



Consistency in social network position over changing environments in a seasonally breeding primate

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Abstract

Social network analysis has become increasingly used to investigate the consequences of individuals' social tendencies in recent years; however, the question of whether individuals are consistent in their social network position over time or situations has received comparatively scant attention. Knowledge of the degree to which individuals are stable in their social behavior can improve our understanding the fitness consequences of processes such as the transmission of disease and social information through networks, as well as the evolution of social behavior and social structure in general. Here, I investigated individual consistency in social behavior in wild vervet monkeys (*Chlorocebus pygerythrus*) residing in a highly seasonal habitat. I constructed grooming networks for three time periods characterized by diverse environmental conditions and explored the repeatability of seven network metrics as well as the effects of sex and dominance rank on these metrics. Both female and male vervets were highly consistent in three correlated, weighted measures of social connectedness—grooming in-strength, out-strength, and eigenvector centrality, and in-degree was moderately repeatable in both sexes. In contrast, only males were consistent in their out-degree and clustering coefficient, and there was no evidence of consistency in betweenness for either sex. High-ranking females had higher in-degree and in-strength scores, and high-ranking males had lower out-degree and out-strength, but controlling for dominance rank did not affect the findings regarding the repeatability of any metric. These results add to the small number of studies that have explored the temporal and situational stability of social network phenotypes in wild animals.

Significance statement

Relatively few animal social network studies have examined whether individuals are consistent in the positions that they occupy within networks. Determining the degree to which individuals are consistent in their social network characteristics over time and across naturally changing conditions is necessary for a better understanding of the ecology and evolution of social behavior. In this study, I examined individual consistency in several components of social network position in vervet monkeys residing in a highly seasonal environment. I also evaluated the effects of sex and dominance rank on these measures of sociality. I found that both male and female vervets were consistent in most measures of direct connectedness in grooming networks across seasons, but metrics capturing indirect social connections were overall less repeatable. Controlling for the effects of dominance rank on sociality measures did not change these results.

Keywords Repeatability · Sociability · Behavioral consistency · Social behavior · Seasonal changes · *Chlorocebus pygerythrus*

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Introduction

In recent years, social network analysis has become a commonly used framework for investigating relationships between individual behavior and social processes in animal societies (Kurvers et al. 2014; Pinter-Wollman et al. 2014; Croft et al. 2016). One topic of particular interest for behavioral ecologists concerns the advantages and disadvantages that individual animals experience when occupying different social network positions, and how these may impact fitness (Wey

et al. 2008; Sih et al. 2009; Croft et al. 2016). Individual differences in social network characteristics have been associated with variation in infant and juvenile survival (Stanton and Mann 2012; Brent et al. 2013; Cheney et al. 2016), reproductive success (McDonald 2007; Oh and Badyaev 2010; Lea et al. 2010; Formica et al. 2012; Wey and Blumstein 2012; Farine and Sheldon 2015), and longevity (Lea et al. 2010) in free-ranging animal populations. The structure of social networks and individuals' position within these networks can additionally influence the transmission of parasites and pathogens (Hamede et al. 2009; VanderWaal et al. 2014; Craft 2015; Rimbach et al. 2015; Friant et al. 2016), as well as social information (Atton et al. 2014; Aplin et al. 2015a; Farine et al. 2015; St Clair et al. 2015).

Variation in social network position may be subject to selection (Wilson et al. 2013; Aplin et al. 2015b), given that network metrics may be heritable (humans: Fowler et al. 2009; *Marmota flaviventris*: Lea et al. 2010; *Macaca mulatta*: Brent et al. 2013). While studies that quantify the heritability of network position are important for understanding the evolution of variation in social behavior, they are restricted to populations for which detailed genetic or pedigree information are available. By contrast, no additional data—apart from behavioral interactions or associations themselves, collected over repeated time periods—are required to examine consistency in individual-level social network measures over time. The animal personality literature provides a theoretical and methodological framework for examining consistency in individuals' behavior across time and contexts (Réale et al. 2007; Bell et al. 2009; Dall and Griffith 2014), and this framework can also be applied to social network measures (Wilson et al. 2013; Aplin et al. 2015b). Examining individual consistency in social network position improves our understanding of the factors shaping social networks and of how social network position is likely to influence fitness (Krause et al. 2010; Wilson et al. 2013; Farine and Whitehead 2015; Formica et al. 2017).

To date, only a handful of studies have examined individual consistency in social network traits in animal populations (Jacoby et al. 2014; Aplin et al. 2015b; Best et al. 2015; Frumkin et al. 2016; Formica et al. 2017). Prior studies reporting consistency in social network traits that capture variation in prosocial or affiliative behavior have interpreted these as evidence of personality differences in “sociability” or “sociality” (Brent et al. 2013; Jacoby et al. 2014; Aplin et al. 2015b; Best et al. 2015). Although sociability is proposed to be one of the five major axes of animal personality (Réale et al. 2007), individual differences in social traits have received very little attention in the animal personality literature compared to variation in traits such as boldness, exploration, activity, and aggression.

Here, I investigated the degree of individual consistency in social network position in a group of wild vervet monkeys

over the course of a year characterized by differing social and ecological environments. The study population resides in a highly seasonal habitat in central South Africa. Vervets mate primarily during the autumn (March–May) and early winter months (June–August) and births occur in the late spring (September–November) and early summer (December–February). There is therefore intra-annual variation in both ecological and social conditions that adult female and male vervets experience. Female vervets are philopatric and remain in their natal groups throughout their lives, while males emigrate around the age of sexual maturity (4–5 years) and thereafter transfer between groups every few years (Henzi and Lucas 1980; Cheney et al. 1988; van de Waal et al. 2013a).

In this study, I considered affiliative social networks based on grooming interactions. Grooming is a commonly examined social behavior in studies of nonhuman primates, and the most commonly studied affiliative behavior in research on vervets specifically (e.g., Seyfarth 1980; Seyfarth and Cheney 1984; Fruteau et al. 2009; Henzi et al. 2013; van de Waal et al. 2013b). Social interactions that involve body contact, such as grooming, are also generally considered to be more reliable indicators of individual's social preferences compared to alternative measures of affiliation such as spatial proximity (Pasquaretta et al. 2014). I investigated consistency in individuals' positions in grooming network.

I further explored sex differences in social network metrics, as well as effects of dominance rank on social behavior for each sex. Although I had no predictions as to whether males or females would be more consistent in their social network positions across seasons, I predicted that females would have higher values for network metrics that capture high rates of social interaction, as vervets are considered a typical “female-bonded” cercopithecine species with the highest rates of affiliative interactions among adults taking place between females (Cheney 1992; Cords 2012). Dominance hierarchies are also important for several aspects of vervet monkey behavior, both among females and males (Cheney and Seyfarth 1992). Therefore, I additionally explored the influence of dominance rank on social network position and evaluated the potential effects of dominance rank on social network consistency. Finally, to improve the interpretability of the results, I explored the degree of collinearity between different network measures (Brent et al. 2013).

Materials and methods

Study site and subjects

Fieldwork was conducted at the Soetdoring Nature Reserve in the Free State Province, South Africa (28° 50' S, 26° 2' E). The reserve occurs in a summer rainfall zone, and

precipitation averages 400–600 mm per annum (Janecke 2002). The climate is classified as arid steppe (Kottek et al. 2006). The predominant vegetation is grassland, with riparian vegetation dominated by *Acacia karoo* flanking the Modder River that bisects the reserve (Janecke 2002; Janecke and du Preez 2005). Six vervet groups live along the river. A large group that averaged ~60 individuals from mid-2011 to the end of 2012 are the subjects of this study. The study group was habituated to human observers over a period of 5 months beginning in July 2011, and behavioral data were collected on all adult and subadult individuals present between March and December 2012. All adults and subadults in the group (17 females and 17 males over the study period) were individually identified based on distinctive facial and body features (Błaszczuk 2017). Juveniles were not all individually recognizable and hence were not included in the study.

Observational data collection

Six observers (five field assistants and I) collected observational behavioral data over the course of the study. All field assistants underwent a period of training that lasted at least 6 weeks, after which we conducted joint focal watches and assessed interobserver reliability monthly. We used 20-min continuous focal animal samples (Altmann 1974) to record all grooming bouts that lasted at least 5 s. The duration of all grooming bouts was recorded to the nearest second. If grooming stopped for five or more seconds, we ended the grooming bout and began a separate bout when grooming resumed. We recorded all dominance interactions involving the focal animal during focal follows, and additionally recorded observations of decided dyadic agonistic interactions between all study subjects using ad libitum sampling (Błaszczuk 2017). Data were recorded using Pendragon Forms software on Palm TX (Palm, Inc.) handheld data loggers. Blind data recording was not possible because the study involved focal animals in the field.

