birth event (Fig. 2a), followed by a stabilization 4 months past birth. In contrast, multiparous females showed an overall steady pattern across their birth events. For grooming strength (Fig. 2b), primiparous females displayed an S-shaped pattern with a substantial increase in strength just after birth, which reached a plateau 2 months later. Multiparous females' strength pattern was stable overall, with a noticeable U-shaped drop centred on the birth event. After reaching its lowest point, strength increased and stabilized again 2 months after birth. For skewness, there was a decrease among primiparous females prior to and just after the birth event (Fig. 2c). Skewness then stabilized 2 months after birth. Multiparous females displayed a comparable pattern, albeit with a delayed onset of decline and subsequent stabilization, compared to primiparous females. Finally, primiparous females maintained high cosine similarity values overall, but there was a temporary U-shaped drop around the birth event (Fig. 2d). This pattern was mirrored by multiparous females but was of lesser magnitude.

Females' social integration

In terms of birth-related shifts in network centrality, primiparous females displayed the predicted pattern but with a slight delay. That is, there was an increase in eigenvector centrality associated with birth, although this took place in the month following the birth event, reaching a plateau 3 months later (Fig. 3). The observed lag can be attributed to our 'moving window' method. Specifically, because we used a 2-month window size for data extraction, which was then shifted in 30-day increments, this meant that, for the period around birth, the data encompassed both a month prior to birth ($t-1$) and the month after ($t+1$). It is only at $t+2$ and onwards that the data capture a period that occurred exclusively after birth. In other words, there was an inevitable lag between a birth event and our being able to clearly detect any effect of birth in our analyses. Multiparous females displayed an overall stable pattern of values through time (Fig. 3).

Grooming bubble structure

With respect to the number of strong grooming partners (Fig. 4), primiparous females showed a very small increase in degree just before birth and across the postpartum period.

Weak ties and the restructuring of primiparous females' relationships

Primiparous females showed an increase in the number of weak grooming partners (from $N = {\sim}17$ prior to first birth to $N = {\sim}21$ partners after it) (Fig. 5). Predictions were estimated with a mean troop size fixed at 44 individuals, revealing that, despite a large number of weak ties, females were not, however, grooming all available females in the troop (i.e. the number of weak ties never exceeded ~24, despite there being an additional 20 partners available).

Knockout Analysis

Eigenvector centrality was slightly higher following birth, as inferred from original unaltered ego-networks. Against our prediction, when all new weak ties were removed, eigenvector centrality remained high and comparable to the unaltered value, compared to the removal of all strong ties. However, the difference

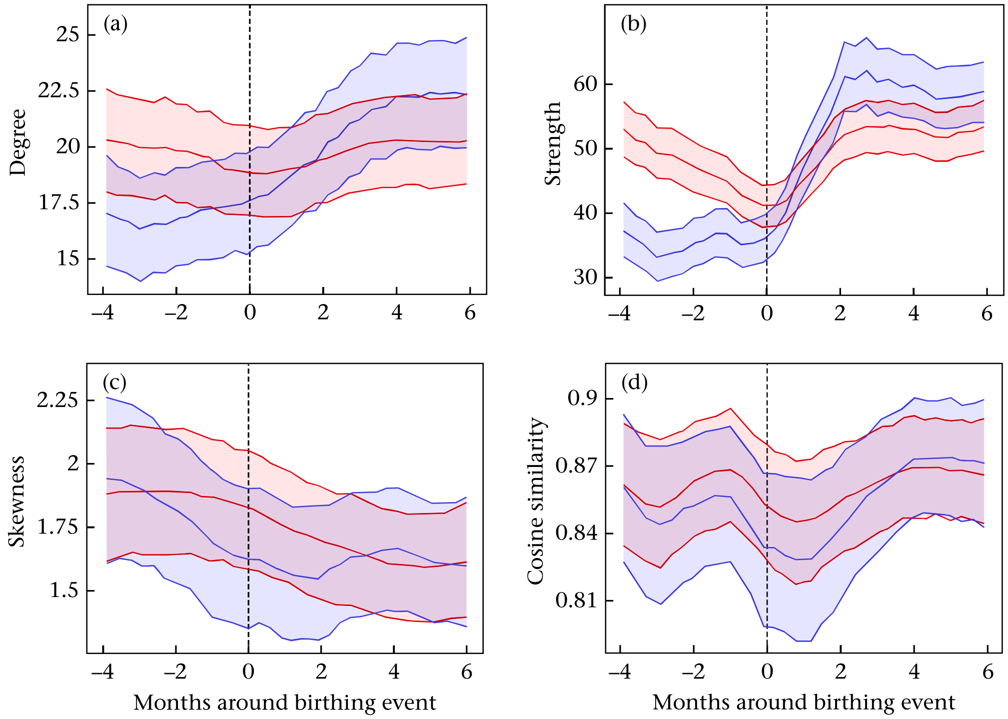

Figure 2. Variation in (a) degree (b) strength (c) skewness and (d) cosine similarity of grooming associations 6 months prior to and past giving birth for primiparous (blue lines) and multiparous (red lines) females. Lines represent the global smooth for the average primiparous and multiparous female, respectively, with upper and lower 95% credible intervals (displayed as bands around these lines). The black dashed line represents the birth event of primiparous and multiparous females and indicates when networks started to contain data following the birth event.

