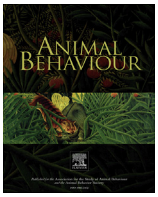
SPECIAL ISSUE: SOCIAL NETWORKS

Animal Behaviour 136 (2018) 217–226

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav



Special Issue: Social Networks

# Consistent individual variation across interaction networks indicates social personalities in lemurs

Ipek G. Kulahci [a, b, *], Asif A. Ghazanfar [a, c, d], Daniel I. Rubenstein [a]

[a] *Department of Ecology & Evolutionary Biology, Princeton University, Princeton, NJ, USA*
[b] *Biological, Earth and Environmental Sciences, University College Cork, Ireland*
[c] *Princeton Neuroscience Institute, Princeton University, Princeton, NJ, USA*
[d] *Department of Psychology, Princeton University, Princeton, NJ, USA*

ARTICLE INFO

*Article history:*
Received 12 June 2017
Initial acceptance 18 August 2017
Final acceptance 4 October 2017
Available online 9 December 2017
MS. number: SI-17-00489

*Keywords:*
animal personality
centrality measure
interaction network
*Lemur catta*
ringtailed lemur
social centrality
social network analysis
social personality

Group members interact with each other during multiple social behaviours that range from aggressive to affiliative interactions. It is not known, however, whether an individual's suite of social behaviours consistently covaries through time and across different types of social interactions. Consistent social behaviour would be advantageous in groups, especially when individuals need to remember their group members' social roles and preferences in order to keep track of social relationships and predict conspecifics' future behaviour. Here, we address whether social behaviour of ringtailed lemurs, *Lemur catta*, is consistent through time and across four interaction networks (aggression, grooming, contact calling, scent marking). We quantified variation in social behaviour through four network centrality measures including outdegree, outstrength, betweenness and eigenvector centrality. Comparing lemurs' measures across 2 years revealed that network centrality remained consistent between years. Lemurs' centrality also stayed consistent across interaction networks: individuals with high centrality in one interaction network also had high centrality in the other networks, even when we controlled for sex-based variation in social behaviour. Thus, regardless of their sex, some individuals were highly social and frequently groomed others, initiated aggressive interactions and responded to others' contact calls and scent marks. Lemurs also had preferred social partners they frequently interacted with across years and across multiple behaviours. In particular, lemurs frequently responded to the contact calls and the scent marks of the conspecifics they had frequently groomed. Together, these results demonstrate that individual variation in lemur social behaviour is not context specific, but instead persists through time and across multiple social interactions. Such consistent behaviour provides evidence of social personalities, which may influence individuals' interaction styles, including how socially active they are and with whom they interact.

Individual variation in social behaviour has key consequences for resource access, mate choice, disease transmission, learning, decision making and fitness (Cameron, Setsaas, & Linklater, 2009; Croft et al., 2009; Frère et al., 2010; Krause, Croft, & James, 2007; Lusseau & Conradt, 2009; Schülke, Bhagavatula, Vigilant, & Ostner, 2010; Seyfarth, Silk, & Cheney, 2012; Weidt, Hofmann, & König, 2008; Wey, Blumstein, Shen, & Jordán, 2008). Some of this variation can be attributed to age, sex, dominance and environmental factors (Monclus, Cook, & Blumstein, 2012; Seyfarth, Silk, & Cheney, 2014; Silk, Altmann, & Alberts, 2006, Silk, Alberts,& Altmann, 2006; Taborsky & Oliveira, 2012). However, variation in social behaviour may also result from some individuals being more social and initiating more interactions than others regardless of their age, sex or dominance status. Such variation may even persist through time and across different types of social interactions. For instance, socially active individuals may frequently groom others while also frequently initiating aggressive interactions.

Social differences that persist through time and across behaviours may provide insight into social personality traits. Human social personalities are identified through consistencies in social activity levels and interaction styles. Social personalities are inferred from measures such as how many interaction partners an individual has, how frequently they interact with others and the identities of their preferred interaction partners (Clifton, 2013; Fang et al., 2015; Golbeck, Robles, Edmondson, & Turner, 2011; John & Srivastava, 1999; Quercia, Lambiotte, Stillwell, Kosinski, &

---

[*] Correspondence: I. G. Kulahci, Biological, Earth and Environmental Sciences, University College Cork, Distillery Fields, North Mall, Cork, Ireland.
*E-mail address:* ipek.kulahci@gmail.com (I. G. Kulahci).

https://doi.org/10.1016/j.anbehav.2017.11.012

Crowcroft, 2012; Staiano et al., 2012). Thus, social personalities can be expressed two ways. Individuals may display consistent social activity levels and they may also have preferred partners with whom they consistently interact during multiple behaviours. Given the high diversity of animal interactions, we propose that an empirical approach similar to that of human social personalities can be utilized to study animal social personalities.

Animal social personalities would have major consequences for how individuals navigate through social environments that feature repeated interactions. Over the past decade, great progress has been made in understanding animal personalities (also referred to as 'behavioural syndromes' or 'temperament') from intraindividual consistencies in exploration, boldness and activity levels (Bell, 2007; Biro & Stamps, 2008; David, Auclair, & Cézilly, 2011; Dingemanse & Réale, 2005; Koolhaas et al., 1999; Réale, Reader, Sol, McDougall, & Dingemanse, 2007, Réale, Dingemanse, Kazem, & Wright, 2010; Seyfarth et al., 2012; Sih, Bell, & Johnson, 2004; Smith & Blumstein, 2008; Wolf & Weissing, 2012). On one hand, consistent behaviour frequently results in trade-offs and may reduce an individual's ability to quickly respond to changing conditions (Sih et al., 2004, Sih, Bell, Johnson, & Ziemba, 2004). On the other hand, consistent social behaviour may be advantageous in groups, especially when individuals need to remember each other's social roles and preferences. Doing so would allow them to predict the future behaviour of others and to modify their own social responses (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005). Reducing uncertainties during social interactions is highly advantageous (Barrett, Henzi, & Lusseau, 2012), and keeping track of others' social personalities may allow animals to reduce uncertainties about their social environment. Furthermore, as individuals vary in their sociability (i.e. response to presence or absence of a conspecific) and aggressiveness (i.e. agonistic interactions towards others) (Réale & Dingemanse, 2010; Réale et al., 2007), consistent variation in these traits may create social niches that reflect individuals' roles in the social environment (Bergmuller & Taborsky, 2010; Montiglio, Ferrari, & Réale, 2013). Social niches can be beneficial at the population level by increasing behavioural diversity, which is essential for dealing with environmental changes (Caro & Sherman, 2011; Rubenstein, 2016).

Identifying social personalities requires analysing individual variation in social behaviour through time and across behaviours. Social network analysis is a robust tool for quantifying social centrality by determining the extent of individuals' connections (Lusseau & Newman, 2004; Wassermann & Faust, 1994). Network position and centrality have multiple consequences (reviewed in Krause, James, Franks, & Croft, 2014). Network position can influence information acquisition (Aplin, Farine, Morand-Ferron, & Sheldon, 2012; Kulahci et al., 2016), disease transmission (Duboscq, Romano, Sueur, & MacIntosh, 2016; Godfrey, Bull, James, & Murray, 2009; Rubenstein, 2015) and reproductive fitness (McDonald, 2007). Social centrality can be defined in multiple ways depending on the question of interest. For instance, some centrality measures address the number of connections an individual has, some measures utilize the frequency of connections, while other measures account for the social importance of one's connections to determine their social centrality (Lusseau & Newman, 2004; Wassermann & Faust, 1994). Using multiple centrality measures is advantageous for analysing different aspects of variation in social behaviour. Similar to inferring personality traits such as boldness, exploration or neophobia from consistencies in behavioural measures through time and across contexts, we can infer social personality traits from consistencies in network centrality measures through time and across contexts (Krause, James, & Croft, 2010; Wilson, Krause, Dingemanse, & Krause, 2013). Social individuals with high centrality in one behaviour, such as aggression, may have high centrality in other behaviours such as grooming.

Several studies have utilized association networks based on physical proximity to address whether network position stays consistent through time (Aplin et al., 2015; Jacoby, Fear, Sims, & Croft, 2014; Krause et al., 2016; Vander Wal, Festa-Bianchet, Réale, Coltman, & Pelletier, 2015). Additional studies have addressed individual consistencies in aggressive interactions (Frumkin et al., 2016), including potential consistencies between social and defensive aggression (Blumstein, Petelle, & Wey, 2013). Yet, only a few studies have explored consistencies across networks based on different types of social behaviours (Castles et al., 2014; Madden, Drewe, Pearce, & Clutton-Brock, 2011). Thus, whether or not individual's network centrality and choice of interaction partners remain stable both through time and across different types of social behaviours has not yet been established.