Data were collected during full-day group follows, and observation days were divided into four equal time blocks, the length of which depended on the time of year. In the winter, we collected data from 0800 to 1600 h and time blocks were each 2 h long. In the summer, we collected data from 0600 to 1800 h and time blocks were 3 h long. We aimed to collect at least one focal sample for each individual per day and to balance individuals' samples as equally as possible for each month, both within and over the four time blocks. No individual was sampled more than three times per day (range of focal samples collected/animal/day: 0–3), and if more than one focal sample on a given individual was collected in a given day, this was always in a different time block and separated from the previous sample by at least 2 h. Observers selected which animal to sample based on whether or not an individual had already been sampled that day and on the total

number of focal minutes that had been amassed for each individual during the time block for that month.

During a focal sample, if an individual went out of view for more than a minute, observers recorded the time that they went out of view, rounding off to the nearest whole minute. If the animal came back into view within 5 min, sampling was resumed until 20 min after the start of the focal sample. The number of minutes the animal spent out of view (1–5 min) was subtracted from 20 min to give the focal sample length. All samples where an animal was observed for less than 5 min were discarded. Focal samples therefore ranged from 5 to 20 min in length, and focal sample lengths thus reflect the actual duration that a focal animal was in view. We collected a total of 2169 focal observation hours for those individuals present in the group for the entire period of March–December 2012 (80.7–84.6 h total focal hours/individual: 18.3–20.6 h/animal in Season 1; 35.5–37.9 h/animal in Season 2; 24.7–28.2 h/animal in Season 3; seasons are described below). Over this time, we recorded a total of 4294 grooming bouts between the 26 study subjects (mean (SD) bouts per individual/period: 59.4 (29.4) in Season 1, 149.9 (55.5) in Season 2, 97.6 (50.9) in Season 3; total 330.3 (137.1) bouts/individual).

Seasons

For social network analyses, I divided the study period between March and December 2012 into three time blocks that tracked sociodemographic changes and seasonal environmental differences as follows. The first time block ("Season 1", S1), March–May, encompassed most of the mating season (generally April–June: Henzi and Lucas 1980; Cheney and Seyfarth 1983; McFarland et al. 2014). This period was also characterized by demographic changes due to male intergroup migration. Three adult males and one subadult male left the study group between March and May, and three adult males migrated in from neighboring groups in April. Daily temperatures were high in March, and days remained warm throughout April and most of May, with cooler temperatures in late May. This time period was characterized by relatively high food availability: many of the vervets' preferred plant food species (e.g., *Diospyros lycioides*, *Ziziphus mucronata*, *Opuntia* sp.) were in fruit, and *Acacia* trees bore abundant seed pods.

The second time block, "Season 2" (S2), comprised the austral winter months, from June to August, and September. The winter months were characterized by frequent below-freezing overnight temperatures, cold mornings with frost, and mild temperatures in the afternoon. Through most of the winter months, vervets fed on desiccated fruit (primarily *Diospyros lycioides* and *Ziziphus mucronata*) and acacia seeds remaining on deciduous trees and bushes that were dormant over the winter. Temperatures got warmer in September and

although there was new growth in the form of new leaves and flowers, there was little fruit available.

The final time block (S3), from October to December, comprised the birth season, with 14 births occurring in October and November, and one female still visibly pregnant at the end of the study in mid-December. Temperatures and rainfall increased between October and December. November 1 marks the beginning of the warm season in central South Africa (WeatherSpark.com). The warm season is characterized by high average daily high temperatures and the highest amount of precipitation for the year, most of which occurs as thunderstorms.

Social networks

Individuals' social network metrics may be affected by the size of the social group and by sampling effort (Aplin et al. 2015b; Farine and Whitehead 2015). Only the subset of individuals that were present over the entire study period from March to December were therefore included in networks and social networks were based on grooming rates. For each network, I extracted all grooming interactions between study individuals and converted total dyadic grooming durations (in seconds) to rates by dividing them by the sum of each individual's total observation seconds for the season, thus correcting for differences in observation time (Farine 2015). I did this separately for grooming in each direction for all dyads, i.e., separating the rate of grooming given versus received for each dyad. I constructed one directed, weighted network (with grooming rate as the weight) for each season using the "igraph" package (Csárdi and Nepusz 2006) in the R statistical computing environment (version 3.3.3., R Core Team 2017).

I calculated seven node-level metrics for each individual in each season. These were an individual's in-degree, out-degree, in-strength, out-strength, betweenness, eigenvector centrality, and clustering coefficient. In-degree and out-degree measure the number of partners that an individual was groomed by and the number of partners that they groomed, respectively, and in-strength and out-strength, respectively, measure an individual's overall rate of being groomed by and of grooming others (Croft et al. 2008). An individual animal's betweenness is the number of shortest paths linking pairs of other individuals in the network that pass through the individual (Freeman 1977), and its eigenvector centrality is a composite measure of how well connected an individual is within a network, taking into account both direct and indirect ties. A high eigenvector centrality can result from an individual having a large number of strong connections or from being connected to social partners who themselves are well connected (Wasserman and Faust 1994). Finally, the local clustering coefficient measures how well connected the social partners of an individual are to each

other, with high clustering coefficients representing a high degree of "cliquishness" (Newman 2003).

I chose the seven network metrics described above because they have all been commonly quantified and examined in studies of primates, where they have been related to variables such as foraging behavior and within-group spatial position (King et al. 2011; Josephs et al. 2016), infection with pathogens (Rushmore et al. 2013; Rimbach et al. 2015; Balasubramaniam et al. 2016; Friant et al. 2016), lice load (Dubosq et al. 2016), over-winter survival and thermoregulation (McFarland et al. 2015; Lehmann et al. 2016), reproductive success (Brent et al. 2013; Gilby et al. 2013), and infant survival (Cheney et al. 2016). These measures of social network position have furthermore all been associated with fitness outcomes or pertinent physiological and behavioral variables in several other animal studies (reviewed in Lehmann et al. 2016; Croft et al. 2016).

Dominance hierarchies

Dominance hierarchies were constructed using data on all decided dominance interactions (Błaszczuk 2017) using the Elo-rating method (Elo 1978; Albers and de Vries 2001). I used the R package "EloRating" (Neumann and Kulik 2014) with the starting score set to 1000 and k (the arbitrary number of points that an individual gains or losses as a result of an interaction) set to 100 (Neumann et al. 2011). Individuals' Elo-ratings on the last day of a season were converted to ranks to give standardized dominance scores for each season (Neumann et al. 2011).

Statistical analysis

I explored the degree to which individuals were consistent in their social network position across seasons by calculating the repeatability, R , of each social network metric. Repeatability is a measure of the proportion of phenotypic variation that is accounted for by variation between individuals (Nakagawa and Schielzeth 2010). I used linear mixed effects models (LMMs) implemented in the R package "rptR" version 0.9.2 (Stoffel et al. 2017) to calculate estimates of repeatability of social network metrics and associated 95% confidence intervals (CIs). I calculated repeatability for each metric for the entire mixed-sex sample ($N = 26$) as well as for females ($N = 16$) and males ($N = 10$) separately, but all analyses were based on networks comprising all nonjuvenile individuals present in the group. I included "Season" as a random effect in all models and all repeatability estimates are therefore "adjusted repeatabilities" within the framework set out by Nakagawa and Schielzeth (2010). Repeatability was calculated as the variance of random individual effect divided by the sum of the random individual effect variance and the residual (within-individual) variance (Nakagawa and Schielzeth 2010).

Residuals of LMMs were inspected for normality and homogeneity of variance. Out-strength values, as well as eigenvector centralities for only the males-only model, were log-transformed to meet model assumptions (Nakagawa and Schielzeth 2010). For betweenness, which is a count (number of shortest paths passing through a node) and for which assumptions of normality and homogeneity of variance in residuals were not met, I used generalized linear mixed effect models (GLMMs) with a Poisson distribution implemented in the rptR package. The rptR package accounts for overdispersion in Poisson data by adding an observational level random effect (Stoffel et al. 2017).

Because individuals' network metrics are not independent of those of other individuals in the network, I used node-based permutation tests to evaluate the significance of repeatability estimates for each metric (Farine 2017). I randomized the individual identities of each node from each seasons' network and then estimated the repeatability of metrics from the resulting random networks using the same models implemented in rptR. I repeated this process 1000 times, and compared the repeatability estimate based on observed data to the distribution of random repeatability estimates. I calculated P values as twice the proportion of random repeatability estimates that exceeded observed estimates; results are therefore significant at $P = 0.05$ when less than 2.5% of the random repeatability values are more extreme than the observed repeatability value (Farine 2017). Collinearity between each pair of network measures was assessed using Spearman rank correlations (Brent et al. 2013). Although some network metrics were highly correlated with each other, I include results for all seven metrics below as this allows more direct comparisons to be made with other animal social network studies reporting repeatability estimates (or sex or rank effects) for different metrics.