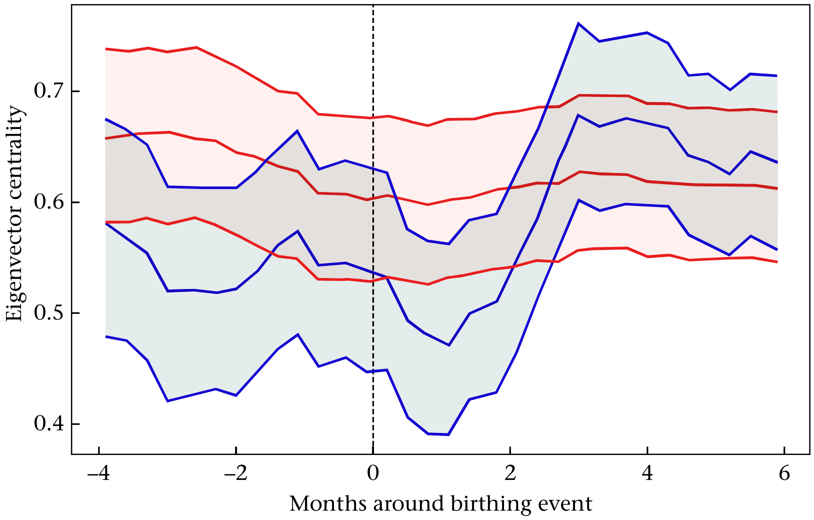

Figure 3. Variation in the undirected eigenvector centrality measure of grooming associations 6 months prior to and past giving birth for primiparous (blue lines) and multiparous (red lines) females. Lines show the global smooth for the average primiparous and multiparous female, respectively, with upper and lower 95% credible intervals (bands). The black dashed line represents the birth event of primiparous and multiparous females and indicates when networks started to contain data after the birthing event.

between the removal of new weak ties versus new strong ties was very small due to the presence of wide credible intervals (Fig. 6). When all new ties were removed, the eigenvector value was even lower, although again the wide credible intervals indicate the difference was small.

DISCUSSION

We found that juveniles' network structure at the end of the developmental period differed from adult female networks in terms of social engagement (strength): juveniles invested less effort in grooming partners than did adult females (Fig. 1b). However, juvenile female networks were similar to those of adult females in terms of degree, skewness and cosine similarity (Fig. 1a, c, d). Thus, by the end of the juvenile period, juvenile females had attained an adult configuration with respect to the size, structure and stability of their ego-networks but continued to differ in their level of social engagement. This partially supports our assumption that juveniles would not have reached a fully adult pattern of social integration by the end of the juvenile period. That is, these patterns

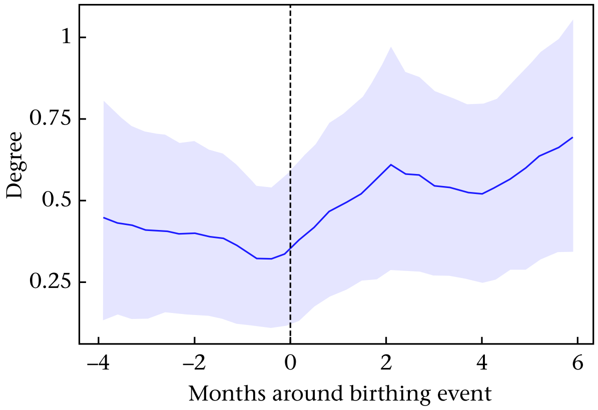

Figure 4. Variation in degree in strong grooming associations 6 months prior to and after giving birth. The blue line shows the global smooth for the average primiparous female, with upper and lower 95% credible intervals (bands). The black dashed line represents the birth event of primiparous females and indicates when networks started to contain data after the birthing event.

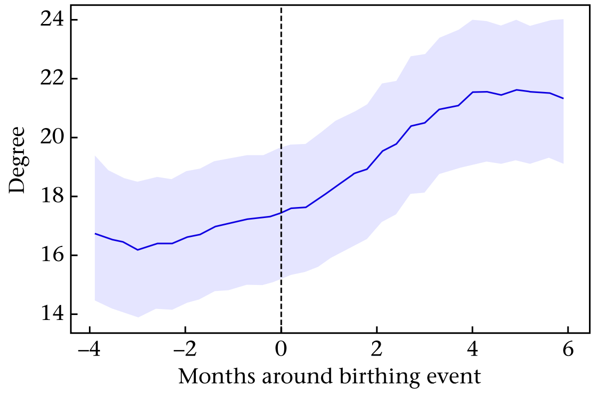

Figure 5. Variation in degree of weak grooming associations 6 months prior to and past giving birth. The blue line shows the global smooth for the average primiparous female, with upper and lower 95% credible intervals (bands). The dashed line represents the birth event of primiparous females. Note that the *Y* axis does not begin at 0, and the dashed black line indicates when networks started to contain data after the birthing event.

do not necessarily conform to the idea that juvenile females are, in fact, less socially integrated, as this depends on the features one considers most relevant. Specifically, one could argue that having a similar number of partners overall means that juveniles females are, in fact, as socially integrated as adult females. Alternatively, one could emphasize the overall quality of engagement, which would suggest the reverse. Nevertheless, we can say that juvenile and adult networks differ in at least one respect by the end of the developmental period.

Having validated that juvenile and adult network structures differ, we then turned to investigating the influence of the onset of reproduction on network structure. Our prediction that primiparous females' network structure would come to more closely resemble that of multiparous females was supported (Fig. 2). That is, following the birth event, primiparous females' network patterns shifted in terms of strength (Fig. 2b). We also observed variation in skewness and cosine similarity across the birth event (Fig. 2c, d), with primiparous and multiparous females exhibiting changes in the same direction, rather than diverging. Additionally, primiparous females increased their number of grooming partners before and after birth (Fig. 2a). Taken together, these findings support the idea that the birth of their first offspring creates the impetus for young females to invest more in grooming. The increase in the number of grooming partners prior to birth of a female's first offspring potentially may reflect the reduced mobility of females during late gestation and an increased risk of predation; pregnant females may therefore have sought safer spatial positions within the troop and used grooming to facilitate this, an effect we have documented in our population more generally (Josephs et al., 2016). Following birth, an increase in grooming may continue to reflect ongoing concerns reducing predation risk, but we can also factor in the increased social attention that the presence of an infant generates. It is also likely that there is an effect on primiparous females themselves produced by increased levels of oxytocin (a hormone involved in social bonding and associated with birth: Morris et al., 1980), which may further increase females' tendency to seek affiliative behaviours (Taylor et al., 2000).