We studied ringtailed lemurs, *Lemur catta*, to detect individual consistencies through time and across different social behaviours. We constructed networks from four behaviours including (1) grooming, (2) aggressive interactions, (3) contact calling and (4) scent marking. Each of these behaviours has a different function. Affiliative interactions such as grooming are essential for forming social bonds, hygiene maintenance, reducing aggression and reducing stress (Barton, 1985; Cords, 1997, pp. 24–49; Enquist & Leimar, 1993; Silk, 2007; Silk & Altmann, 2006). Strongly bonded lemurs frequently groom each other to maintain their social bonds (Kulahci, Rubenstein, & Ghazanfar, 2015). In comparison to grooming, aggressive interactions are important in intra and intersexual competition, territoriality, group stability and dominance in many species including ringtailed lemurs (Clutton-Brock et al., 2006; Flack, Girvan, de Waal, & Krakauer, 2006; Marler, 1976).

While grooming and aggression are direct interactions that involve physical contact, animals also interact indirectly through social signals. Social signals allow conspecifics to communicate when they are separated from each other and are thus comparable to an interaction. Signals can influence association and interaction networks, and they play a critical role in individual recognition, which is necessary for selectivity in social interactions (Kulahci & Ghazanfar, 2013, pp. 3–27; Kulahci, Drea, Rubenstein, & Ghazanfar, 2014; Snijders & Naguib, 2017). For instance, in many primate species including lemurs, contact calls carry individual signatures and allow group members to keep in touch over long distances (Macedonia, 1993). Besides contact calls, scent marks carry individual signatures, and investigating a scent mark provides information on the scent owner's identity, reproductive status and location (Charpentier, Boulet, & Drea, 2008; Kappeler, 1998; Scordato & Drea, 2007). In lemurs, scent marking is critical in communication, reproductive status advertisement and territoriality (Kappeler, 1998; Kulahci et al., 2014; Macedonia, 1986, 1993; Scordato & Drea, 2007). We focused on these four social behaviours to determine whether individual variation in social activity levels and interaction partners persisted through time and across behaviours with different functional consequences.

We predicted that social variation that persisted through time and across different types of behaviours would indicate presence of social personalities in lemurs. We utilized two complementary approaches to infer social personalities. First, we analysed consistencies in centrality metrics to explore whether individuals had consistently high (or low) centrality through time and across the four behaviours. We predicted that some lemurs would be more social and thus have higher network centrality than others, and that this variation would be carried over through time and across different types of behaviours, resulting in consistencies in network centrality across all four behaviours we studied. Second, we analysed whether individuals interacted with the same conspecifics through time and during different behaviours. If the pairs that interact frequently during one behaviour also interact frequently during other behaviours, then this would result in correlations between the matrices of these networks, suggesting that individuals had preferred interaction partners. We predicted that lemurs would respond to the contact calls and the scent marks of the conspecifics they groomed. Because grooming reinforces social bonds, complementing grooming interactions with contact calling and scent marking would allow bonded lemurs to keep in touch and receive up to date information about each other. Alternatively, if we did not detect consistencies through time or different behaviours, then this would suggest that individual variation in social behaviour is explained by other variables such as sex and/or age. For instance, if age influences variation in social behaviour, then individuals' centrality and choice of interaction partners should differ between years instead of remaining consistent. This difference should be most noticeable when juveniles become adults.

## METHODS

### *Social Network Data*

Lemurs live in female-dominated groups of up to 25 individuals (Jolly, 1966, 1966; Wilson & Hanlon, 2010). Such group sizes are perfect for network analyses, because they are large enough to detect individual variation, but also small enough to observe all individuals simultaneously to avoid sampling biases. We observed four ringtailed lemur groups. Two groups (NHE4: $N = 7–9$; NHE2: $N = 8$ individuals) semifree-ranged in large natural habitat enclosures at the Duke Lemur Center (Durham, NC, U.S.A.), while two larger groups (WM: $N = 17$; YB: $N = 21$ individuals) free-ranged on St Catherines Island (GA, U.S.A.) (Supplementary Table S1). The groups at Duke Lemur Center were separated from each other by chain-link fences, which allowed visual, acoustic and olfactory contact but prevented intergroup movement. In contrast, lemurs at St Catherines Island free-ranged on the island and were free to move between groups.

We observed two of the groups for two consecutive years (NHE4: $N = 9$ in 2010, $N = 7$ in 2011; YB: $N = 21$ in 2011 and 2012; Supplementary Table S1). Each group was observed for a minimum of four times per week during 2 months (number of observation hours per group: NHE4: 116 h in 2010, 105 h in 2011; NHE2: 120 h in 2010; WM: 107 h in 2013; YB: 128 h in 2011, 120 h in 2012). All lemurs were individually identifiable through visual features, collars, and tail shaves. We used all-occurrence sampling to collect social data, which we then converted into network matrices and analysed in UCINET (version 6.624) (Borgatti, Everett, & Freeman, 2002). We constructed networks from four behaviours including grooming, aggression, contact calling and scent marking. Each network had a distinct actor and a receiver (directed network) and also included information on how frequently an interaction occurred between each pair (weighted network). Procedures were consistent with the guidelines of, and approved by, the Institutional Animal Care and Use Committees at Duke University (A121-10-05) and Princeton University (Protocol number 1868).

Grooming networks included both reciprocal grooming (two lemurs simultaneously groom each other) and directed grooming (one lemur grooms another). We converted reciprocal grooming into directed grooming by adding the mutually grooming lemurs as both the actor and the receiver of the interaction. Each grooming bout was separated from others either by suspension of grooming for at least 5 min or by a change in grooming partners.

Aggression networks included chases and aggressive physical contact such as fights. The actor was the lemur initiating the aggressive interaction. If a lemur initiated an aggressive interaction towards a specific conspecific multiple times in a row, without engaging in any other interaction with another group member, this was recorded as a single aggressive interaction.

Contact-calling networks were based on producing a vocal response after hearing a contact call. It is not always possible to determine whether the initial calls are directed towards specific lemurs. However, responses are usually directed towards the lemur who produces the initial call (Kulahci et al., 2015). Therefore, the lemurs who vocalized first and received vocal responses were defined as the receivers of the contact-calling networks, and the lemurs who produced a vocal response after hearing another lemur's contact call were defined as the actors.

Scent-marking networks were based on countermarking after investigating a previously placed mark at the same location. Lemurs who placed the initial marks were defined as the receivers of the scent-marking networks and the lemurs who marked the same place after investigating were defined as the actors. Scent-marking data were collected only if we witnessed both the initial mark and the countermark within the same observational period. During our observations, all countermarks were placed within a few minutes of the first mark. By quantifying networks based on four distinct behaviours, we aimed to obtain an accurate picture of each lemur's social activity levels and their preferences for specific interaction partners.

### *Network Metrics*

To quantify individual variation in social behaviour and to address whether some individuals were highly active regardless of the type of social behaviour they engaged in, we calculated four network metrics (degree, strength, betweenness and eigenvector centrality). Each of these metrics addresses a different aspect of social centrality. The first measure, degree, depends on the number of direct connections (neighbours) that an individual has (Freeman & Gosling, 2010). Individuals who are connected to more conspecifics have higher degree than individuals who are connected to fewer conspecifics. We calculated degree from directed but unweighted networks, which we obtained by dichotomizing the network matrices by assigning a value of ‘1’ to each cell with a value of greater than ‘0’ (i.e. when an interaction was present between two individuals). In directed networks, outdegree indicates the number of group members towards whom an individual initiates an interaction and indegree indicates the number of group members from whom an individual receives an interaction. We focused on outdegree to determine the social activity levels of individuals by quantifying the number of conspecifics towards whom they initiated interactions.

The second measure, strength, focuses on the frequency of interactions and is calculated from weighted networks. We focused on outstrength to determine the frequency with which each lemur initiated interactions towards others. We used outdegree and outstrength to quantify whether certain individuals were more socially active than others through time and across different types of social behaviours.

The third measure, betweenness, depends on the shortest path length, which is the least number of connections required to connect two individuals (Croft, James, & Krause, 2008). Pairs that are directly connected have a shorter path length than pairs that are indirectly connected only through others. Betweenness reflects the number of shortest paths that go through an individual to connect other pairs (Borgatti, Everett, & Johnson, 2013; Lusseau & Newman, 2004). Individuals with high betweenness are critical in connecting the pairs that are not directly connected to each other (Freeman, 1979). Therefore, an individual with low degree can have high betweenness if some of its neighbours are not otherwise connected to each other.