As dominance rank could potentially affect estimates of repeatability, I repeated all of the analytical steps described above except with dominance ranks included in models as a fixed effect. The resulting repeatability estimates are thus additionally adjusted to control for effects of rank. Given that the effect of dominance status on social behavior may differ by sex (Cheney and Seyfarth 1992), I conducted analyses that include dominance rank on females and males separately.

I additionally used (G)LMMs to explore sex differences and the effects of dominance rank on all social network metrics. To explore differences in social behavior between sexes, I constructed mixed models for each metric using the mixed-sex sample of individuals and included "sex" as a fixed effect in addition to the random effects of individual and season. For the Poisson GLMM for betweenness, I also included an observational level random effect to account for overdispersion (Harrison 2014). I again conducted independent node permutation tests to assess the statistical significance of sex differences, randomizing the "sex" attribute of all individuals 1000

times and then fitting the same model on the randomized data. Two-tailed P values were calculated as before, taking the proportion of instances coefficient values from permuted data were more extreme than the observed coefficients (Farine 2017).

Finally, I carried out the same procedure to investigate effects of dominance rank. I used the same models as for calculating adjusted repeatability including the effect of dominance rank, only now extracting the coefficient value of the rank effect for models fit to the observed data. I analyzed males and females separately as before. I performed independent node permutations, randomizing the dominance rank attribute of nodes for each season 1000 times, fit models, and extracted coefficient values for the randomized data, which I compared against observed coefficient values for significance testing as described above. All mixed models were fit in the R package "lme4" version 1.1–13 (Bates et al. 2015).

Data availability The datasets analyzed for the study are included as supplementary material.

Results

All direct metrics co-varied positively with each other and with the composite metric eigenvector centrality, such that individuals with high degrees also tended to have high strengths and had a high eigenvector centrality (Table 1). Clustering coefficient was however negatively correlated with each of the direct metrics and with eigenvector centrality, and there was no correlation between betweenness and any social network measure. All node-based measures except for betweenness were significantly repeatable across season-based social networks (Fig. 1) for the complete, mixed-sex sample (Table 2). In-degree, in-strength, out-strength, and eigenvector centrality were also all repeatable in both males and females considered separately, while out-degree and clustering coefficient were repeatable for males but not for females. Individuals were not at all consistent in their betweenness. For those network measures that were repeatable for the complete sample, repeatabilities ranged from $R = 0.31$ (in-degree) to $R = 0.83$ (out-strength) (Fig. 2). Results where P values from node permutation tests were close to 0.05 or whose confidence intervals either overlapped zero or had lower confidence bounds that were close to zero, i.e., in-degree in males and clustering coefficient in the complete sample and in males, should be treated with caution. In no case did controlling for an effect of dominance rank lead to a qualitative change in repeatability results.

Individuals were more consistent in measures reflecting outward-directed grooming compared to grooming received both in terms of degree (in-degree vs. out-degree: 0.31 vs. 0.36) and strength (in-strength vs. out-strength: 0.70 vs.

Table 1 Spearman correlation coefficients between each pair of social network metrics with associated *P* values

	In-degree	Out-degree	In-strength	Out-strength	Eigenvector centrality	Clustering coefficient	Betweenness
In-degree	X	0.71 (<0.001)	0.69 (<0.001)	0.46 (<0.001)	0.56 (<0.001)	−0.29 (0.01)	0.05 (0.69)
Out-degree		X	0.36 (0.001)	0.75 (<0.001)	0.53 (<0.001)	−0.39 (<0.001)	0.13 (0.24)
In-strength			X	0.44 (<0.001)	0.82 (<0.001)	−0.27 (0.02)	−0.08 (0.49)
Out-strength				X	0.80 (<0.001)	−0.47 (<0.001)	−0.07 (0.51)
Eigenvector centrality					X	−0.31 (<0.01)	−0.08 (0.51)
Clustering coefficient						X	0.00 (0.99)
Betweenness							X

0.83). Overall, strength metrics were more highly repeatable than degree metrics.

There were significant sex differences for all network metrics except for betweenness (Table 3). Females had higher in- and out-degree, in- and out-strength, and eigenvector centralities, while males had higher clustering coefficients. Females had consistently higher median values than males for in- and out-degree, in- and out-strength, and eigenvector centrality across all seasons, while males had a higher median clustering coefficient in all seasons (Fig. 3). There was no consistent pattern of differences between the sexes for betweenness centrality.

There was no instance in which dominance rank was predictive of the same measure of social network position for both males and females (Table 4). Among females, higher dominance rank was associated with higher in-degree, in-strength, and eigenvector centrality. Among males, higher rank was associated with a lower out-degree and lower out-strength. The effect of rank on male clustering coefficients was in the opposite direction, with dominant males having slightly higher clustering coefficients, but this effect was marginal.

Discussion

Vervet monkeys were consistent in several aspects of social network position over three time periods with varying social and ecological environments. Three of the four positively correlated network measures reflecting direct interactions of individuals with their neighbors—namely, in-degree, in-strength and out-strength—were repeatable in the mixed sex sample as well as in each sex, and out-degree was repeatable only among males when males and females were analyzed separately. Of the three measures of indirect connectedness, only eigenvector centrality—a composite measure reflecting direct as well as indirect connections—was repeatable in each sample considered, and clustering coefficient was only repeatable in the mixed-sex and males-only samples. Individuals were not at all consistent in their betweenness centrality across seasons.

The magnitudes of repeatability estimates for degree and strength centrality metrics in this study (range 0.31–0.83) are similar to those found for degree and strength in proximity networks in great tits, *Parus major* (range 0.41–0.64), using a similar analytical approach (Aplin et al. 2015b). These

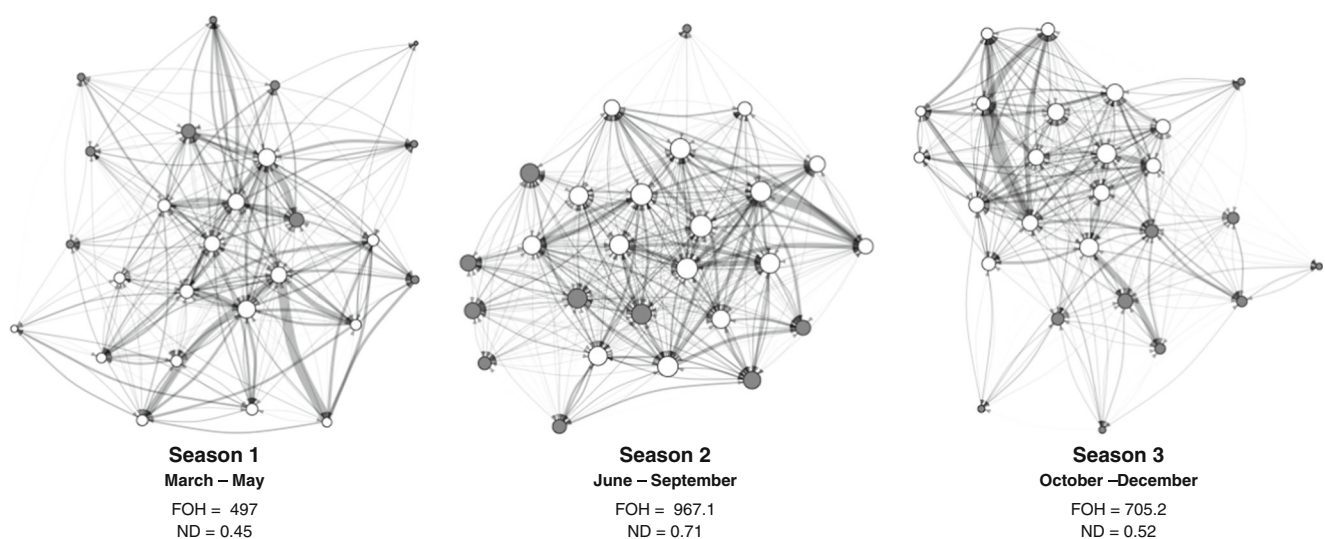


Fig. 1 Social networks for each of the three seasons including only individuals present across all three time periods ($N=26$). White circles are females and gray circles are males. Arrowheads show directionality of

grooming interactions. Node size is scaled by unweighted degree, and edge widths are scaled by grooming time as a proportion of observation time for a dyad. *FOH* total focal observation hours, *ND* network density