Another point worth highlighting is that the transition to motherhood did not disrupt the stability of primiparous females' ego-networks, although the existing ego-network structure appeared less distinct prior to and following the birth event (as evidenced by the decline in skewness values: Fig. 2c). That is, there was a reduced contrast in grooming engagement between strong and weak ties. Despite this, the fundamental structure of their networks remained unchanged. This is notable because it suggests that, in our population, a stable network structure is in place from the very beginning of the juvenile period (Vilette et al., 2022) and persists through the motherhood transition, demonstrating high levels of robustness across development and into adult life. It is therefore plausible that this kind of structure actively enables individual flexibility in social engagement, accommodating the specific needs of females as they experience changes in their own status and broader demographic shifts within the group. Ultimately, it is the consistency and stability of ego-network structure that stands out as the key feature of juveniles' social development (Vilette et al., 2022).

Given these changes in direct centrality measures (degree and strength) around the birth period, we proceeded to assess whether the birth event was also associated with changes to indirect measures of centrality and patterns of social integration (Fig. 3). Accordingly, we observed an increase in eigenvector centrality following the birth event for primiparous females, which then reached a plateau 3 months after birth. The multiparous females' pattern, however, was continuous and stable and was not impacted by their birth events. This supports the idea that the transition to motherhood, rather than any subsequent birth events, drives a shift in sociality. This also prompts further inquiry into the underlying mechanisms of this integration. Specifically, does integration occur primarily due to the presence of dependent offspring, and the received social attention, that drives these observed shifts? Alternatively, birth itself and associated hormonal changes (i.e. increased levels of oxytocin) may increase females' tendency to seek affiliative behaviours (Taylor et al., 2000).

Considering multiparous females in more detail, we found that there were no major effects of their birth events on engagement style in terms of degree, although strength declined across gestation and rose again in the 2 months following birth (Fig. 2a, b). One potential explanation for these patterns is that, during late gestation, pregnant females may see their time budgets change due to energetic demands, hence favouring foraging over grooming. After birth, the increased social attention around the birth of their infant may lead females to capitalize on this attention and to reinvest in grooming. In turn, this reinvestment may serve to reduce the likelihood of predation, as previously noted above (Josephs et al., 2016). There was also no overall effect on network stability (i.e. cosine similarity, Fig. 2d), but skewness slightly decreased in association with impending birth (Fig. 2c). In other words, despite

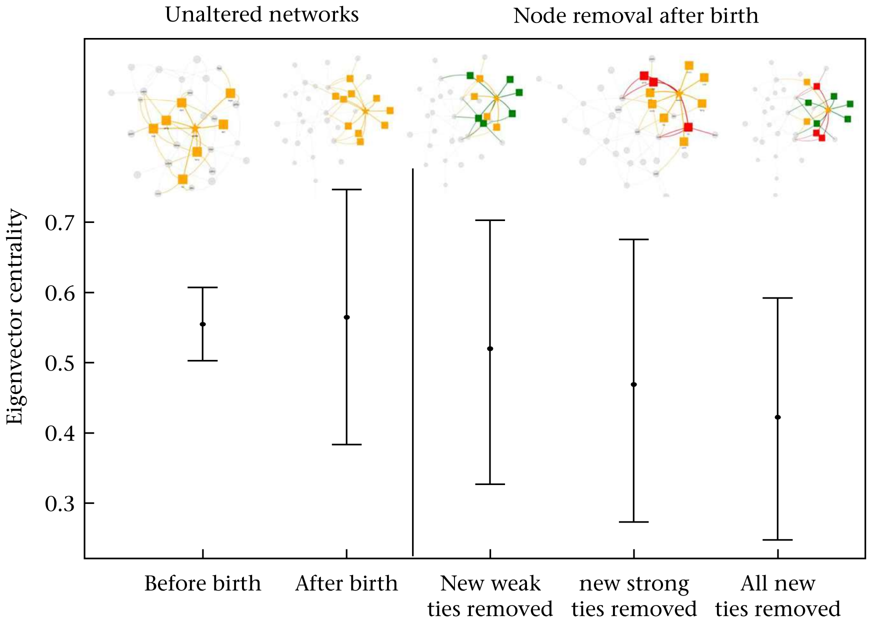

Figure 6. (a) Group level networks across the motherhood transition and knockout procedure. A specific node focal (star shape) is highlighted in orange with its direct and indirect links. New weak and strong ties, and their corresponding edges, removed after birth are represented in green and red, respectively. (b) Primiparous females' eigenvector centrality values inferred over the motherhood transition (before and after birth), based on unaltered and altered ego-networks.

changes in grooming engagement, ego-networks of multiparous females remained stable, reinforcing the notion that the overall structure of ego-networks permits flexibility in grooming effort, without compromising ego-network stability.

The formation of new strong ties among primiparous females (Fig. 4) showed only a very minor increase across the birth event (~<1), which was somewhat surprising. The birth of a first offspring, associated with the heightened attention received from group members, marks an important social change in a female's life. To cope with this potentially stressful event, and to integrate further into the group, it would be reasonable to expect females to expand the size of their grooming bubbles in order to buffer and protect both themselves and their offspring. Yet, primiparous females did not do so. However, new mothers did form less demanding weak ties (Fig. 5), potentially achieving social buffering by alternative means. To reiterate the point made above, the most striking social change associated with motherhood was the reallocation of grooming effort within females' ego-networks; there was both an increase in social effort (strength) and a decline in skewness values, suggesting that females spread their effort more equally across their partners. Motherhood largely influenced the style of females' social engagement and had a small effect on network size, rather than inducing overt changes in network structure.

The increase in new tie formation, and weak ties in particular, prompted us to test whether these changes could account for the observed increase in eigenvector centrality. Contrary to our initial prediction, we found that the addition of both strong and weak ties contributed to the increase in centrality values, but the large credible intervals meant that we could not tease apart which type of tie had more effect. As expected, the removal of all new ties (weak and strong) led to a decrease in eigenvector centrality (Fig. 6). Due to wide credible intervals, however, it is not certain that these removals resulted in a reversion to centrality values seen before birth. Our knockout analyses, therefore, suggest that the increase in primiparous females' centrality may be attributed to these additional weak and strong ties. The large uncertainty around the mean estimates seen in this analysis may have arisen from individual variation and/or a lack of data, something that may be inevitable for a study of this nature given that, by definition, a female can only be classified as primiparous once, which limits the amount of data that can be collected. Longitudinal data are necessary to gather sufficient data on this specific class of female to enable us to effectively investigate the extent and consequences of individual variation.