The final measure, eigenvector centrality, is a more global measure than the previous three, because it depends on the centrality of one's neighbours. Highly connected individuals can have high eigenvector centrality only if their neighbors are also well connected to others (Borgatti et al., 2013; Kasper & Voelkl, 2009; Newman, 2004). Both betweenness and eigenvector centrality can provide insight into the social role that individuals play in their group, either by connecting the otherwise unconnected pairs or by being connected to others who play important roles in the group.

Overall, we calculated four measures for each of the four behaviours. These measures allowed us to quantify social centrality using different criteria, including the number of interaction partners (outdegree), the frequency with which individuals initiated interactions (outstrength), their importance in connecting the otherwise unconnected pairs (betweenness) and the centrality of their interaction partners (eigenvector centrality).

## *Social Network Analyses*

### *Consistency of network centrality through time*

We compared centralities between two years to determine whether lemurs retained their centrality through time. We used data from two groups (NHE4, YB; Supplementary Table S1) for this analysis because we did not have sufficient data for temporal comparisons from other groups. Only the lemurs who were in the same group during both years were included in the temporal analyses. We used the R code from Wilson et al. (2013) to test consistencies in network centrality and to determine whether individuals with high centrality in one year also had high centrality the next year. Using this network position consistency test, we ranked each individual based on a centrality metric of interest, and then analysed whether individual ranks were correlated across networks. We were interested in whether or not some individuals consistently had higher centrality relative to the others in their group. Therefore, using ranks was preferable to using raw metric values in our study. Because metrics arising from the same network are not independent of each other, this network position consistency test includes a randomization procedure (we ran 10 000 randomizations) (Wilson et al., 2013). A significant *P* value indicates that individual ranks are similar across networks, providing evidence for individual consistencies across networks of interest. We had four behaviours and four measures per behaviour, giving us a total of 16 ranks per lemur. We used the Benjamini–Hochberg false discovery rate (FDR) to correct for multiple comparisons at the 0.05 level (Benjamini & Hochberg, 1995, Benjamini & Hochberg, 2000).

### *Consistency of network centrality across different social behaviours*

To determine whether lemurs with high centrality in one social behaviour also had high centrality in other social behaviours, we again used the network position consistency test from Wilson et al. (2013). We analysed whether individual ranks were consistent across four behaviours (grooming, aggression, contact calling and scent marking). We used the Benjamini–Hochberg FDR test to correct for multiple comparisons. Because metrics arising from the same network are frequently correlated (Borgatti et al., 2013), we only compared the same metrics to each other. For example, while we compared grooming outdegree to outdegrees of aggression, contact calling and scent marking, we did not compare grooming outdegree to outstrength, betweenness or eigenvector from any network including the grooming network. If the same individuals consistently rank high in multiple interactions, while others consistently rank low, this would suggest that network centrality stays consistent regardless of the nature of the social connections between conspecifics, thus providing evidence in favour of social personalities.

Because variation in group size may influence whether ranks stay consistent across different behaviours, we calculated network densities and centrality ranges for each network from each group. We calculated network densities from unweighted networks. Low network density means that the majority of connections that could potentially exist in the network do not actually exist (Hanneman & Riddle, 2005). Because the probability of being connected to more conspecifics increases as group size increases, large groups are likely to have lower densities and higher centrality ranges than smaller groups.

Lemurs are a female-dominated species in which females stay in their natal group and interact frequently, while males disperse into new groups when they reach sexual maturity (Jolly, 1966, 1966; Wilson & Hanlon, 2010). Therefore, it is possible that females are more social than males and have higher centrality. To determine whether sex-based variation in social behaviour was responsible for consistencies across behaviours, we used ANOVA to compare the centrality ranks of males to those of females. We then checked the *P* values using a permutation test (‘Simple-PermutationTest’ add-in for JMP) by running 1000 permutations on centrality ranks of males and females, and comparing the resulting *P* values to those we obtained from our data set. Because females do not inherit their dominance status from their mothers (Nakamichi & Koyama, 1997), and lemur dominance hierarchies are subject to fluctuations, we did not include dominance as a variable but focused on the role of sex-based differences in social behaviour.

### *Consistency of interaction partners through time*

We used the quadratic assignment procedure (QAP) (Borgatti et al., 2013) to determine whether lemurs consistently interacted with the same group members through time. QAP runs a correlation test for the corresponding cells of each matrix, permutes the rows and the columns of one of the matrices, and runs the correlation again before repeating this procedure multiple times (we ran 10 000 permutations). We used QAP to analyse whether individuals were consistent in their choice of interaction partners across years in two groups (NHE4, YB; Supplementary Table S1). Only the networks based on the same social behaviour were compared to each other (e.g. the grooming network from the first year was compared only to the grooming network from the following year).

### *Consistency of interaction partners across social behaviours*

To analyse whether lemurs consistently interacted with the same set of conspecifics across different types of social behaviours, we again used the QAP analysis. When analysing weighted networks, QAP is informative about whether or not the pairs with strong connections in one network also have strong connections in other networks. Running QAP with weighted networks allowed us to determine whether lemurs had preferred social partners that they frequently interacted with during multiple behaviours.

# RESULTS

## *Network Centrality Was Consistent Across Years*

In the two groups for which we had multiple years of data ($N = 7$, 21), the majority of the centrality ranks were consistent across years (Table 1; the Benjamini–Hochberg adjusted $P$ values are provided in Supplementary Table S2). For example, individuals with high grooming outstrength and eigenvector ranks in the first year also had high ranks the following year (network position consistency test: grooming outstrength test score = 1, $N = 7$, $P < 0.001$; grooming outstrength test score = 163.5, $N = 21$, $P = 0.02$; grooming eigenvector test score = 4, $N = 7$, $P = 0.008$; grooming eigenvector test score = 104, $N = 21$, $P = 0.001$; Table 1, Fig. 1). Grooming network betweenness ranks were consistent across years in one group but not in the other group (network position consistency test: grooming betweenness test score = 6.5, $N = 7$, $P = 0.03$; grooming betweenness test score = 212, $N = 21$, $P = 0.07$; Table 1). Overall, for the majority of the network measures, lemurs with high centrality in the first year also had high centrality in the following year, suggesting that individual variation in social behaviour stayed consistent across years.

### *Consistency of Network Centrality Across Multiple Social Behaviours*

To determine whether some individuals had high centrality regardless of the type of social behaviour they engaged in, we compared each lemur's centrality rank across four behaviours. In the larger groups, almost all of the centrality ranks were consistent across behaviours ($N = 17$, 21 individuals) (Table 2; the Benjamini–Hochberg adjusted $P$ values are provided in Supplementary Table S3). For example, all ranks were consistent across different social behaviours in one of the groups (YB 2011, $N = 21$) (network position consistency test: outdegree test score = 523.833, $P = 0.002$; outstrength test score = 505.625, $P < 0.001$; eigenvector centrality test score = 526.125, $P = 0.002$; betweenness test score = 516.542, $P = 0.001$). However, none of the ranks were consistent across behaviours in the smaller groups ($N = 7$, 8 individuals). We note that the networks from the smaller groups had high densities and most lemurs interacted with the majority of their group members in these groups (Supplementary Table S4). The grooming networks had particularly high densities (grooming network density: 0.982, 0.861, 0.81, 0.449, 0.479 and 0.319 for $N = 8$, 9, 7, 17, 21 and 21 individuals). Additionally, interindividual variation in centrality measures was lower in the small groups than in the larger groups (Supplementary Tables S5, S6).

Females had higher centrality than males in all networks except the scent-marking networks, where the difference between the sexes was not significant (regression results; Table 3). We checked the $P$ values using a permutation test and found that the majority of the $P$ values from the permutation test were consistent with those we obtained from our data set, thereby confirming our observational $P$ values. Only scent-marking outdegree ($P = 0.211$ versus 0.206) and scent-marking betweenness ($P = 0.228$ versus 0.224) showed nonsignificant differences. Despite sex-based differences in social behaviour, analysing females' ranks separately from males' ranks revealed that intraindividual consistencies in centrality still persisted even after accounting for behavioural differences between sexes (network consistency test results; Table 4; the Benjamini–Hochberg adjusted $P$ values are provided in Supplementary Table S7). This suggests that even though sex played a major role in determining variation in lemur social centrality, with females being more central than males, intraindividual consistencies across networks were not exclusively due to sex-based differences.