Table 2 Repeatability estimates (R) and 95% confidence intervals (CI) for seven social network measures over three seasons. Repeatabilities are presented for the complete mixed-sex sample as well as estimates calculated for females ($N=16$) and males ($N=10$) separately

Metric	Sample	R	CI	<i>P</i>
In-degree	All	0.31	0.11–0.62	< 0.001
	Females	0.22	0.03–0.59	0.006
	with rank	0.25	0.05–0.61	0.002
	Males	0.26	0–0.62	0.022
	with rank	0.27	0–0.66	0.036
Out-degree	All	0.36	0.13–0.66	< 0.001
	Females	0.16	0–0.47	0.082
	with rank	0.17	0–0.51	0.090
	Males	0.31	0.05–0.72	0.006
	with rank	0.26	0.03–0.71	0.010
In-strength	All	0.70	0.5–0.82	< 0.001
	Females	0.66	0.36–0.84	< 0.001
	with rank	0.50	0.13–0.75	< 0.001
	Males	0.56	0.11–0.81	0.006
	with rank	0.58	0.11–0.83	< 0.001
Out-strength	All	0.83	0.69–0.91	< 0.001
	Females	0.62	0.32–0.81	< 0.001
	with rank	0.63	0.34–0.81	< 0.001
	Males	0.78	0.39–0.92	< 0.001
	with rank	0.78	0.44–0.93	< 0.001
Eigenvector centrality	All	0.71	0.5–0.84	< 0.001
	Females	0.54	0.2–0.74	< 0.001
	with rank	0.42	0.08–0.68	0.010
	Males	0.45	0.12–0.83	< 0.001
	with rank	0.49	0.14–0.85	< 0.001
Clustering coefficient	All	0.35	0.08–0.56	0.004
	Females	0.04	0–0.29	0.690
	with rank	0.07	0–0.36	0.534
	Males	0.44	0–0.74	0.044
	with rank	0.50	0.03–0.8	0.028
Betweenness	All	0.02	0–0.25	0.802
	Females	0.00	0–0.28	0.854
	with rank	0.00	0–0.27	0.572
	Males	0.28	0–0.62	0.102
	with rank	0.16	0–0.53	0.478

P values are from independent node permutation tests. Repeatability estimates that are significant at the $P < 0.05$ level are highlighted in italics. Adjusted repeatability estimates controlling for the effect of dominance rank among females and males are also shown

repeatability estimates can all be considered as comparatively high, given that a meta-analysis of the repeatability in a variety of taxa found the average repeatability of a range of behaviors in to be 0.37 (Bell et al. 2009). The magnitudes of the significant repeatability estimates in the present study are also generally higher than the repeatability of boldness towards novel objects (0.37) in this population of vervets (Błaszczuk 2017).

Higher repeatability values could be expected for network measures that capture behavior over which an individual has more control (Lea et al. 2010; Formica et al. 2017). Thus, metrics reflecting outgoing connections, such as giving grooming, may be expected to be more repeatable than those measuring incoming interactions, such as receiving grooming. Likewise, metrics reflecting interactions in which an individual is directly involved are expected to be more repeatable than those capturing indirect or higher-order interactions (Lea et al. 2010; Formica et al. 2017). Lea et al. (2010) explored the heritability (closely conceptually related to repeatability: Boake 1989; Bell et al. 2009) of social network traits in marmots (*Marmota flaviventris*) and found that indirect network metrics were not heritable, but neither were direct metrics reflecting initiated interactions, such as out-degree. By contrast, direct metrics capturing received social interactions (e.g., in-degree) were heritable (Lea et al. 2010). In a social network study on fungus beetles, *Bolitotherus cornutus*, Formica et al. (2017) tested the hypothesis that a direct network metric (strength) would be repeatable, and that two metrics reflecting indirect connections (betweenness and clustering coefficient) would not be. They found that strength and betweenness were similarly repeatable, while clustering coefficient was not repeatable. The results of the present study in vervets provide some support for these authors' hypotheses: vervets were generally more consistent in behavior captured by direct than by indirect metrics.

Other animal social network studies that have examined consistency in social network measures provide further mixed support for the hypothesis that metrics reflecting behavior over which an individual has greater levels of control should be more repeatable. In wild great tits (*Parus major*), degree and strength had higher repeatability estimates than betweenness and clustering coefficient within three winter sampling seasons as well as across seasons (Aplin et al. 2015b). However, wild female kangaroos, *Macropus giganteus*, showed greater consistency in their clustering coefficient than strength in association networks (Best et al. 2015), and wild marmots (*Marmota flaviventris*) were similarly consistent in their in- and out-strength in directed social aggression networks (Blumstein et al. 2013).

In a recent study of wild chacma baboons, *Papio ursinus*, Cheney et al. (2016) explored individual consistency in networks constructed from a composite of affiliative behaviors ("composite sociality index," CSI, scores). They examined four indirect network metrics, namely betweenness, eigenvector centrality, clustering coefficient, and reach, and found evidence of consistency in eigenvector centrality only. The findings of Cheney et al. (2016) are therefore similar to those of the present study in vervets, where females were also consistent in their eigenvector centralities in affiliative networks but not in other indirect measures of social connectedness. Cheney et al. (2016) further found that eigenvector centrality

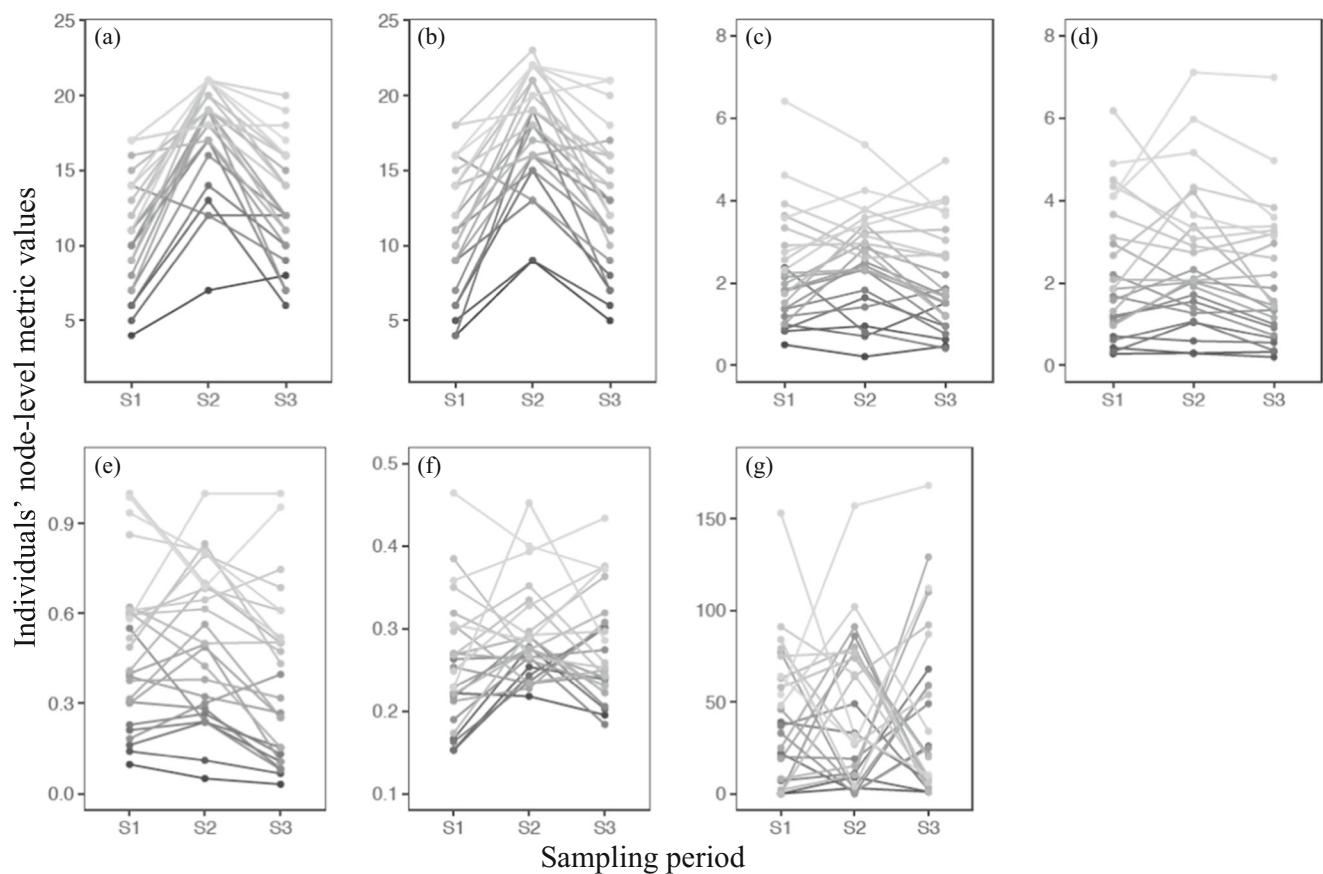


Fig. 2 Vervets' social network metrics across three environmentally and sociodemographically distinct time periods (S1–S3). Individuals are points and lines connect their scores in each season. Seven social network measures are shown: **a** unweighted in-degree ($R=0.31$), **b** unweighted out-degree ($R=0.36$), **c** in-strength ($R=0.70$), **d** out-