Lastly, our findings underscore the importance of investigating not only individual changes but also the overall dynamics of the group. Specifically, our results suggest that, as primiparous and multiparous females all give birth within a defined season, there is a reconfiguration of social ties and social engagement that occurs across the group as whole, as well as within individual ego-networks. The particular patterns shown will likely reflect the relative proportion of primiparous versus multiparous females in a given birth season, and can ultimately be traced back to ecological conditions that determine group demographic structure. It is also likely that any group level effects produced due to the onset of motherhood will feed back and subsequently influence networks at the individual level. Consequently, our study prompts consideration of a broader perspective on the dynamics of social integration: specifically, a focus on the interplay between individual and group network structure in relation to both the onset of motherhood and birth events in general, and how variation in these structures over time can be traced to group demographics and the ecological conditions to which they are a response. Future studies could also explore additional factors influencing females' social integration, such as food availability (NDVI) and troop size. High food availability might promote social integration by allowing individuals to allocate more time to social interactions. Conversely, smaller troop sizes could reduce aggression levels, potentially facilitating easier integration among group members.

Author Contributions

C. Vilette: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

T.R. Bonnell: Writing – review & editing, Validation, Supervision, Methodology, Formal analysis. **M.J. Dostie:** Data curation. **S.P. Henzi:** Writing – review & editing, Supervision, Investigation, Funding acquisition, Conceptualization. **L. Barrett:** Writing – review & editing, Validation, Supervision, Funding acquisition, Conceptualization.

Data Availability

All code and data used to generate this paper are available at: github.com/ChloeVilette/Parity_status_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.2024.11.006.

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Appendix

Table A1

Summary statistics of a Bayesian hierarchical generalized additive mixed model (HGAM) for the number of grooming partners (degree) for juvenile females, using a Poisson distribution

Effect	Parameter	Estimate	Estimate error	Lower 95% CI	Upper 95% CI
Population level effects	Intercept	2.44	0.32	1.75	3.11
	s(age)	1.82	0.85	0.13	3.51
	s(scan.nb)	0.81	0.82	−0.79	2.4
	s(NDVI)	−0.03	0.94	−1.89	1.79
	s(troop.nb)	0.72	0.66	−0.44	2.12
	s(rank)	0.03	0.26	−0.58	0.51
Smooth terms	sds(age)	3.22	1.01	1.71	5.58
	sds(age ID1)	1.52	0.14	1.25	1.8
	sds(age ID2)	1.02	0.32	0.35	1.65
	sds(cohortID)	0.26	0.32	0.02	1.19
	sds(troopID)	0.37	0.4	0.06	1.51
	sds(age mumID1)	0.31	0.23	0.02	0.85
	sds(age mumID2)	0.52	0.35	0.03	1.3
	sds(scan.nb)	1.8	0.73	0.58	3.5
	sds(NDVI)	2.17	0.82	0.93	4.1
	sds(troop.nb)	0.45	0.27	0.12	1.13
	sds(rank)	0.11	0.12	0	0.42
		Estimate	Estimate error	Q2.5	Q97.5
R^2 marginal		0.31	0.08	0.20	0.51

CI = credible interval; NDVI: normalized difference vegetation index; ID: identity; s() = spline; smooth term sds() = spline 'wiggliness' (spline variance parameter).

Table A2

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

Effect	Parameter	Estimate	Estimate error	Lower	Upper
				95% CI	95% CI
Population level effects	Intercept	3.35	0.34	2.60	4.12
	s(age)	0.69	0.85	−0.97	2.37
	s(scan.nb)	0.60	0.71	−0.76	2.00
	s(NDVI)	−0.26	0.82	−1.87	1.40
	s(troop.nb)	0.99	0.71	−0.38	2.40
	s(rank)	−0.66	0.57	−1.85	0.40
Smooth terms	sds(age)	4.14	1.18	2.36	6.87
	sds(age ID1)	3.11	0.18	2.76	3.47
	sds(age ID2)	2.39	0.60	1.35	3.65
	sds(cohortID)	0.46	0.45	0.06	1.81
	sds(troopID)	0.16	0.24	0.00	0.82
	sds(age mumID1)	0.53	0.37	0.03	1.38
	sds(age mumID2)	1.80	0.79	0.17	3.31
	sds(scan.nb)	2.92	0.81	1.77	4.87
	sds(NDVI)	2.88	0.82	1.62	4.88
	sds(troop.nb)	1.10	0.40	0.52	2.05
	sds(rank)	1.06	0.46	0.32	2.12
		Estimate	Estimate error	Q2.5	Q97.5
R^2 marginal		0.44	0.03	0.39	0.53

CI = credible interval; NDVI: normalized difference vegetation index; sd = standard deviation; ID: identity; 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 distribution of grooming weights (skewness) for juvenile females, using a skew-normal distribution

Effect	Parameter	Estimate	Estimate error	Lower	Upper
				95% CI	95% CI
Population level effects	Intercept	1.61	0.33	0.91	2.35
	s(age)	−0.20	0.92	−2.00	1.62
	s(scan.nb)	1.16	0.46	0.14	1.99
	s(NDVI)	−0.69	0.97	−2.61	1.18
	s(troop.nb)	0.00	0.61	−1.12	1.35
	s(rank)	−0.08	0.48	−1.13	0.86
Smooth terms	sds(age)	3.19	1.07	1.55	5.69
	sds(age ID1)	2.13	0.23	1.70	2.57
	sds(age ID2)	2.79	0.61	1.66	4.03
	sds(cohortID)	0.39	0.43	0.03	1.59
	sds(troopID)	0.20	0.30	0.00	1.10
	sds(age mumID1)	0.42	0.32	0.01	1.18
	sds(age mumID2)	1.59	0.93	0.09	3.43
	sds(scan.nb)	0.21	0.23	0.01	0.86
	sds(NDVI)	2.14	0.90	0.79	4.18
	sds(troop.nb)	0.42	0.30	0.02	1.16
	sds(rank)	0.25	0.24	0.01	0.85
Family-specific parameters	Sigma	0.55	0.01	0.52	0.57
	Alpha	0.51	0.60	−0.67	1.42
		Estimate	Estimate error	Q2.5	Q97.5
R^2 marginal		0.50	0.03	0.42	0.55

CI = credible interval; NDVI: normalized difference vegetation index; sd = standard deviation; ID: identity; s() = spline; smooth term sds() = spline ‘wiggliness’ (spline variance parameter).