**Table 1**
The majority of the network centrality measures were consistent over time

| Network | $N$ | Outdegree | Outstrength | Eigenvector | Betweenness |
|---|---|---|---|---|---|
| Aggression | 7 | **0.009** | **0.003** | **0.001** | **0.008** |
| Grooming | 7 | 0.078 | **<0.001** | **0.008** | **0.030** |
| Scent marking | 7 | 0.039 | **0.006** | **0.016** | 0.174 |
| Contact calling | 7 | 0.139 | **0.005** | **<0.001** | 0.422 |
| Aggression | 21 | **<0.001** | **<0.001** | 0.663 | **0.003** |
| Grooming | 21 | 0.418 | **0.020** | **0.001** | 0.070 |
| Scent marking | 21 | 0.118 | 0.083 | 0.316 | 0.065 |
| Contact calling | 21 | **0.003** | **0.018** | 0.065 | 0.068 |

$P$ values are from the network position consistency test. $P$ values in bold are the results that were deemed significant in the Benjamini–Hochberg FDR test and indicate the measures that were similar between the two years. The FDR adjusted $P$ values are provided in Supplementary Table S2. Except for scent-marking network measures from one group (YB, $N = 21$), the majority of the measures were correlated between years in both groups.

### *Lemurs' Choice of Interaction Partners Was Consistent Through Time*

To address whether individuals interacted with the same conspecifics, we analysed the similarities between network matrices from two consecutive years. QAP analysis revealed that lemurs were highly consistent in their interaction partners. During both years in both groups, lemurs initiated aggressive interactions towards the same conspecifics (QAP: $r = 0.982$, $N = 7$, $P < 0.001$; $r = 0.22$, $N = 21$, $P = 0.014$), groomed the same conspecifics ($r = 0.993$, $N = 7$, $P < 0.001$; $r = 0.519$, $N = 21$, $P < 0.001$) and responded to the calls of the same conspecifics ($r = 0.918$, $N = 7$, $P < 0.001$; $r = 0.191$, $N = 21$, $P = 0.031$). Scent marking was an exception to this trend: in one group but not in the other group, lemurs investigated the marks of the same conspecifics during both years ($r = 0.662$, $N = 7$, $P < 0.001$; $r = -0.005$, $N = 21$, $P = 0.652$; Table 5). These results revealed that lemurs had high temporal consistency in their choice of interaction partners for the majority of the social interactions we analysed.

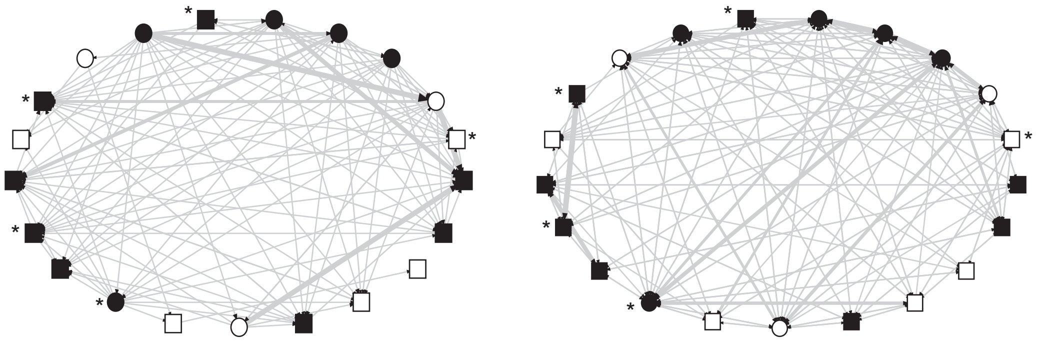
### *Lemurs Engaged in Multiple Types of Interactions with Their Preferred Partners*

We used QAP to determine whether lemurs interacted with the same conspecifics during multiple social behaviours. In all groups except one ($N = 7$), lemurs responded to the calls of, and investigated the scents of, the conspecifics they frequently groomed (Table 6). Even though the relationship between grooming, vocalizations and scent marks was not significant in this group, there was a strong tendency in the same direction as in the other groups ($N = 7$: grooming versus scent marking: $P = 0.059$; grooming versus contact calling: $P = 0.057$). In addition, lemurs investigated the scent marks of the conspecifics whose vocalizations they frequently responded to in two of the groups (QAP: $r = 0.2$, $N = 17$, $P = 0.016$; $r = 0.122$, $N = 21$, $P = 0.043$). Notably, there were no correlations between aggression networks and any of the other networks in any of the groups. Overall, lemurs responded to the social signals of the same conspecifics they groomed, demonstrating that their choice of interaction partners stayed consistent across multiple social behaviours with different social functions.

## DISCUSSION

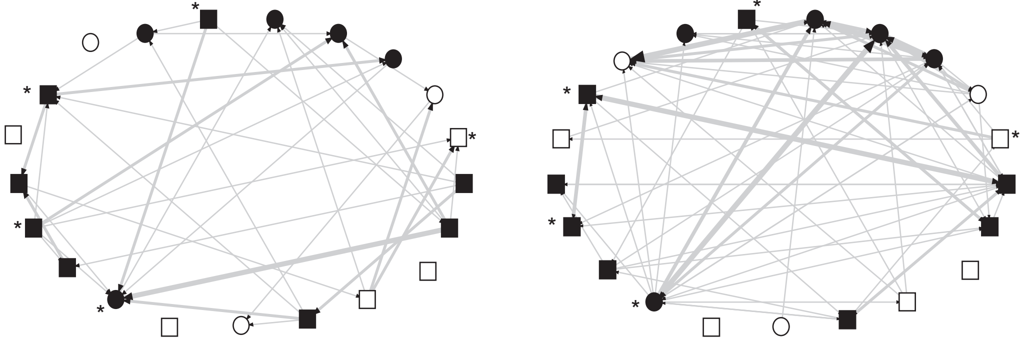
We demonstrate that individual differences in social behaviour persist through time and across multiple interaction networks. Lemurs' network centrality and choice of interaction partners were consistent between years. In the larger groups, lemurs with high centrality in one network also had high centrality in the other networks, even when we controlled for sex-based differences in social behaviour. These central lemurs frequently groomed conspecifics, initiated aggressive interactions and also frequently responded to the contact calls and the scents of conspecifics, suggesting that some individuals are highly social regardless of the context in which their interactions occur. Lemurs also had preferred interaction partners; they frequently groomed, kept in vocal

2011 Networks



(a) Aggression

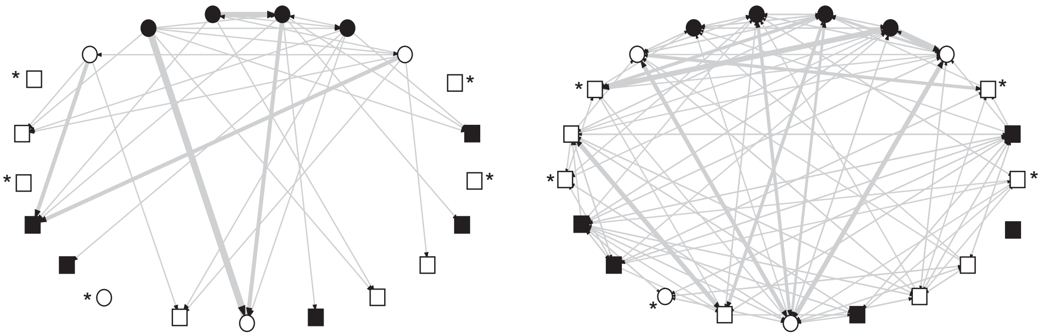
(b) Grooming



(c) Scent marking

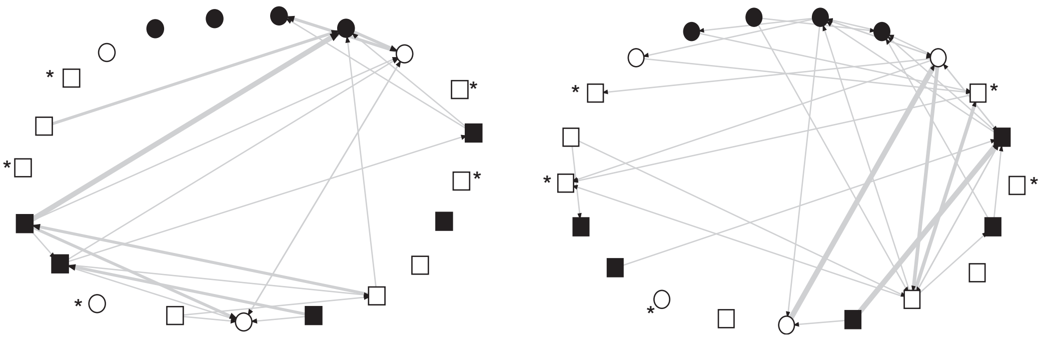
(d) Contact calling

2012 Networks



(e) Aggression

(f) Grooming



(g) Scent marking

(h) Contact calling

**Figure 1.** Networks of four behaviours during 2011 (a–d) and 2012 (e–h) from one of the groups (YB, $N = 21$ individuals). The circular layout is based on lemur names and is used for ease of comparison between behaviours and years. Line thickness is proportional to the interaction frequency. Node shape is based on sex (circles represent females, squares represent males) and node colour is based on age (black nodes are adults, white nodes are juveniles). An asterisk next to a node indicates that the lemur was present in the group during only 1 year.