strength ($R=0.83$), **e** eigenvector centrality ($R=0.71$), **f** clustering coefficient ($R=0.35$), and **g** betweenness centrality ($R=0.02$). All measures except for betweenness were significantly repeatable for the complete mixed-sex sample ($N=26$)

was a better predictor of offspring survival than was the strength of females' dyadic social bonds (Silk et al. 2003). Among free-ranging rhesus macaques (*Macaca mulatta*), Brent et al. (2013) investigated the heritability in- and out-strength in grooming and aggression networks and strength in proximity networks, and betweenness and eigenvector centrality in all three types of networks, and found that grooming

betweenness and aggression out-strength were significantly heritable (Brent et al. 2013). They also found that proximity eigenvector centrality was associated with female reproductive success, with number of offspring increasing as proximity eigenvector increased.

In line with my prediction that females would have higher values than males for network metrics that capture high rates of social interaction, female vervets had higher values for all of the positively correlated degree and strength measures and for eigenvector centrality. Females thus tended to have more and stronger social connections, and to be connected to other individuals who themselves were well connected in the network. In contrast, males had higher clustering coefficients, indicating that their grooming behavior was more confined to interconnected subgroups or small cliques. Clustering coefficient was also negatively correlated with all degree, strength, and eigenvector centrality. Overall, then, males were less broadly and strongly integrated into grooming networks than were females.

Vervet monkeys are considered to be a typical “female-bonded” cercopithecine species, with the strongest and most enduring social relationships found between females (Cheney

Table 3 Coefficient estimates for sex differences from mixed models of seven social network metrics. P values are from independent node permutation tests. The reference category for the sex effect estimates is females. Individual identity and season were included as random effects in all models

Metric	Estimate (sex)	SE	P
In-degree	− 3.296	1.112	0.006*
Out-degree	− 4.488	1.130	0.002*
In-strength	− 1.194	0.397	0.006*
Out-strength	− 1.151	0.235	< 0.001**
Eigenvector centrality	− 0.360	0.065	< 0.001**
Clustering coefficient	0.052	0.018	0.004*
Betweenness	0.200	0.367	0.622

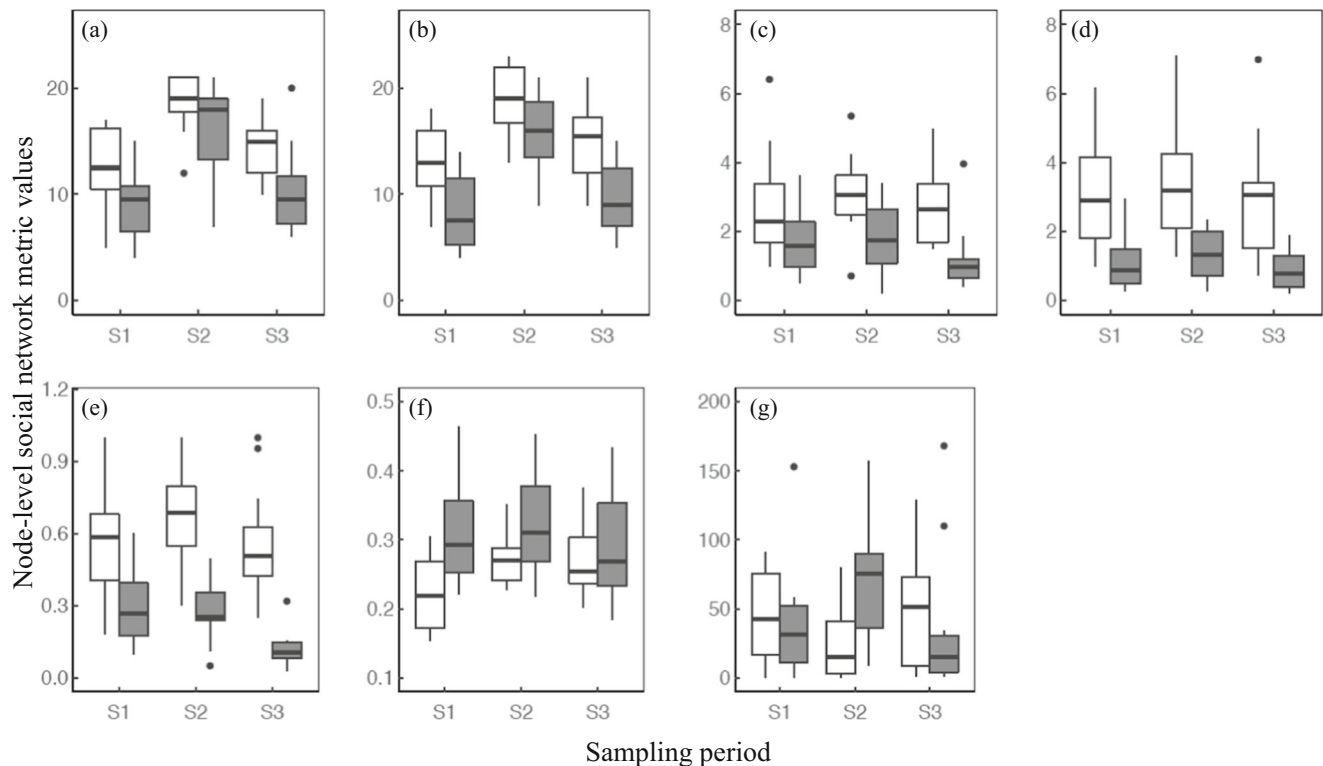


Fig. 3 Illustrative boxplots showing median values and interquartile ranges (IQR) for females (white) and males (gray) for **a** in-degree, **b** out-degree, **c** in-strength, **d** out-strength, **e** eigenvector centrality, **f** clustering coefficient, and **g** betweenness in each season. Whiskers

extend to the largest and smallest value no further than $1.5 \times \text{IQR}$ from the upper and lower hinges, respectively, outlying values beyond this range are shown as points

1992; Cords 2012). In other female-philopatric cercopithecine species such as baboons, measures of sociability have been linked to linked to increased offspring survival (*Papio*

cynocephalus: Silk et al. 2003; *Papio ursinus*: Silk et al. 2009; Cheney et al. 2016) and longevity (*P. ursinus*: Silk et al. 2010; *P. cynocephalus*: Archie et al. 2014) for females. Additionally, female vervets (*C. pygerythrus*) with a greater degree in grooming networks were more effective in maintaining their core body temperature under periods of cold thermal stress (McFarland et al. 2015). For species such as vervets that live in matrilineal societies, the proclivity to be social is suggested to be particularly adaptive for females, and females are expected to invest more in affiliative behavior such as grooming compared to males (Silk et al. 2006; Silk 2007). Nonetheless, social integration is also demonstrably important for males in some cercopithecine primate species (*Macaca assamensis*: Schülke et al. 2010; *Macaca sylvanus*: McFarland and Majolo 2013; Lehmann et al. 2016). Indeed, another study of vervets found that grooming out-strength and in-strength were both associated with lower exposure to risky spatial positions for both female and male vervets (Josephs et al. 2016).

Other factors that commonly influence patterns of affiliative interactions in primate groups are dominance hierarchies and kinship (Silk 2007). In the present study, the effects of kinship could not be determined as familial relationships between group members were not known. The effects of rank on metrics capturing received grooming—in-degree and in-strength—among females in this study are, however, in line with previous

Table 4 Coefficient estimates for effects of dominance rank from mixed models of seven social network metrics, considering females ($N=16$) and males ($N=10$) separately. Ranks were reserve-scored for analyses, so higher values reflect a higher dominance rank. P values are based on independent node permutation tests

Metric	Sample	Estimate (rank)	SE	P
In-degree	Females	0.104	0.079	0.046
	Males	0.011	0.146	0.984
Out-degree	Females	-0.015	0.081	0.834
	Males	-0.269	0.123	0.002*
In-strength	Females	0.086	0.024	< 0.001**
	Males	-0.007	0.035	0.858
Out-strength	Females	0.004	0.014	0.658
	Males	-0.042	0.019	< 0.001**
Eigenvector centrality	Females	0.013	0.005	< 0.001**
	Males	-0.014	0.020	0.270
Clustering coefficient	Females	0.000	0.001	0.840
	Males	0.004	0.003	0.044
Betweenness	Females	-0.002	0.031	0.918
	Males	-0.076	0.047	0.090

research showing that high-ranking females receive more grooming than low-ranking individuals in vervet groups (Seyfarth 1980; Cheney and Seyfarth 1992). One hypothesis for this pattern is that grooming is traded for coalitionary support in agonistic interactions, and given that high-ranking individuals will be most valuable in this context, they should be most sought after as grooming partners (Seyfarth 1977; Seyfarth and Cheney 1984). Subordinates may also groom higher-ranking individuals in exchange for tolerance at feeding sites (Barrett et al. 1999).