Table A4

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

Effect	Parameter	Estimate	Estimate error	Lower	Upper
				95% CI	95% CI
Population level effects	Intercept	1.90	0.68	0.17	3.05
	s(age)	−0.56	0.86	−2.37	1.05
	s(scan.nb)	1.01	0.89	−0.74	2.74
	s(NDVI)	−0.35	0.90	−2.13	1.44
	s(troop.nb)	0.32	0.88	−1.14	2.14
	s(rank)	0.16	0.51	−0.84	1.21
Smooth terms	sds(age)	1.06	0.63	0.24	2.64
	sds(age ID1)	1.47	0.37	0.64	2.04
	sds(age ID2)	3.48	0.96	1.96	5.63
	sds(cohortID)	0.73	0.68	0.14	2.71
	sds(troopID)	0.53	0.75	0.02	2.34
	sds(age mumID1)	0.58	0.39	0.03	1.37
	sds(age mumID2)	3.39	1.30	0.56	5.81
	sds(scan.nb)	2.26	1.07	0.69	4.77
	sds(NDVI)	1.76	0.76	0.75	3.64
	sds(troop.nb)	0.77	0.76	0.03	3.02
	sds(rank)	0.26	0.26	0.01	1.02
Family-specific parameters	Phi	11.93	0.53	10.93	12.99
	Zoi	0.02	0.00	0.01	0.03
	Coi	0.63	0.08	0.46	0.78
		Estimate	Estimate error	Q2.5	Q97.5
R^2 marginal		0.47	0.03	0.38	0.51

CI = credible interval; NDVI: normalized difference vegetation index; sd = standard deviation; ID: identity; s() = spline; smooth term sds() = spline ‘wiggliness’ (spline variance parameter).

Table A5

Summary statistics of a Bayesian hierarchical generalized additive mixed model (HGAM) for the number of grooming partners (degree) for adult females, using a Poisson distribution

Effect	Parameter	Estimate	Estimate error	Lower	Upper
				95% CI	95% CI
Population level effects	Intercept	2.93	0.09	2.72	3.14
	s(day.nb)	1.39	0.94	−0.48	3.16
	s(scan.nb)	0.91	0.67	−0.68	1.90
	s(NDVI)	−0.69	0.45	−1.53	0.25
	s(troop.nb)	0.01	0.39	−0.82	0.77
	s(rank)	0.13	0.30	−0.51	0.71
Smooth terms	sds(day.nb)	3.61	1.15	1.99	6.39
	sds(day.nb ID1)	0.65	0.07	0.52	0.79
	sds(day.nb ID2)	1.60	0.25	1.17	2.16
	sds(troopID)	0.12	0.18	0.00	0.66
	sds(syday)	0.02	0.01	0.01	0.04
	sds(scan.nb)	0.35	0.26	0.07	1.04
	sds(NDVI)	0.37	0.19	0.13	0.86
	sds(troop.nb)	0.35	0.23	0.05	0.92
	sds(rank)	0.16	0.12	0.02	0.49
		Estimate	Estimate error	Q2.5	Q97.5
R^2 marginal		0.59	0.03	0.53	0.65

CI = credible interval; NDVI: normalized difference vegetation index; sd = standard deviation; ID: identity; s() = spline; smooth term sds() = spline ‘wiggliness’ (spline variance parameter).

Table A6
Summary statistics of a Bayesian hierarchical generalized additive mixed model (HGAM) for the frequency of grooming interactions (strength) for adult females, using a Poisson distribution

Effect	Parameter	Estimate	Estimate error	Lower	Upper
				95% CI	95% CI
Population level effects	Intercept	3.89	0.41	2.98	3.89
	s(day.nb)	1.8	0.97	−0.14	1.8
	s(scan.nb)	−0.57	0.7	−1.96	−0.57
	s(NDVI)	−2.47	0.5	−3.44	−2.47
	s(troop.nb)	2.8	0.44	1.94	2.8
	s(rank)	1.14	0.37	0.44	1.14
Smooth terms	sds(day.nb)	7.67	2.07	4.67	12.63
	sds(day.nb ID1)	2.68	0.19	2.33	3.08
	sds(day.nb ID2)	4.06	0.69	2.9	5.56
	sds(troopID)	0.65	0.5	0.16	2.14
	sds(syday)	0.09	0.03	0.05	0.16
	sds(scan.nb)	1.64	0.51	0.91	2.88
	sds(NDVI)	1.46	0.49	0.76	2.62
	sds(troop.nb)	2.35	0.66	1.39	4
	sds(rank)	0.59	0.28	0.2	1.25
		Estimate	Estimate error	Q2.5	Q97.5
R^2 marginal		0.52	0.01	0.51	0.55

CI = credible interval; NDVI: normalized difference vegetation index; sd = standard deviation; ID: identity; s() = spline; smooth term sds() = spline 'wiggliness' (spline variance parameter).

Table A7
Summary statistics of a Bayesian hierarchical generalized additive mixed model (HGAM) for the distribution of grooming weights (skewness) for adult females, using a skew-normal distribution

Effect	Parameter	Estimate	Estimate error	Lower	Upper
				95% CI	95% CI
Population level effects	Intercept	1.6	0.14	1.3	1.91
	s(day.nb)	0.41	0.87	−1.31	2.11
	s(scan.nb)	1.44	0.59	0.01	2.38
	s(NDVI)	−1.42	0.88	−3.07	0.35
	s(troop.nb)	0.51	0.59	−0.62	1.67
	s(rank)	0.69	0.59	−0.39	1.97
Smooth terms	sds(day.nb)	2.6	1.09	0.71	5.13
	sds(day.nb ID1)	1.94	0.22	1.52	2.37
	sds(day.nb ID2)	2.33	0.4	1.63	3.19
	sds(troopID)	0.18	0.26	0	0.92
	sds(syday)	0.03	0.02	0.01	0.09
	sds(scan.nb)	0.28	0.28	0.01	1.03
	sds(NDVI)	1.29	0.59	0.45	2.68
	sds(troop.nb)	0.43	0.28	0.08	1.18
	sds(rank)	0.51	0.45	0.02	1.65
Family-specific parameters	Sigma	0.62	0.01	0.59	0.65
	Alpha	2.81	0.4	2.1	3.66
		Estimate	Estimate error	Q2.5	Q97.5
R^2 marginal		0.49	0.03	0.42	0.53

CI = credible interval; NDVI: normalized difference vegetation index; sd = standard deviation; ID: identity; s() = spline; smooth term sds() = spline 'wiggliness' (spline variance parameter).