**Table 2**
Individual centrality was consistent across four behaviours in the larger groups

| Group | *N* | Outdegree | Outstrength | Eigenvector | Betweenness |
|---|---|---|---|---|---|
| DLC − NHE2 | 8 | 0.148 | 0.072 | 0.574 | 0.249 |
| DLC − NHE4 (2010) | 9 | 0.470 | 0.661 | 0.619 | 0.424 |
| DLC − NHE4 (2011) | 7 | 0.493 | 0.605 | 0.823 | 0.138 |
| SCI − WM | 17 | **0.002** | **<0.001** | 0.626 | 0.048 |
| SCI − YB (2011) | 21 | **0.002** | **<0.001** | **0.002** | **0.001** |
| SCI − YB (2012) | 21 | **0.004** | **0.001** | **<0.001** | **<0.001** |

DLC: Duke Lemur Center; SCI: St Catherines Island; NHE2, NHE4, WM and YB are the group name abbreviations. YB ($N = 21$) group size stayed the same between years, even though the group composition changed due to births and male movement between groups. *P* values are from the network position consistency test. *P* values in bold are the results that were deemed significant in the Benjamini–Hochberg FDR test and indicate the measures that were similar between all four behaviours. The FDR adjusted *P* values are provided in Supplementary Table S3.

**Table 3**
Regression results for sex-based differences in network centrality

| Metric | Aggression | Grooming | Scent marking | Contact calling |
|---|---|---|---|---|
| Outdegree | **<0.001** | **<0.001** | 0.206 | **<0.001** |
| Outstrength | **<0.001** | **<0.001** | 0.173 | **<0.001** |
| Eigenvector | 0.214 | **<0.001** | 0.389 | **0.002** |
| Betweenness | **<0.001** | **<0.001** | 0.228 | **0.001** |

Significant *P* values are shown in bold.

**Table 5**
Lemurs' interaction partner choices were consistent through time

| Network | *N* | *r* | *P* |
|---|---|---|---|
| Aggression | 7 | 0.982 | **<0.001** |
| Grooming | 7 | 0.993 | **<0.001** |
| Scent marking | 7 | 0.662 | **<0.001** |
| Contact calling | 7 | 0.918 | **<0.001** |
| Aggression | 21 | 0.220 | **0.014** |
| Grooming | 21 | 0.519 | **<0.001** |
| Scent marking | 21 | -0.005 | 0.652 |
| Contact calling | 21 | 0.191 | **0.031** |

Results are from the QAP analysis in which similarities between the network matrices of four behaviours were analysed. Significant *P* values are indicated in bold.

contact with and investigated the scent marks of their preferred partners. Network consistencies through time and across different behaviours provide evidence of social personalities, which may underlie individual variation in interaction styles, including how socially active individuals are and their choice of interaction partners.

Social differences have major consequences both at the individual level and at the group level (Wilson et al., 2013; Wolf & Krause, 2014) . For example, in pigtailed macaque, *Macaca nemestrina,* groups, a small set of group members play a key role in reducing within-group conflicts and in maintaining the stability of the group structure (Flack et al., 2006). Similarly, highly social individuals have a major influence on group-level processes such as transmission of disease or information (Rubenstein, 2015). Furthermore, social centrality is correlated with exploration in great tits, *Parus major* (Aplin et al., 2013), predicts future breeding success in juvenile manakins, *Pipra filicauda* (McDonald, 2009; Ryder, McDonald, Blake, Parker, & Loiselle, 2008), and is also linked to the tendency to give alarm calls in yellow-bellied marmots, *Marmota flaviventris* (Fuong, Maldonado-Chaparro, & Blumstein, 2015). Therefore, consistent social differences that persist through time and across behaviours may significantly affect how individuals and groups adapt to changing conditions.

However, despite the growing interest in personalities and in networks, only a limited number of empirical studies have addressed whether network centrality remains consistent through time and across contexts. For example, a long-term study has demonstrated that bighorn sheep, *Ovis canadensis*, have consistent centrality in association networks across years (Vander Wal et al., 2015). Another long-term study has shown that great tits occupy consistent positions in foraging networks, as evidenced by both short-term (weekly) and long-term (yearly) data. Because great tit social data were based on a gambit-of-the-group approach, it was suggested that these consistencies may have been influenced by variation in space use (Aplin et al., 2015). Guppies also occupy consistent network positions, and some of these consistencies were explained in part by the tendency to be social and in part by sex-specific preferences (Krause et al., 2016). Similarly, aggression centrality measures of small spotted sharks, *Scyliorhinus canicula*, were found to be consistent across different habitats, but it was noted that these consistencies could have been driven by individual preferences for specific group sizes (Jacoby et al., 2014). In contrast, comparison of grooming, dominance and foraging competition networks in meerkats, *Suricata suricatta*, showed that network centrality and partner choice are not always consistent across networks (Madden et al., 2011). Similarly, measures of defensive aggression (i.e. aggression during live trapping) did not correlate with measures of social aggression in yellow-bellied marmots (Blumstein et al., 2013). Furthermore, a 3-year study on chacma baboons, , *Papio hamadryas ursinus*, revealed high temporal variation between grooming networks, affiliative interaction networks and proximity networks, but also demonstrated consistencies between grooming networks and networks based on other affiliative interactions (Castles et al., 2014).

**Table 4**
Intraindividual consistencies in centrality persist after accounting for sex-based differences

| Group | *N* | Sex | Outdegree | Outstrength | Eigenvector | Betweenness |
|---|---|---|---|---|---|---|
| SCI–WM | 17 | Females | **0.001** | **0.002** | 0.796 | 0.190 |
| | | Males | 0.642 | 0.176 | 0.453 | 0.276 |
| SCI–YB (2011) | 21 | Females | **0.011** | 0.044 | **0.024** | **0.009** |
| | | Males | **0.005** | **0.001** | **0.007** | 0.088 |
| SCI–YB (2012) | 21 | Females | 0.130 | 0.137 | **<0.001** | **0.034** |
| | | Males | **0.007** | **0.004** | 0.137 | **0.010** |

SCI: St Catherines Island; WM and YB are the group name abbreviations. *P* values are from the network position consistency test. *P* values in bold are the results that were deemed significant in the Benjamini–Hochberg FDR test. The FRD adjusted *P* values are provided in Supplementary Table S7.

**Table 6**
Consistency in interaction partners across different networks

| Networks | *N* | *P* |
|---|---|---|
| Aggression – Grooming | 7 | 0.280 |
| Aggression – Scent marking | 7 | 0.133 |
| Aggression – Contact calling | 7 | 0.319 |
| Grooming – Scent marking | 7 | 0.059 |
| Grooming – Contact calling | 7 | 0.057 |
| Scent marking – Contact calling | 7 | 0.366 |
| Aggression – Grooming | 8 | 0.078 |
| Aggression – Scent marking | 8 | 0.249 |
| Aggression – Contact calling | 8 | 0.535 |
| Grooming – Scent marking | 8 | **0.049** |
| Grooming – Contact calling | 8 | **0.007** |
| Scent marking – Contact calling | 8 | 0.425 |
| Aggression – Grooming | 17 | 0.312 |
| Aggression – Scent marking | 17 | 0.356 |
| Aggression – Contact calling | 17 | 0.083 |
| Grooming – Scent marking | 17 | **0.008** |
| Grooming – Contact calling | 17 | **<0.001** |
| Scent marking – Contact calling | 17 | **0.016** |
| Aggression – Grooming | 21 | 0.384 |
| Aggression – Scent marking | 21 | 0.222 |
| Aggression – Contact calling | 21 | 0.164 |
| Grooming – Scent marking | 21 | **0.004** |
| Grooming – Contact calling | 21 | **0.001** |
| Scent marking – Contact calling | 21 | **0.043** |

Significant *P* values from the QAP analysis are shown in bold. Lemurs' interaction partners remained consistent across grooming and contact-calling networks and in some groups' scent-marking networks.