Rank predicted outgoing social behavior rather than incoming interactions among male vervets. As in previous studies (Cheney and Seyfarth 1992), male vervets' dominance ranks were related to age in the present study: of the 10 males present throughout the study, three were classified as adults (Błaszczuk 2017) and two of these adult males were the alpha and beta male throughout the study period. Low-ranking, generally younger, males may invest in grooming to facilitate tolerance by dominant males, and may groom females at higher rates than high-ranking males potentially as a strategy to gain mating opportunities (Muller and Emery Thompson 2012).

Regardless of the factors underlying relationships between dominance rank and the patterning of social interactions, an important finding of the present study is that controlling for rank effects did not result in any qualitative differences in estimates of consistency of social network metrics. Vervets of both sexes were highly consistent in both in- and out-strength as well as eigenvector centrality, and both males and females showed moderate consistency in in-degree. Males were further consistent in their out-degree. These metrics could therefore be used as measures of social personality traits in vervets, labeled for example "gregariousness" in the case of degree and "sociability" in the case of strength (following Aplin et al. 2015b). By contrast, only equivocal evidence of consistency in clustering coefficient among males was found, and individuals were not at all consistent in their betweenness. These higher-order social network measures therefore do not seem to capture trait-like individual differences in social behavior that are stable over time and contexts among vervets, but may rather capture the ways in which individuals adjust their social behavior across changing environmental conditions.

The present study was conducted only on sexually mature individuals, the ages of adult individuals were not known, and the number of subadults versus adults within each sex was not large enough to test for differences between these two age classes. An interesting avenue for future research would be to examine the ontogeny of social network traits as well as consistency in social behavior over several years and ideally the entire lifespan, including juveniles and separating adults into younger and older adults, as individuals may also show differences in social behavior as they age (Almeling et al. 2016).

Understanding the degree to which individuals are consistent in their social behavior over time and across contexts is

important for improving our understanding of the ecological and evolutionary determinants and consequences of animal social networks (Wilson et al. 2013; Aplin et al. 2015b; Farine and Whitehead 2015). Evaluating the stability of social network measures may also have practical applications, for instance, if network analyses are used to plan vaccination or infectious disease treatment campaigns where individuals scoring highly on particular network metrics are targeted for interventions (Rushmore et al. 2014; Craft 2015; White et al. 2017). For example, if high grooming betweenness were found to be associated with increased disease transmission risk in vervets in a given season, it may not help to target high-betweenness individuals for treatment in a future season given that grooming betweenness is not a stable network trait among vervets. Given these practical applications as well as potential theoretical implications for understanding links between fitness and network structure, future animal social network studies should consider the issue of consistency in individuals' network measures over time and changing conditions.

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Compliance with ethical standards

Conflict of interest The author declares that they have no conflict of interest.

Ethical approval The observational protocols were approved by New York University's University Animal Welfare Committee (Protocol number 12-1391) and the study was conducted with the permission of the Department of Economic Development, Tourism and Environmental Affairs of the Free State Province in South Africa (Permit number 01/9912).

References

- Albers PCH, de Vries H (2001) Elo-rating as a tool in the sequential estimation of dominance strengths. *Anim Behav* 61(2):489–495. <https://doi.org/10.1006/anbe.2000.1571>
- Almeling L, Hammerschmidt K, Sennhenn-Reulen H, Freund AM, Fischer J (2016) Motivational shifts in aging monkeys and the

- origins of social selectivity. *Curr Biol* 26(13):1744–1749. <https://doi.org/10.1016/j.cub.2016.04.066>
- Altmann J (1974) Observational study of behavior: sampling methods. *Behaviour* 49(3):227–267. <https://doi.org/10.1163/156853974X00534>
- Aplin LM, Farine DR, Morand-Ferron J, Cockburn A, Thornton A, Sheldon BC (2015a) Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature* 518(7540):538–541. <https://doi.org/10.1038/nature13998>
- Aplin LM, Firth JA, Farine DR, Voelkl B, Crates RA, Culina A, Garroway CJ, Hinde CA, Kidd LR, Psorakis I, Milligan ND, Radersma R, Verhelst BL, Sheldon BC (2015b) Consistent individual differences in the social phenotypes of wild great tits, *Parus major*. *Anim Behav* 108:117–127. <https://doi.org/10.1016/j.anbehav.2015.07.016>
- Archie EA, Tung J, Clark M, Altmann J, Alberts SC (2014) Social affiliation matters: both same-sex and opposite-sex relationships predict survival in wild female baboons. *Proc R Soc B* 281(1793):20141261. <https://doi.org/10.1098/rspb.2014.1261>
- Atton N, Galef BJ, Hoppitt W, Webster MM, Laland KN (2014) Familiarity affects social network structure and discovery of prey patch locations in foraging stickleback shoals. *Proc R Soc B* 281(1789):20140579. <https://doi.org/10.1098/rspb.2014.0579>
- Balasubramaniam K, Beisner B, Vandeleeuw J, Atwill E, McCowan B (2016) Social buffering and contact transmission: network connections have beneficial and detrimental effects on *Shigella* infection risk among captive rhesus macaques. *PeerJ* 4:e2630. <https://doi.org/10.7717/peerj.2630>
- Barrett L, Henzi SP, Weingill T, Lycett JE, Hill RA (1999) Market forces predict grooming reciprocity in female baboons. *Proc R Soc Lond B* 266(1420):665–670. <https://doi.org/10.1098/rspb.1999.0687>
- Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *J Stat Softw* 67:1–48
- Bell AM, Hankison SJ, Laskowski KL (2009) The repeatability of behaviour: a meta-analysis. *Anim Behav* 77(4):771–783. <https://doi.org/10.1016/j.anbehav.2008.12.022>
- Best EC, Blomberg SP, Goldizen AW (2015) Shy female kangaroos seek safety in numbers and have fewer preferred friendships. *Behav Ecol* 26(2):639–646. <https://doi.org/10.1093/beheco/arv003>
- Błaszczak M (2017) Boldness towards novel objects predicts predator inspection in wild vervet monkeys. *Anim Behav* 123:91–100. <https://doi.org/10.1016/j.anbehav.2016.10.017>
- Blumstein DT, Petelle MB, Wey TW (2013) Defensive and social aggression: repeatable but independent. *Behav Ecol* 24(2):457–461. <https://doi.org/10.1093/beheco/ars183>
- Boake CRB (1989) Repeatability: its role in evolutionary studies of mating behavior. *Evol Ecol* 3(2):173–182. <https://doi.org/10.1007/BF02270919>
- Brent LJ, Heilbronner SR, Horvath JE, Gonzalez-Martinez J, Ruiz-Lambides A, Robinson AG, Skene JP, Platt ML (2013) Genetic origins of social networks in rhesus macaques. *Sci Rep* 3(1):1042. <https://doi.org/10.1038/srep01042>
- Cheney DL (1992) Intragroup cohesion and intergroup hostility: the relation between grooming distributions and intergroup competition among female primates. *Behav Ecol* 3(4):334–345. <https://doi.org/10.1093/beheco/3.4.334>
- Cheney DL, Seyfarth RM (1983) Nonrandom dispersal in free-ranging vervet monkeys: social and genetic consequences. *Am Nat* 122(3):392–412. <https://doi.org/10.1086/284142>
- Cheney DL, Seyfarth RM (1992) How monkeys see the world: inside the mind of another species. University of Chicago Press, Chicago
- Cheney DL, Seyfarth RM, Andelman SJ, Phyllis CL (1988) Reproductive success in vervet monkeys. In: Clutton-Brock TH (ed) Reproductive success. Chicago University Press, Chicago, pp 384–402
- Cheney DL, Silk JB, Seyfarth RM (2016) Network connections, dyadic bonds and fitness in wild female baboons. *R Soc Open Sci* 3(7):160255. <https://doi.org/10.1098/rsos.160255>
- Cords M (2012) The behavior, ecology, and social evolution of cercopithecine monkeys. In: Mitani JC, Call J, Kappeler PM, Palombit RA, Silk JB (eds) The evolution of primate societies. University of Chicago Press, Chicago, pp 92–112
- Craft ME (2015) Infectious disease transmission and contact networks in wildlife and livestock. *Philos T Roy Soc B* 370(1669):20140107. <https://doi.org/10.1098/rstb.2014.0107>
- Croft DP, Darden SK, Wey TW (2016) Current directions in animal social networks. *Curr Opin Behav Sci* 12:52–58. <https://doi.org/10.1016/j.cobeha.2016.09.001>
- Croft DP, James R, Krause J (2008) Exploring animal social networks. Princeton University Press, Princeton. <https://doi.org/10.1515/9781400837762>
- Csárdi G, Nepusz T (2006) The igraph software package for complex network research. *Int J Complex Syst* 1695 <http://igraph.org/>
- Dall SRX, Griffith SC (2014) An empiricist guide to animal personality variation in ecology and evolution. *Front Ecol Evol* 2:3
- Duboscq J, Romano V, Sueur C, MacIntosh AJJ (2016) Network centrality and seasonality interact to predict lice load in a social primate. *Sci Rep* 6(1):22095. <https://doi.org/10.1038/srep22095>
- Elo AE (1978) The rating of chessplayers, past and present. Arco, New York
- Farine DR (2017) A guide to null models for animal social network analysis. *Methods Ecol Evol* 8(10):1309–1320. <https://doi.org/10.1111/2041-210X.12772>
- Farine DR (2015) Proximity as a proxy for interactions: issues of scale in social network analysis. *Anim Behav* 104:e1–e5. <https://doi.org/10.1016/j.anbehav.2014.11.019>
- Farine DR, Aplin LM, Sheldon BC, Hoppitt W (2015) Interspecific social networks promote information transmission in wild songbirds. *Proc R Soc B* 282(1803):20142804. <https://doi.org/10.1098/rspb.2014.2804>
- Farine DR, Sheldon BC (2015) Selection for territory acquisition is modulated by social network structure in a wild songbird. *J Evol Biol* 28(3):547–556. <https://doi.org/10.1111/jeb.12587>
- Farine DR, Whitehead H (2015) Constructing, conducting and interpreting animal social network analysis. *J Anim Ecol* 84(5):1144–1163. <https://doi.org/10.1111/1365-2656.12418>
- Formica V, Wood C, Cook P, Brodie E (2017) Consistency of animal social networks after disturbance. *Behav Ecol* 28(1):85–93. <https://doi.org/10.1093/beheco/arw128>
- Formica VA, Wood CW, Larsen WB, Butterfield RE, Augat ME, Hougen HY, Brodie E (2012) Fitness consequences of social network position in a wild population of forked fungus beetles (*Bolitotherus cornutus*). *J Evol Biol* 25(1):130–137. <https://doi.org/10.1111/j.1420-9101.2011.02411.x>
- Fowler JH, Dawes CT, Christakis NA (2009) Model of genetic variation in human social networks. *Proc Natl Acad Sci U S A* 106(6):1720–1724. <https://doi.org/10.1073/pnas.0806746106>
- Freeman LC (1977) A set of measures of centrality based on betweenness. *Sociometry* 40(1):35–41. <https://doi.org/10.2307/3033543>
- Friant S, Ziegler TE, Goldberg TL (2016) Primate reinfection with gastrointestinal parasites: behavioural and physiological predictors of parasite acquisition. *Anim Behav* 117:105–113. <https://doi.org/10.1016/j.anbehav.2016.04.006>
- Frumkin NB, Wey TW, Exnicios M, Benham C, Hinton MG, Lantz S, Atherton C, Forde D, Karubian J (2016) Inter-annual patterns of aggression and pair bonding in captive American flamingos (*Phoenicopterus ruber*). *Zoo Biol* 35(2):111–119. <https://doi.org/10.1002/zoo.21274>
- Fruteau C, Voelkl B, van Damme E, Noë R (2009) Supply and demand determine the market value of food providers in wild vervet