Table A8

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

Effect	Parameter	Estimate	Estimate error	Lower 95% CI	Upper 95% CI
Population level effects	Intercept	1.92	0.14	1.61	2.17
	s(day.nb)	0.93	0.87	−0.83	2.67
	s(scan.nb)	0.64	0.89	−1.04	2.43
	s(NDVI)	−0.52	0.74	−1.96	1.04
	s(troop.nb)	−0.54	0.87	−1.98	1.23
	s(rank)	0.67	0.58	−0.47	1.87
Smooth terms	sds(day.nb)	2.69	1.36	0.83	6.08
	sds(day.nb ID1)	0.81	0.12	0.59	1.05
	sds(day.nb ID2)	2.28	0.39	1.61	3.15
	sds(troopID)	0.16	0.24	0	0.81
	sds(syday)	0.21	0.08	0.11	0.41
	sds(scan.nb)	2.21	0.98	0.75	4.56
	sds(NDVI)	0.74	0.47	0.12	1.91
	sds(troop.nb)	0.65	0.53	0.03	2.05
	sds(rank)	0.4	0.31	0.04	1.22
Family-specific parameters	Phi	21.18	0.83	19.57	22.82
	Zoi	0	0	0	0
		Estimate	Estimate error	Q2.5	Q97.5
R^2 marginal		0.42	0.08	0.27	0.54

CI = credible interval; NDVI: normalized difference vegetation index; sd = standard deviation; ID: identity; s() = spline; smooth term sds() = spline ‘wiggliness’ (spline variance parameter).

Table A9

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

Effect	Parameter	Estimate	Estimate error	Lower 95% CI	Upper 95% CI
Population level effects	Intercept	2.67	0.5	1.51	3.78
	hu_Intercept	−0.78	2.02	−5.37	2.74
	s(time)	−0.01	0.2	−0.45	0.37
	s(scan.nb)	0.41	0.02	0.38	0.44
	s(troop.nb)	1.19	0.73	−0.23	2.64
	s(NDVI)	0.38	0.29	−0.24	0.99
	s(rank)	0.23	0.25	−0.34	0.7
Smooth terms	sds(time)	0.09	0.09	0	0.33
	sds(time primiparous0)	0.04	0.03	0	0.13
	sds(time primiparous1)	0.1	0.05	0.02	0.23
	sds(primiparous)	0.61	0.75	0.03	2.77
	sds(ID)	0.16	0.02	0.12	0.2
	sds(troopID)	0.12	0.21	0	0.63
	sds(scan.nb)	2.86	2.01	0.9	7.94
	sds(troop.nb)	1.31	0.53	0.54	2.58
	sds(NDVI)	0.16	0.15	0.01	0.54
	sds(rank)	0.11	0.12	0	0.44
	sds(year)	0.16	0.08	0.07	0.36
Family-specific parameters	Shape	552	171.92	291.78	957.71
		Estimate	Estimate error	Q2.5	Q97.5
R^2 marginal		0.29	0.02	0.25	0.33

CI = credible interval; NDVI: normalized difference vegetation index; sd = standard deviation; ID: identity; s() = spline; smooth term sds() = spline ‘wiggliness’ (spline variance parameter).

Table A10

Summary statistics of a Bayesian hierarchical generalized additive mixed model (HGAM) for the number of grooming partners (degree) for females, using a Poisson distribution

Effect	Parameter	Estimate	Estimate error	Lower	Upper
				95% CI	95% CI
Population level effects	Intercept	2.76	0.46	1.7	3.85
	s(time)	0	0.2	−0.45	0.38
	s(scan.nb)	0.4	0.01	0.37	0.43
	s(NDVI)	0.94	0.71	−0.39	2.39
	s(troop.nb)	0.42	0.3	−0.21	1.05
	s(rank)	0.18	0.22	−0.31	0.57
Smooth terms	sds(time)	0.1	0.09	0	0.32
	sds(time primiparous0)	0.05	0.04	0	0.13
	sds(time primiparous1)	0.09	0.05	0.01	0.22
	sds(primiparous)	0.56	0.7	0.03	2.62
	sds(ID)	0.15	0.02	0.12	0.2
	sds(troopID)	0.13	0.23	0	0.79
	sds(scan.nb)	2.85	1.99	0.92	8.1
	sds(troop.nb)	1.17	0.49	0.46	2.37
	sds(NDVI)	0.15	0.15	0.01	0.53
	sds(rank)	0.1	0.1	0	0.37
	sds(year)	0.16	0.09	0.07	0.37
		Estimate	Estimate error	Q2.5	Q97.5
R^2 marginal		0.28	0.02	0.24	0.33

CI = credible interval; NDVI: normalized difference vegetation index; sd = standard deviation; ID: identity; s() = spline; smooth term sds() = spline ‘wiggliness’ (spline variance parameter).