Our study adds to these previous studies and demonstrates social consistencies through time and across multiple types of social behaviours with different functions. Understanding consistencies across multiple types of behaviours is advantageous when determining social personalities, as these consistencies can have far-reaching implications at the group level. For example, strongly bonded ringtailed lemurs frequently respond to each other's contact calls (Kulahci et al., 2015). Repeatedly interacting with the same conspecifics during different behaviours provides increased opportunities for forming and maintaining strong social bonds. Strong social relationships play a critical role in fitness (Seyfarth & Cheney, 2012) and may even be one of the precursors to the evolution of cooperation (Allen et al., 2017). Furthermore, consistencies across multiple behaviours would allow animals to keep track of the past behaviours and the preferences of their group members, allowing them to predict others' future behaviour and to adjust their own responses accordingly (Dall et al., 2005; Drewe, Madden, & Pearce, 2009; Madden, Drewe, Pearce, & Clutton-Brock, 2009; Wassermann & Faust, 1994; Wolf & Krause, 2014). One of the exciting but relatively unexplored questions in social cognition is whether animals know about and keep track of conspecifics' social centrality (Seyfarth & Cheney, 2015). If centrality remains stable across different types of interactions, then this may allow animals to predict conspecifics' behaviour and adjust their own behaviour. Therefore, it is possible that in addition to dominance, kinship, age and sex, social personalities also provide key information that shapes animals' social decisions and relationships. For example, chacma baboons use different strategies when approaching conspecifics with different personalities (i.e. nice, aloof, loner) (Seyfarth et al., 2012), suggesting that they do in fact pay attention to, and keep track of, different personality types in their group and their own relationships with them. Thus, knowing and remembering the social personalities of their group members may help animals make informed decisions about how to best respond to their social environment.

Network position and centrality are likely to be influenced by factors such as sex, age and group structure (Krause et al., 2014). The role of these factors on network position can make it difficult to infer social personalities. For instance, in our study populations, females had higher centrality than males. However, analysing females' centrality ranks separately from males' ranks revealed that consistencies still existed even after we controlled for sex-based differences. Furthermore, centrality ranks remained consistent across 2 years, during which some juveniles reached adulthood. If age were the only factor responsible for differences in centrality, then the centrality ranks of these juveniles should have changed when they became adults. We note that our group sizes varied from 7 to 21 individuals, and we detected some variation in our results from different groups. For example, smaller groups were more connected than larger groups, as evidenced by the high network densities and the low interindividual variation in centrality measures. Additional studies are needed to clarify whether these varying results are due to a real biological difference arising from group size differences, or due to a lack of confidence arising from small sample sizes in smaller groups. Overall, our results suggest that social consistencies can still be present even beyond the influence of factors that are known to affect social behaviour.

Our temporal analyses spanned 2 years of data and provided evidence that interaction partners stayed consistent through time. Even though 2 years does not include all possible group composition changes such as multiple births and deaths, the promising results from our study suggest that assessing social personalities through consistencies in time and across social behaviours is a fruitful direction for studies with access to longitudinal data from multiple years. In our study, the main exception to temporal consistencies was the scent-marking network in one of the groups ($N = 21$; Tables 1, 5), where scent-marking ranks were not consistent between years, and the central lemurs from the first year did not occupy central positions during the following year. Similarly, lemurs in this group did not mark the same conspecifics' marks during both years. Adult males frequently investigate and countermark conspecifics' marks, therefore scent-marking networks are highly dependent on the behaviour of the adult males. We removed data from the adult males who switched groups between years, which allowed us to keep the network matrices comparable for the temporal analyses. It is possible that removing data from the adult males reduced our power to detect consistencies in the scent-marking networks. This was not an issue in the other group ($N = 7$), which was in a different field site where movement between groups was restricted. Therefore, we note that it is important to account for the ecology of the species of interest when looking at temporal consistencies in long-term data sets, especially when group composition changes significantly through time.

Quantifying social personalities through networks is a new approach in animal behaviour. Yet, human studies have already provided evidence that network metrics reliably reflect social personalities, by demonstrating that the five main personality traits (extraversion, neuroticism, agreeableness, conscientiousness and openness; John & Srivastava, 1999) strongly correlate with consistencies in network centrality measures (Clifton, 2013; Fang et al., 2015; Golbeck et al., 2011; Quercia et al., 2012; Staiano et al., 2012). In contrast, only a handful of animal studies have addressed consistencies in animal social networks. Here, we demonstrate consistencies in both social centrality and in choice of interaction partners through time and across multiple types of social behaviours. The positive results from our study encourage further exploration of social personalities in long-term data sets, where major life history events and significant group changes will provide additional insights into consistent differences. We suggest that combining network analysis and social personality studies with social cognition experiments provides a fruitful area of future research, in which we can address how knowledge of conspecifics' social personalities aids social decision making in animals.

## Acknowledgments

We thank Duke Lemur Center and St Catherines Island. This study was funded by grants to I.G.K. from the Animal Behavior Society, American Society of Mammalogists, American Society of Primatologists and the Department of Ecology & Evolutionary Biology at Princeton University. We thank Jacinta C. Beehner and two referees for comments on the manuscript. This is Duke Lemur Center publication number 1359.

## Supplementary Material

Supplementary Material associated with this article is available, in the online version, at https://doi.org/10.1016/j.anbehav.2017.11.012.

## References

Allen, B., Lippner, G., Chen, Y.-T., Fotouhi, B., Momeni, N., Yau, S.-T., et al. (2017). Evolutionary dynamics on any population structure. *Nature, 544*(7649), 227–230.

Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cole, E. F., Cockburn, A., & Sheldon, B. C. (2013). Individual personalities predict social behaviour in wild networks of great tits (*Parus major*). *Ecology Letters, 16*(11), 1365–1372.

Aplin, L., Farine, D., Morand-Ferron, J., & Sheldon, B. (2012). Social networks predict patch discovery in a wild population of songbirds. *Proceedings of the Royal Society B: Biological Sciences, 279*(1745), 4199–4205. https://doi.org/10.1098/rspb.2012.1591.

Aplin, L. M., Firth, J. A., Farine, D. R., Voelkl, B., Crates, R. A., Culina, A., et al. (2015). Consistent individual differences in the social phenotypes of wild great tits, *Parus major*. *Animal Behaviour, 108*, 117–127.

Barrett, L., Henzi, S. P., & Lusseau, D. (2012). Taking sociality seriously: The structure of multi-dimensional social networks as a source of information for individuals. *Philosophical Transactions of the Royal Society B: Biological Sciences, 367*(1599), 2108–2118. https://doi.org/10.1098/rstb.2012.0113.

Barton, R. (1985). Grooming site preferences in primates and their functional implications. *International Journal of Primatology, 6*(5), 519–532.

Bell, A. M. (2007). Future directions in behavioural syndromes research. *Proceedings of the Royal Society B: Biological Sciences, 274*(1611), 755–761.

Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society B: Methodological, 57*(1), 289–300.

Benjamini, Y., & Hochberg, Y. (2000). On the adaptive control of the false discovery rate in multiple testing with independent statistics. *Journal of Educational and Behavioral Statistics, 25*(1), 60–83.

Bergmuller, R., & Taborsky, M. (2010). Animal personality due to social niche specialisation. *Trends in Ecology & Evolution, 25*(9), 504–511.

Biro, P. A., & Stamps, J. A. (2008). Are animal personality traits linked to life-history productivity? *Trends in Ecology & Evolution, 23*(7), 361–368.

Blumstein, D. T., Petelle, M. B., & Wey, T. W. (2013). Defensive and social aggression: Repeatable but independent. *Behavioral Ecology, 24*(2), 457–461. https://doi.org/10.1093/beheco/ars183.

Borgatti, S. P., Everett, M. G., & Freeman, L. C. (2002). *Ucinet 6 for Windows: Software for social network analysis*. Harvard, MA: Analytical Technologies.

Borgatti, S. P., Everett, M. G., & Johnson, J. C. (2013). *Analyzing social networks*. Thousand Oaks, CA: Sage.

Cameron, E. Z., Setsaas, T. H., & Linklater, W. L. (2009). Social bonds between unrelated females increase reproductive success in feral horses. *Proceedings of the National Academy of Sciences of the United States of America, 106*(33), 13850–13853.

Caro, T., & Sherman, P. W. (2011). Endangered species and a threatened discipline: Behavioural ecology. *Trends in Ecology & Evolution, 26*(3), 111–118.