- monkeys. *Proc Natl Acad Sci U S A* 106(29):12007–12012. <https://doi.org/10.1073/pnas.0812280106>
- Gilby IC, Brent LJ, Wroblewski EE, Rudicell RS, Hahn BH, Goodall J, Pusey AE (2013) Fitness benefits of coalitionary aggression in male chimpanzees. *Behav Ecol Sociobiol* 67(3):373–381. <https://doi.org/10.1007/s00265-012-1457-6>
- Hamede RK, Bashford J, McCallum H, Jones M (2009) Contact networks in a wild Tasmanian devil (*Sarcophilus harrisii*) population: using social network analysis to reveal seasonal variability in social behaviour and its implications for transmission of devil facial tumour disease. *Ecol Lett* 12(11):1147–1157. <https://doi.org/10.1111/j.1461-0248.2009.01370.x>
- Harrison XA (2014) Using observation-level random effects to model overdispersion in count data in ecology and evolution. *PeerJ* 2: e616. <https://doi.org/10.7717/peerj.616>
- Henzi SP, Forshaw N, Boner R, Barrett L, Lusseau D (2013) Scalar social dynamics in female vervet monkey cohorts. *Philos T Roy Soc B* 368(1618):20120351. <https://doi.org/10.1098/rstb.2012.0351>
- Henzi SP, Lucas JW (1980) Observations on the inter-troop movement of adult vervet monkeys. (*Cercopithecus aethiops*). *Folia Primatol* 33(3):220–235. <https://doi.org/10.1159/000155936>
- Jacoby DMP, Fear LN, Sims DW, Croft DP (2014) Shark personalities? Repeatability of social network traits in a widely distributed predatory fish. *Behav Ecol Sociobiol* 68(12):1995–2003. <https://doi.org/10.1007/s00265-014-1805-9>
- Janecke BB (2002) Vegetation ecology of Soetdoring Nature Reserve: pan, grassland, and karroid communities. MSc Thesis, University of the Free State, South Africa
- Janecke BB, du Preez P (2005) A synoptic view on the grassland vegetation of Soetdoring Nature Reserve, Free State Province. *S Afr J Bot* 71(3–4):339–348. [https://doi.org/10.1016/S0254-6299\(15\)30107-1](https://doi.org/10.1016/S0254-6299(15)30107-1)
- Josephs N, Bonnell T, Dostie M, Barrett L, Henzi SP (2016) Working the crowd: sociable vervets benefit by reducing exposure to risk. *Behav Ecol* 27(4):988–994. <https://doi.org/10.1093/beheco/arw003>
- King AJ, Clark FE, Cowlshaw G (2011) The dining etiquette of desert baboons: the roles of social bonds, kinship, and dominance in co-feeding networks. *Am J Primatol* 73(8):768–774. <https://doi.org/10.1002/ajp.20918>
- Kottek M, Grieser J, Beck C, Rudolf B, Rubel F (2006) World map of the Köppen-Geiger climate classification updated. *Meteorol Z* 15(3): 259–263. <https://doi.org/10.1127/0941-2948/2006/0130>
- Krause J, James R, Croft DP (2010) Personality in the context of social networks. *Philos T Roy Soc B* 365(1560):4099–4106. <https://doi.org/10.1098/rstb.2010.0216>
- Kurvers RH, Krause J, Croft DP, Wilson AD, Wolf M (2014) The evolutionary and ecological consequences of animal social networks: emerging issues. *Trends Ecol Evol* 29(6):326–335. <https://doi.org/10.1016/j.tree.2014.04.002>
- Lea AJ, Blumstein DT, Wey TW, Martin JG (2010) Heritable victimization and the benefits of agonistic relationships. *Proc Natl Acad Sci U S A* 107(50):21587–21592. <https://doi.org/10.1073/pnas.1009882107>
- Lehmann J, Majolo B, McFarland R (2016) The effects of social network position on the survival of wild Barbary macaques, *Macaca sylvanus*. *Behav Ecol* 27(1):20–28. <https://doi.org/10.1093/beheco/arv169>
- McDonald DB (2007) Predicting fate from early connectivity in a social network. *Proc Natl Acad Sci U S A* 104(26):10910–10914. <https://doi.org/10.1073/pnas.0701159104>
- McFarland R, Barrett L, Boner R, Freeman NJ, Henzi SP (2014) Behavioral flexibility of vervet monkeys in response to climatic and social variability. *Am J Phys Anthropol* 154(3):357–364. <https://doi.org/10.1002/ajpa.22518>
- McFarland R, Fuller A, Hetem RS, Mitchell D, Maloney SK, Henzi SP, Barrett L (2015) Social integration confers thermal benefits in a gregarious primate. *J Anim Ecol* 84(3):871–878. <https://doi.org/10.1111/1365-2656.12329>
- McFarland R, Majolo B (2013) Coping with the cold: predictors of survival in wild Barbary macaques, *Macaca sylvanus*. *Biol Lett* 9(4): 20130428. <https://doi.org/10.1098/rsbl.2013.0428>
- Muller MN, Emery Thompson M (2012) Mating, parenting, and male reproductive strategies. In: Mitani JC, Call J, Kappeler PM, Palombit RA, Silk JB (eds) *The evolution of primate societies*. University of Chicago Press, Chicago, pp 388–411
- Nakagawa S, Schielzeth H (2010) Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. *Biol Rev* 85(4):935–956. <https://doi.org/10.1111/j.1469-185X.2010.00141.x>
- Neumann C, Duboscq J, Dubuc C, Ginting A, Irwan AM, Agil M, Widdig A, Engelhardt A (2011) Assessing dominance hierarchies: validation and advantages of progressive evaluation with Elo-rating. *Anim Behav* 82(4):911–921. <https://doi.org/10.1016/j.anbehav.2011.07.016>
- Neumann C, Kulik L (2014) EloRating: Animal Dominance Hierarchies by Elo Rating. <https://cran.r-project.org/web/packages/EloRating/index.html>
- Newman MEJ (2003) The structure and function of complex networks. *SIAM Rev* 45(2):167–256. <https://doi.org/10.1137/S003614450342480>
- Oh KP, Badyaev AV (2010) Structure of social networks in a passerine bird: consequences for sexual selection and the evolution of mating strategies. *Am Nat* 176:E80–E89
- Pasquaretta C, Levé M, Claidière N et al (2014) Social networks in primates: smart and tolerant species have more efficient networks. *Sci Rep* 4:7600
- Pinter-Wollman N, Hobson EA, Smith JE, Edelman AJ, Shizuka D, de Silva S, Waters JS, Prager SD, Sasaki T, Wittemyer G, Fewell J, McDonald DB (2014) The dynamics of animal social networks: analytical, conceptual, and theoretical advances. *Behav Ecol* 25(2): 242–255. <https://doi.org/10.1093/beheco/art047>
- R Core Team (2017) R: a language and environment for statistical computing, version 3.3.3. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>
- Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ (2007) Integrating animal temperament within ecology and evolution. *Biol Rev* 82(2):291–318
- Rimbach R, Bisanzio D, Galvis N, Link A, Di Fiore A, Gillespie TR (2015) Brown spider monkeys (*Ateles hybridus*): a model for differentiating the role of social networks and physical contact on parasite transmission dynamics. *Philos T Roy Soc B* 370(1669):20140110. <https://doi.org/10.1098/rstb.2014.0110>
- Rushmore J, Caillaud D, Hall RJ, Stumpf RM, Meyers LA, Altizer S (2014) Network-based vaccination improves prospects for disease control in wild chimpanzees. *J R Soc Interface* 11(97):20140349. <https://doi.org/10.1098/rsif.2014.0349>
- Rushmore J, Caillaud D, Matamba L, Stumpf RM, Borgatti SP, Altizer S (2013) Social network analysis of wild chimpanzees provides insights for predicting infectious disease risk. *J Anim Ecol* 82(5): 976–986. <https://doi.org/10.1111/1365-2656.12088>
- Schülke O, Bhagavatula J, Vigilant L, Ostner J (2010) Social bonds enhance reproductive success in male macaques. *Curr Biol* 20(24): 2207–2210. <https://doi.org/10.1016/j.cub.2010.10.058>
- Seyfarth R, Cheney D (1984) Grooming, alliances and reciprocal altruism in vervet monkeys. *Nature* 308(5959):541–543. <https://doi.org/10.1038/308541a0>
- Seyfarth RM (1977) A model of social grooming among adult female monkeys. *J Theor Biol* 65(4):671–698. [https://doi.org/10.1016/0022-5193\(77\)90015-7](https://doi.org/10.1016/0022-5193(77)90015-7)
- Seyfarth RM (1980) The distribution of grooming and related behaviours among adult female vervet monkeys. *Anim Behav* 28(3):798–813. [https://doi.org/10.1016/S0003-3472\(80\)80140-0](https://doi.org/10.1016/S0003-3472(80)80140-0)