Table A11

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

Effect	Parameter	Estimate	Estimate error	Lower	Upper
				95% CI	95% CI
Population level effects	Intercept	3.71	0.83	2.01	5.4
	hu_Intercept	−0.8	2.09	−5.82	2.81
	s(time)	−0.11	0.41	−0.87	0.72
	s(scan.nb)	0.77	0.02	0.73	0.8
	s(troop.nb)	1.11	0.75	−0.37	2.66
	s(NDVI)	0.54	0.41	−0.28	1.4
	s(rank)	0.82	0.4	−0.05	1.62
Smooth terms	sds(time)	0.36	0.22	0.04	0.88
	sds(time primiparous0)	0.1	0.07	0.01	0.27
	sds(time primiparous1)	0.19	0.09	0.03	0.42
	sds(primiparous)	1.18	1.5	0.1	6.16
	sds(ID)	0.34	0.04	0.27	0.43
	sds(troopID)	0.44	0.53	0.07	1.91
	sds(scan.nb)	3.47	2.13	1.3	8.99
	sds(troop.nb)	1.46	0.68	0.41	3.02
	sds(NDVI)	0.27	0.17	0.05	0.7
	sds(rank)	0.27	0.18	0.07	0.75
	sds(year)	0.12	0.08	0.04	0.32
Family-specific parameters	Shape	14.76	0.92	13.06	16.68
		Estimate	Estimate error	Q2.5	Q97.5
R^2 marginal		0.30	0.03	0.26	0.36

CI = credible interval; NDVI: normalized difference vegetation index; sd = standard deviation; ID: identity; s() = spline; smooth term sds() = spline ‘wiggliness’ (spline variance parameter).

Table A12

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

Effect	Parameter	Estimate	Estimate error	Lower 95% CI	Upper 95% CI
Population level effects	Intercept	3.67	0.7	2.16	5.34
	s(time)	−0.06	0.38	−0.81	0.76
	s(scan.nb)	0.74	0.01	0.72	0.76
	s(NDVI)	2.66	0.67	1.37	3.99
	s(troop.nb)	0.8	0.36	0.1	1.53
	s(rank)	0.64	0.35	−0.02	1.37
Smooth terms	sds(time)	0.49	0.22	0.12	1.01
	sds(time primiparous0)	0.1	0.07	0	0.27
	sds(time primiparous1)	0.21	0.09	0.06	0.44
	sds(primiparous)	0.83	0.78	0.1	3.01
	sds(ID)	0.34	0.04	0.28	0.42
	sds(troopID)	0.34	0.49	0.05	1.66
	sds(scan.nb)	3.24	2.06	1.14	8.81
	sds(troop.nb)	2.24	0.63	1.27	3.71
	sds(NDVI)	0.37	0.19	0.15	0.83
	sds(rank)	0.42	0.21	0.13	0.94
	sds(year)	0.16	0.08	0.07	0.35
		Estimate	Estimate error	Q2.5	Q97.5
R^2 marginal		0.31	0.02	0.28	0.34

CI = credible interval; NDVI: normalized difference vegetation index; sd = standard deviation; ID: identity; s() = spline; smooth term sds() = spline 'wiggliness' (spline variance parameter).

Table A13

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

Effect	Parameter	Estimate	Estimate error	Lower 95% CI	Upper 95% CI
Population level effects	Intercept	1.5	0.46	0.47	2.35
	s(time)	−0.23	0.38	−0.85	0.64
	s(scan.nb)	0.27	0.03	0.2	0.34
	s(NDVI)	0.22	0.81	−1.49	1.7
	s(troop.nb)	−0.45	0.59	−1.68	0.79
	s(rank)	0.58	0.43	−0.32	1.41
Smooth terms	sds(time)	0.16	0.15	0.01	0.57
	sds(time primiparous0)	0.1	0.08	0	0.28
	sds(time primiparous1)	0.19	0.12	0.01	0.48
	sds(primiparous)	0.8	1.17	0.02	4.54
	sds(ID)	0.21	0.04	0.15	0.28
	sds(troopID)	0.17	0.28	0	0.91
	sds(scan.nb)	1.55	1.68	0.07	5.85
	sds(troop.nb)	1.11	0.59	0.29	2.51
	sds(NDVI)	0.43	0.37	0.02	1.35
Family-specific parameters	Sigma	0.68	0.02	0.65	0.71
	Alpha	2.59	0.31	2.03	3.24
	Estimate	Estimate error	Q2.5	Q97.5	
R^2 marginal	0,25	0.06	0.15	0.38	

CI = credible interval; NDVI: normalized difference vegetation index; sd = standard deviation; ID: identity; s() = spline; smooth term sds() = spline 'wiggliness' (spline variance parameter).

Table A14

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

Effect	Parameter	Estimate	Estimate error	Lower 95% CI	Upper 95% CI
Population level effects	Intercept	1.38	0.81	−0.83	2.76
	s(time)	−0.43	0.66	−1.87	0.71
	s(scan.nb)	0.51	0.04	0.44	0.59
	s(NDVI)	0.09	0.8	−1.32	1.76
	s(troop.nb)	−0.03	0.64	−1.28	1.43
	s(rank)	0.29	0.57	−0.88	1.41
Smooth terms	sds(time)	0.56	0.46	0.02	1.69
	sds(time primiparous0)	0.15	0.11	0.01	0.42
	sds(time primiparous1)	0.21	0.16	0.01	0.61
	sds(primiparous)	0.85	1.08	0.03	4.57
	sds(ID)	0.16	0.04	0.09	0.24
	sds(troopID)	0.58	0.55	0.12	2.19
	sds(scan.nb)	1.96	1.72	0.25	6.51
	sds(troop.nb)	0.77	0.44	0.16	1.85
	sds(NDVI)	0.44	0.31	0.07	1.26
Family-specific parameters	Phi	2.51	0.53	11.52	13.56
		Estimate	Estimate error	Q2.5	Q97.5
R^2 marginal		0.20	0.05	0.11	0.31

CI = credible interval; NDVI: normalized difference vegetation index; sd = standard deviation; ID: identity; s() = spline; smooth term sds() = spline ‘wiggliness’ (spline variance parameter).