Castles, M., Heinsohn, R., Marshall, H. H., Lee, A. E. G., Cowlishaw, G., & Carter, A. J. (2014). Social networks created with different techniques are not comparable. *Animal Behaviour, 96*, 59–67.

Charpentier, M. J., Boulet, M., & Drea, C. M. (2008). Smelling right: The scent of male lemurs advertises genetic quality and relatedness. *Molecular Ecology, 17*(14), 3225–3233. https://doi.org/10.1111/j.1365-294X.2008.03831.x.

Clifton, A. (2013). Variability in personality expression across contexts: A social network approach. *Journal of Personality, 82*(2), 103–115. https://doi.org/10.1111/jopy.12038.

Clutton-Brock, T., Hodge, S., Spong, G., Russell, A., Jordan, N., Bennett, N., et al. (2006). Intrasexual competition and sexual selection in cooperative mammals. *Nature, 444*(7122), 1065.

Cords, M. (1997). Friendships, alliances, reciprocity and repair. In A. Whiten, & R. W. Byrne (Eds.), *Machiavellian intelligence II: Extensions and evaluations*. Cambridge, U.K.: Cambridge University Press.

Croft, D. P., James, R., & Krause, J. (2008). *Exploring animal social networks*. Princeton, NJ: Princeton University Press.

Croft, D., Krause, J., Darden, S., Ramnarine, I., Faria, J., & James, R. (2009). Behavioural trait assortment in a social network: Patterns and implications. *Behavioral Ecology and Sociobiology, 63*(10), 1495–1503.

Dall, S. R., Giraldeau, L.-A., Olsson, O., McNamara, J. M., & Stephens, D. W. (2005). Information and its use by animals in evolutionary ecology. *Trends in Ecology & Evolution, 20*(4), 187–193.

David, M., Auclair, Y., & Cézilly, F. (2011). Personality predicts social dominance in female zebra finches, *Taeniopygia guttata*, in a feeding context. *Animal Behaviour, 81*, 219–224.

Dingemanse, N. J., & Réale, D. (2005). Natural selection and animal personality. *Behaviour, 142*, 1159–1184.

Drewe, J. A., Madden, J. R., & Pearce, G. P. (2009). The social network structure of a wild meerkat population: 1. Inter-group interactions. *Behavioral Ecology and Sociobiology, 63*(9), 1295–1306.

Duboscq, J., Romano, V., Sueur, C., & MacIntosh, A. J. (2016). Network centrality and seasonality interact to predict lice load in a social primate. *Scientific Reports, 6*, 22095. https://doi.org/10.1038/srep22095.

Enquist, M., & Leimar, O. (1993). The evolution of cooperation in mobile organisms. *Animal Behaviour, 45*, 747–757.

Fang, R., Landis, B., Zhang, Z., Anderson, M. H., Shaw, J. D., & Kilduff, M. (2015). Integrating personality and social networks: A meta-analysis of personality, network position, and work outcomes in organizations. *Organization Science, 26*(4), 1243–1260. https://doi.org/10.1287/orsc.2015.0972.

Flack, J. C., Girvan, M., de Waal, F. B. M., & Krakauer, D. C. (2006). Policing stabilizes construction of social niches in primates. *Nature, 439*(7075), 426–429.

Freeman, L. C. (1979). Centrality in social networks conceptual clarification. *Social Networks, 1*(3), 215–239.

Freeman, H. D., & Gosling, S. D. (2010). Personality in nonhuman primates: A review and evaluation of past research. *American Journal of Primatology, 72*(8), 653–671.

Frère, C. H., Krützen, M., Mann, J., Connor, R. C., Bejder, L., & Sherwin, W. B. (2010). Social and genetic interactions drive fitness variation in a free-living dolphin population. *Proceedings of the National Academy of Sciences of the United States of America, 107*(46), 19949–19954.

Frumkin, N. B., Wey, T. W., Exnicios, M., Benham, C., Hinton, M. G., Lantz, S., et al. (2016). Inter-annual patterns of aggression and pair bonding in captive American flamingos (*Phoenicopterus ruber*). *Zoo Biology, 35*(2), 111–119.

Fuong, H., Maldonado-Chaparro, A., & Blumstein, D. T. (2015). Are social attributes associated with alarm calling propensity? *Behavioral Ecology, 26*(2), 587–592. https://doi.org/10.1093/beheco/aru235.

Godfrey, S. S., Bull, C. M., James, R., & Murray, K. (2009). Network structure and parasite transmission in a group living lizard, the gidgee skink. *Egernia stokesii. Behavioral Ecology and Sociobiology, 63*(7), 1045–1056. https://doi.org/10.1007/s00265-009-0730-9.

Golbeck, J., Robles, C., Edmondson, M., & Turner, K. (2011). Predicting personality from twitter. In *Proceedings of the IEEE Third International Conference on Privacy, Security, Risk and Trust (PASSAT) and Social Computing (SocialCom), Boston, MA, 9–11 October, 2011*. New York, NY: IEEE. https://doi.org/10.1109/PASSAT/SocialCom.2011.33.

Hanneman, R. A., & Riddle, M. (2005). *Introduction to social network methods*. Riverside, CA: University of California.

Jacoby, D. M. P., Fear, L. N., Sims, D. W., & Croft, D. P. (2014). Shark personalities? Repeatability of social network traits in a widely distributed predatory fish. *Behavioral Ecology and Sociobiology, 68*(12), 1995–2003.

John, O. P., & Srivastava, S. (1999). The big five trait taxonomy: History, measurement, and theoretical perspectives. *Handbook of Personality: Theory and Research, 2*(1999), 102–138.

Jolly, A. (1966). *Lemur behavior*. Chicago, IL: University of Chicago Press.

Jolly, A. (1966). Lemur social behavior and primate intelligence. *Science, 153*(3735), 501–506.

Kappeler, P. M. (1998). To whom it may concern: The transmission and function of chemical signals in *Lemur catta*. *Behavioral Ecology and Sociobiology, 42*(6), 411–421.

Kasper, C., & Voelkl, B. (2009). A social network analysis of primate groups. *Primates, 50*(4), 343–356.

Koolhaas, J. M., Korte, S. M., De Boer, S. F., Van Der Vegt, B. J., Van Reenen, C. G., Hopster, H., et al. (1999). Coping styles in animals: Current status in behavior and stress-physiology. *Neuroscience & Biobehavioral Reviews, 23*(7), 925–935.

Krause, J., Croft, D., & James, R. (2007). Social network theory in the behavioural sciences: Potential applications. *Behavioral Ecology and Sociobiology, 62*(1), 15–27.

Krause, J., James, R., & Croft, D. P. (2010). Personality in the context of social networks. *Philosophical Transactions of the Royal Society B: Biological Sciences, 365*(1560), 4099–4106.

Krause, J., James, R., Franks, D. W., & Croft, D. P. (2014). *Animal social networks*. New York, NY: Oxford University Press.

Krause, S., Wilson, A. D., Ramnarine, I. W., Herbert-Read, J. E., Clément, R. J., & Krause, J. (2016). Guppies occupy consistent positions in social networks: Mechanisms and consequences. *Behavioral Ecology, 28*(2), 429–438.

Kulahci, I. G., Drea, C. M., Rubenstein, D. I., & Ghazanfar, A. A. (2014). Individual recognition through olfactory–auditory matching in lemurs. *Proceedings of the Royal Society B: Biological Sciences, 281*(1784), 20140071.

Kulahci, I. G., & Ghazanfar, A. A. (2013). Multisensory recognition in vertebrates (especially primates). In P. Belin, S. Campanella, & T. Ethofer (Eds.), *Integrating face and voice in person perception*. New York, NY: Springer.

Kulahci, I. G., Rubenstein, D. I., Bugnyar, T., Hoppitt, W., Mikus, N., & Schwab, C. (2016). Social networks predict selective observation and information spread in ravens. *Royal Society Open Science, 3*(7), 160256. https://doi.org/10.1098/rsos.160256.

Kulahci, I. G., Rubenstein, D. I., & Ghazanfar, A. A. (2015). Lemurs groom-at-a-distance through vocal networks. *Animal Behaviour, 110*, 179–186.

Lusseau, D., & Conradt, L. (2009). The emergence of unshared consensus decisions in bottlenose dolphins. *Behavioral Ecology and Sociobiology, 63*(7), 1067–1077.

Lusseau, D., & Newman, M. E. (2004). Identifying the role that animals play in their social networks. *Proceedings of the Royal Society B: Biological Sciences, 271*(Suppl. 6), S477–S481.