- Sih A, Hanser SF, McHugh KA (2009) Social network theory: new insights and issues for behavioral ecologists. *Behav Ecol Sociobiol* 63(7):975–988. <https://doi.org/10.1007/s00265-009-0725-6>
- Silk JB (2007) The adaptive value of sociality in mammalian groups. *Philos T Roy Soc B* 362(1480):539–559. <https://doi.org/10.1098/rstb.2006.1994>
- Silk JB, Alberts SC, Altmann J (2003) Social bonds of female baboons enhance infant survival. *Science* 302(5648):1231–1234. <https://doi.org/10.1126/science.1088580>
- Silk JB, Altmann J, Alberts SC (2006) Social relationships among adult female baboons (*Papio cynocephalus*) I. Variation in the strength of social bonds. *Behav Ecol Sociobiol* 61(2):183–195. <https://doi.org/10.1007/s00265-006-0249-2>
- Silk JB, Beehner JC, Bergman TJ, Crockford C, Engh AL, Moscovice LR, Wittig RM, Seyfarth RM, Cheney DL (2010) Strong and consistent social bonds enhance the longevity of female baboons. *Curr Biol* 20(15):1359–1361. <https://doi.org/10.1016/j.cub.2010.05.067>
- Silk JB, Beehner JC, Bergman TJ, Crockford C, Engh AL, Moscovice LR, Wittig RM, Seyfarth RM, Cheney DL (2009) The benefits of social capital: close social bonds among female baboons enhance offspring survival. *Proc R Soc Lond B* 276(1670):3099–3104. <https://doi.org/10.1098/rspb.2009.0681>
- St Clair JJH, Bums ZT, Bettaney EM, Morrissey MB, Otis B, Ryder TB, Fleischer RC, James R, Rutz C (2015) Experimental resource pulses influence social-network dynamics and the potential for information flow in tool-using crows. *Nat Commun* 6:7197. <https://doi.org/10.1038/ncomms8197>
- Stanton MA, Mann J (2012) Early social networks predict survival in wild bottlenose dolphins. *PLoS One* 7(10):e47508. <https://doi.org/10.1371/journal.pone.0047508>
- Stoffel MA, Nakagawa S, Schielzeth H (2017) rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. *Methods Ecol Evol* 8(11):1639–1644. <https://doi.org/10.1111/2041-210X.12797>
- van de Waal E, Borgeaud C, Whiten A (2013a) Potent social learning and conformity shape a wild primate's foraging decisions. *Science* 340(6131):483–485. <https://doi.org/10.1126/science.1232769>
- van de Waal E, Spinelli M, Bshary R, Ros AFH, Noë R (2013b) Negotiations over grooming in wild vervet monkeys (*Chlorocebus pygerythrus*). *Int J Primatol* 34(6):1153–1171. <https://doi.org/10.1007/s10764-013-9729-1>
- VanderWaal KL, Atwill ER, Isbell LA, McCowan B (2014) Linking social and pathogen transmission networks using microbial genetics in giraffe (*Giraffa camelopardalis*). *J Anim Ecol* 83(2):406–414. <https://doi.org/10.1111/1365-2656.12137>
- Wasserman S, Faust K (1994) Social network analysis: methods and applications. Cambridge University Press, Cambridge. <https://doi.org/10.1017/CBO9780511815478>
- WeatherSpark.com Average yearly weather for Bloemfontein, South Africa. <https://weatherspark.com/averages/29013/Bloemfontein-Free-State-South-Africa>
- Wey TW, Blumstein DT (2012) Social attributes and associated performance measures in marmots: bigger male bullies and weakly affiliating females have higher annual reproductive success. *Behav Ecol Sociobiol* 66(7):1075–1085. <https://doi.org/10.1007/s00265-012-1358-8>
- Wey T, Blumstein DT, Shen W, Jordán F (2008) Social network analysis of animal behaviour: a promising tool for the study of sociality. *Anim Behav* 75(2):333–344. <https://doi.org/10.1016/j.anbehav.2007.06.020>
- White LA, Forester JD, Craft ME (2017) Using contact networks to explore mechanisms of parasite transmission in wildlife. *Biol Rev* 92(1):389–409. <https://doi.org/10.1111/brv.12236>
- Wilson ADM, Krause S, Dingemanse NJ, Krause J (2013) Network position: a key component in the characterization of social personality types. *Behav Ecol Sociobiol* 67(1):163–173. <https://doi.org/10.1007/s00265-012-1428-y>