Table A15

Summary statistics of a Bayesian hierarchical generalized additive mixed model (HGAM) for the social integration of females in their grooming networks (eigenvector centrality), using a zero-one-inflated beta distribution

Effect	Parameter	Estimate	Estimate error	Lower 95% CI	Upper 95% CI
Population level effects	s(time)	−0.12	0.5	−1.1	0.95
	s(scan.nb)	0.4	0.05	0.3	0.49
	s(NDVI)	−0.09	0.93	−1.94	1.71
	s(troop.nb)	0.26	0.91	−1.52	2.05
	s(rank)	1.35	0.7	−0.17	2.64
Smooth terms	sds(time)	0.27	0.28	0.01	1.04
	sds(time primiparous0)	0.15	0.12	0.01	0.44
	sds(time primiparous1)	0.76	0.28	0.36	1.45
	sds(primiparous)	1.26	1.01	0.24	4
	sds(ID)	0.8	0.1	0.63	1.01
	sds(troopID)	0.49	0.6	0.01	2.13
	sds(scan.nb)	3.45	2.18	1.19	8.97
	sds(troop.nb)	3.08	1.35	1.04	6.16
	sds(NDVI)	3.04	1.26	1.24	5.95
Family-specific parameters	Phi	5.93	0.24	5.49	6.42
	Zoi	0.09	0.01	0.07	0.1
	Coi	0.97	0.02	0.93	0.99
		Estimate	Estimate error	Q2.5	Q97.5
R^2 marginal		0.36	0.03	0.30	0.42

CI = credible interval; NDVI: normalized difference vegetation index; sd = standard deviation; ID: identity; s() = spline; smooth term sds() = spline ‘wiggliness’ (spline variance parameter).

Table A16

Summary statistics of a Bayesian hierarchical generalized additive mixed model (HGAM) for the number of strong grooming partners (degree) for primiparous females, using a Poisson distribution

Effect	Parameter	Estimate	Estimate error	Lower 95% CI	Upper 95% CI
Population level effects	Intercept	−1.25	0.99	−3.6	0.63
	s(time)	−0.09	0.54	−1.26	0.94
	s(scan.nb)	1.09	0.08	0.94	1.24
	s(NDVI)	0.13	0.72	−1.26	1.63
	s(troop.nb)	−0.25	0.67	−1.74	0.95
	s(rank)	1.02	0.89	−0.82	2.51
Smooth terms	sds(time)	0.3	0.25	0.02	0.96
	sds(time primiparous1)	0.12	0.1	0	0.37
	sds(time primiparous0)	0.5	0.35	0.03	1.3
	sds(primiparous)	1.19	1.05	0.15	4.02
	sds(ID)	0.46	0.09	0.3	0.66
	sds(troopID)	0.84	0.74	0.15	2.89
	sds(scan.nb)	4.83	2.97	1.82	12.43
	sds(troop.nb)	0.5	0.46	0.02	1.71
	sds(NDVI)	0.46	0.45	0.01	1.64
	sds(rank)	0.7	0.6	0.02	2.24
	sds(year)	0.25	0.19	0.02	0.71
		Estimate	Estimate error	Q2.5	Q97.5
R^2 marginal		0.30	0.06	0.19	0.42

CI = credible interval; NDVI: normalized difference vegetation index; sd = standard deviation; ID: identity; s() = spline; smooth term sds() = spline ‘wiggliness’ (spline variance parameter).

Table A17

Summary statistics of a Bayesian hierarchical generalized additive mixed model (HGAM) for the number of weak grooming partners (degree) for primiparous females, using a Poisson distribution

Effect	Parameter	Estimate	Estimate error	Lower 95% CI	Upper 95% CI
Population level effects	Intercept	2.7	0.43	1.73	3.69
	s(time)	0	0.19	−0.44	0.36
	s(scan.nb)	0.38	0.02	0.35	0.41
	s(NDVI)	1.1	0.74	−0.35	2.6
	s(troop.nb)	0.6	0.4	−0.27	1.4
	s(rank)	0.01	0.3	−0.68	0.52
Smooth terms	sds(time)	0.1	0.09	0	0.33
	sds(time primiparous1)	0.04	0.03	0	0.12
	sds(time primiparous0)	0.09	0.05	0.01	0.22
	sds(primiparous)	0.55	0.65	0.03	2.46
	sds(ID)	0.16	0.02	0.13	0.21
	sds(troopID)	0.14	0.28	0	0.81
	sds(scan.nb)	2.79	1.99	0.83	7.67
	sds(troop.nb)	1.56	0.57	0.74	2.88
	sds(NDVI)	0.27	0.19	0.03	0.72
	sds(rank)	0.16	0.16	0.01	0.58
	sds(year)	0.15	0.08	0.07	0.33
		Estimate	Estimate error	Q2.5	Q97.5
R^2 marginal		0.32	0.06	0.24	0.47

CI = credible interval; NDVI: normalized difference vegetation index; sd = standard deviation; ID: identity; s() = spline; smooth term sds() = spline ‘wiggliness’ (spline variance parameter).

Table A18

Summary statistics of a Bayesian hierarchical generalized additive mixed model (HGAM) for the social integration of primiparous females in their grooming networks (eigenvector centrality), depending on node removal, using a zero-one-inflated beta distribution

Effect	Parameter	Estimate	Estimate error	Lower 95% CI	Upper 95% CI
Population level effects	Intercept	0.03	0.36	−0.71	0.93
	eigen_mod_s	−0.24	0.12	−0.47	0
	eigen_mod_w	−0.09	0.1	−0.29	0.11
	eigen_mod_all	−0.59	0.09	−0.77	−0.4
	primiparous	0.14	0.18	−0.21	0.49
	scan.nb	0.13	0.08	−0.02	0.31
	troop.nb	0.25	0.12	0.02	0.51
	NDVI	0.12	0.11	−0.06	0.36
	Rank	−0.08	0.06	−0.21	0.04
	eigen.start	0.87	0.06	0.74	0.99
	eigen_mod : primiparous	−0.19	0.33	−0.86	0.47
	eigen_mod_w : primiparous	−0.11	0.25	−0.59	0.39
	eigen_mod_all : primiparous	−0.05	0.24	−0.53	0.41
Family-specific parameters	Phi	8.38	0.6	7.23	9.56
	Zoi	0.06	0.01	0.04	0.08
	Coi	0.96	0.03	0.87	1
		Estimate	Estimate error	Q2.5	Q97.5
R^2 marginal		0.59	0.02	0.55	0.63

CI = credible interval; NDVI: normalized difference vegetation index; sd = standard deviation; ID: identity; s() = spline; smooth term sds() = spline ‘wiggliness’ (spline variance parameter).