Macedonia, J. M. (1986). Individuality in a contact call of the ringtailed lemur (*Lemur catta*). *American Journal of Primatology, 11*, 163–179.

Macedonia, J. M. (1993). The vocal repertoire of the ringtailed lemur (*Lemur catta*). *Folia Primatologica, 61*(4), 186–217.

Madden, J. R., Drewe, J. A., Pearce, G. P., & Clutton-Brock, T. H. (2009). The social network structure of a wild meerkat population: 2. Intragroup interactions. *Behavioral Ecology and Sociobiology, 64*(1), 81–95.

Madden, J. R., Drewe, J. A., Pearce, G. P., & Clutton-Brock, T. H. (2011). The social network structure of a wild meerkat population: 3. Position of individuals within networks. *Behavioral Ecology and Sociobiology, 65*(10), 1857–1871. https://doi.org/10.1007/s00265-011-1194-2.

Marler, P. (1976). On animal aggression: The roles of strangeness and familiarity. *American Psychologist, 31*(3), 239–246.

McDonald, D. B. (2007). Predicting fate from early connectivity in a social network. *Proceedings of the National Academy of Sciences of the United States of America, 104*(26), 10910–10914.

McDonald, D. B. (2009). Young-boy networks without kin clusters in a lek-mating manakin. *Behavioral Ecology and Sociobiology, 63*(7), 1029–1034.

Monclus, R., Cook, T., & Blumstein, D. T. (2012). Masculinized female yellow-bellied marmots initiate more social interactions. *Biology Letters, 8*(2), 208–210. https://doi.org/10.1098/rsbl.2011.0754.

Montiglio, P.-O., Ferrari, C., & Réale, D. (2013). Social niche specialization under constraints: Personality, social interactions and environmental heterogeneity. *Philosophical Transactions of the Royal Society B: Biological Sciences, 368*(1618), 20120343.

Nakamichi, M., & Koyama, N. (1997). Social relationships among ring-tailed lemurs (*Lemur catta*) in two free-ranging troops at Berenty Reserve, Madagascar. *International Journal of Primatology, 18*(1), 73–93. https://doi.org/10.1023/a:1026393223883.

Newman, M. E. (2004). Analysis of weighted networks. *Physical Review E, 70*, 056131.

Quercia, D., Lambiotte, R., Stillwell, D., Kosinski, M., & Crowcroft, J. (2012). The personality of popular facebook users. In *Proceedings of the ACM 2012 Conference on Computer Supported Cooperative Work, Seattle, WA, 11–15 February 2012* (pp. 955–964). New York, NY: Association for Computing Machinery. https://doi.org/10.1145/2145204.2145346.

Réale, D., & Dingemanse, N. J. (2010). Personality and individual social specialisation. In T. Székely, A. J. Moore, & J. Komdeur (Eds.), *Social behaviour: Genes, ecology and evolution* (pp. 417–441). Cambridge, U.K.: Cambridge University Press.

Réale, D., Dingemanse, N. J., Kazem, A. J. N., & Wright, J. (2010). Evolutionary and ecological approaches to the study of personality. *Philosophical Transactions of the Royal Society B: Biological Sciences, 365*(1560), 3937–3946.

Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews, 82*(2), 291–318.

Rubenstein, D. I. (2015). Networks of terrestrial ungulates: Linking form and function. In J. Krause, R. James, D. W. Franks, & D. P. Croft (Eds.), *Animal social networks* (pp. 184–196). Oxford, U.K.: Oxford University Press.

Rubenstein, D. I. (2016). Anthropogenic impacts on behavior: The pros and cons of plasticity. In O. Berger-Tal, & D. Saltz (Eds.), *Conservation behavior: Applying behavioral ecology to wildlife conservation and management* (pp. 121–146). Cambridge, U.K.: Cambridge University.

Ryder, T. B., McDonald, D. B., Blake, J. G., Parker, P. G., & Loiselle, B. A. (2008). Social networks in the lek-mating wire-tailed manakin (*Pipra filicauda*). *Proceedings of the Royal Society B: Biological Sciences, 275*(1641), 1367–1374.

Schülke, O., Bhagavatula, J., Vigilant, L., & Ostner, J. (2010). Social bonds enhance reproductive success in male macaques. *Current Biology, 20*(24), 2207–2210.

Scordato, E. S., & Drea, C. M. (2007). Scents and sensibility: Information content of olfactory signals in the ringtailed lemur. *Lemur catta. Animal Behaviour, 73*, 301–314.

Seyfarth, R. M., & Cheney, D. L. (2012). The evolutionary origins of friendship. *Annual Review of Psychology, 63*(1), 153–177. https://doi.org/10.1146/annurev-psych-120710-100337.

Seyfarth, R. M., & Cheney, D. L. (2015). Social cognition. *Animal Behaviour, 103*, 191–202.

Seyfarth, R. M., Silk, J. B., & Cheney, D. L. (2012). Variation in personality and fitness in wild female baboons. *Proceedings of the National Academy of Sciences of the United States of America, 109*(42), 16980–16985.

Seyfarth, R. M., Silk, J. B., & Cheney, D. L. (2014). Social bonds in female baboons: The interaction between personality, kinship and rank. *Animal Behaviour, 87*, 23–29.

Sih, A., Bell, A., & Johnson, J. C. (2004). Behavioral syndromes: An ecological and evolutionary overview. *Trends in Ecology & Evolution, 19*(7), 372–378.

Sih, A., Bell, A., Johnson, J. C., & Ziemba, R. E. (2004). Behavioral syndromes: An integrative overview. *Quarterly Review of Biology, 79*(3), 241–277. https://doi.org/10.1086/422893.

Silk, J. B. (2007). Social components of fitness in primate groups. *Science, 317*(5843), 1347–1351.

Silk, J. B., Alberts, S. C., & Altmann, J. (2006). Social relationships among adult female baboons (*Papio cynocephalus*) II. Variation in the quality and stability of social bonds. *Behavioral Ecology and Sociobiology, 61*, 197–204.

Silk, J., Altmann, J., & Alberts, S. (2006). Social relationships among adult female baboons (*Papio cynocephalus*) I. Variation in the strength of social bonds. *Behavioral Ecology and Sociobiology, 61*(2), 183–195.

Smith, B. R., & Blumstein, D. T. (2008). Fitness consequences of personality: A meta-analysis. *Behavioral Ecology, 19*(2), 448–455.

Snijders, L., & Naguib, M. (2017). Communication in animal social networks: A missing link? *Advances in the Study of Behavior, 49*, 297–359.

Staiano, J., Lepri, B., Aharony, N., Pianesi, F., Sebe, N., & Pentland, A. (2012). Friends don't lie: Inferring personality traits from social network structure. In *Proceedings of the 2012 ACM Conference on Ubiquitous Computing, Pittsburgh, PA, 5–8 September* (pp. 321–330). New York, NY: Association for Computing Machinery. https://doi.org/10.1145/2370216.2370266.

Taborsky, B., & Oliveira, R. F. (2012). Social competence: An evolutionary approach. *Trends in Ecology & Evolution, 27*(12), 679–688. https://doi.org/10.1016/j.tree.2012.09.003.

Vander Wal, E., Festa-Bianchet, M., Réale, D., Coltman, D. W., & Pelletier, F. (2015). Sex-based differences in the adaptive value of social behavior contrasted against morphology and environment. *Ecology, 96*(3), 631–641. https://doi.org/10.1890/14-1320.1.

Wassermann, S., & Faust, K. (1994). *Social networks analysis*. Cambridge, U.K.: Cambridge University Press.

Weidt, A., Hofmann, S. E., & König, B. (2008). Not only mate choice matters: Fitness consequences of social partner choice in female house mice. *Animal Behaviour, 75*, 801–808.

Wey, T., Blumstein, D. T., Shen, W., & Jordán, F. (2008). Social network analysis of animal behaviour: A promising tool for the study of sociality. *Animal Behaviour, 75*, 333–344.

Wilson, D. E., & Hanlon, E. (2010). *Lemur catta* (Primates: Lemuridae). *Mammalian Species, 42*, 58–74.

Wilson, A. D. M., Krause, S., Dingemanse, N. J., & Krause, J. (2013). Network position: A key component in the characterization of social personality types. *Behavioral Ecology and Sociobiology, 67*(1), 163–173.

Wolf, M., & Krause, J. (2014). Why personality differences matter for social functioning and social structure. *Trends in Ecology & Evolution, 29*(6), 306–308.

Wolf, M., & Weissing, F. J. (2012). Animal personalities: Consequences for ecology and evolution. *Trends in Ecology & Evolution, 27*(8), 452–461.