Original Article

Age differences in the temporal stability of a male African elephant (*Loxodonta africana*) social network

Derek Murphy,[a,◉] Hannah S. Mumby,[a,b,c,d,◉] and Michelle D. Henley[e,f]

[a]Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK, [b]College for Life Sciences, Wissenschaftskolleg zu Berlin, Wallotstraße 19, 14193 Berlin, Germany, [c]Centre for African Ecology, School of Animal, Plant and Environmental Sciences, University of Witwatersrand, Private Bag 3, Wits 2050, South Africa, [d]School of Biological Sciences, University of Hong Kong, Pok Fu Lam, Hong Kong, [e]Elephants Alive, Hoedspruit, South Africa, and [f]Applied Ecosystem and Conservation Research Unit, University of South Africa, Johannesburg, South Africa

Social animals live in complex and variable socio-ecological environments where individuals adapt their behavior to local conditions. Recently, there have been calls for studies of animal social networks to take account of temporal dynamics in social relationships as these have implications for the spread of information and disease, group cohesion, and the drivers of sociality, and there is evidence that maintaining stable social relationships has fitness benefits. It has recently been recognized that male elephants form strong social bonds with other males. The nature of these relationships, and thus network structure, may vary over time in response to varying environmental conditions and as individuals age. Using social network analysis, we examine the stability of relationships and network centrality in a population of male African elephants. Our results suggest that males may maintain stable social relationships with others over time. Older males show greater stability in network centrality than younger males, suggesting younger males face uncertainty in transitioning to adult society. For elephants, where older individuals function as social repositories of knowledge, maintaining a social network underpinned by older males could be of particular importance.

Key words: **African elephant, age differences, conservation, male–male associations, social behavior, temporal stability.**

INTRODUCTION

Many species of social animals—especially long-lived species such as elephants, cetaceans, and primates (including humans)—live in complex and variable socio-ecological environments (Wittemyer et al. 2005; Lusseau 2007; Poole and Moss 2008; Henzi et al. 2009; Rand et al. 2011; Apicella et al. 2012; Kramer et al. 2014; McFarland et al. 2014; Connor and Krützen 2015; Goldenberg et al. 2016). Individuals must continuously adjust their social behavior in response to inconstant local environmental conditions, the behavior of conspecifics, and their own motivational states to maintain group cohesion and benefit from the advantages of living in a social group (Cheney et al. 1986; Silk 2007; Henzi et al. 2009; Barrett et al. 2012; McFarland et al. 2014; Josephs et al. 2016). Information about the temporal dynamics of a social network can have important implications for understanding and predicting group fission (Sueur

and Maire 2014; Haulsee et al. 2016), as well as processes of flow through a social group such as how information is shared or disease is spread among individuals (Böhm et al. 2009; Hamede et al. 2009; Hobaiter et al. 2014; Silk et al. 2017; Farine 2018), and may reveal new insights into the relationship between the ecological and social environments that may be hidden when examining static social networks (Henzi et al. 2009; Leu et al. 2016).

A number of recent studies have examined or accounted for temporal dynamics in social networks (e.g., Henzi et al. 2009; Hobaiter et al. 2014; Shizuka et al. 2014; Ilany et al. 2015; Tranmer et al. 2015), but despite recent calls for studies to take temporal dynamics into account (Blonder et al. 2012; Hobson et al. 2013; Pinter-Wollman et al. 2014; Farine 2018), they are not very numerous. Some studies have found evidence for temporal stability in social relationships among females in animal groups (e.g., yellow baboons [*Papio cynocephalus*, Silk et al. 2006] and chacma baboons [*Papio hamadryas ursinus*, Silk et al. 2010a], giraffes (*Giraffa camelopardalis*, Carter et al. 2013), Asian elephants [*Elephas maximus*, Nandini

Address correspondence to H.S. Mumby. E-mail: hsmumby@hku.hk.

et al. 2017]), but fewer have found evidence for stable relationships among adult males (e.g., chimpanzees [*Pan troglodytes*, Mitani 2009], bottlenose dolphins [*Tursiops truncatus*, Parsons et al. 2003]). There is some evidence that there are fitness advantages to maintaining stable social relationships (Cameron et al. 2009; Silk et al. 2009; Silk et al. 2010b), such as increased longevity and greater rates of infant survival found in female baboons (Silk et al. 2009; Silk et al. 2010b) and greater infant fledging success for female ani (*Crotophaga major*), a cooperatively breeding tropical bird (Riehl and Strong 2018). However, others have found no evidence for stability in female baboon relationships and have argued that social relationships among female baboons reflect contingent responses to a variable socio-ecological environment to meet short-term goals (Henazi and Barrett 1999; Barrett and Henzi 2002; Henzi et al. 2009; McFarland et al. 2017).

In terms of long-lived social mammals, the social structure of female African elephants and female sperm whales (*Physeter macrocephalus*) is remarkably similar, where females of both species form temporally stable social relationships in complex, multi-tiered societies (Wittemyer et al. 2005, Whitehead et al. 2012). However, adult male sperm whales do not appear to form preferred social relationships or maintain stable social bonds with other males (Lettevall et al. 2002). To our knowledge, there have been no attempts to determine whether male elephants maintain stable social roles over time.

In fact, until recently, it was assumed that adult male elephants are similarly unsocial or weakly social, but a recent study has shown that it is important to account for the fact that they are periodically unavailable as social partners when they are in a sexually active state (Goldenberg et al. 2014). The results of this study suggest that male elephants do form stronger social bonds than previously expected, which may be driven partly by age and genetic relatedness (Chiyo et al. 2011). Despite these interesting findings, it is not known whether male elephants maintain these social relationships over time. One study found that younger male elephants may benefit more from the social structure provided by a stable, linear dominance hierarchy than older males (O'Connell-Rodwell et al. 2011). During periods in which there was no linear dominance hierarchy observed, younger males showed increased levels of aggression (O'Connell-Rodwell et al. 2011).

Another important aspect of an individual's sociality is the position they occupy within their social network. Individuals occupy different roles within their social groups (Lusseau and Newman 2004) and these roles may be quantified using social network centrality measures such as strength (a measure of general gregariousness) or eigenvector centrality (EC—a measure of how well connected an individual is to other important individuals in the network) (Whitehead 2008). More central individuals within a social network may be important for maintaining network structure and group cohesion (Flack et al. 2005; Flack, Girvan, de Waal, et al. 2006), and they may gain fitness benefits as a result of their more central positions (Stanton and Mann 2012, Cheney et al. 2016, Ellis et al. 2017). Among African elephants, older females have been found to occupy more central positions in their networks (Goldenberg et al. 2016). However, there is conflicting evidence as to whether older males also occupy more central positions in their social networks. Chiyo and his colleagues found that older males had greater strength and EC than younger males (Chiyo et al. 2011), whereas Evans and Harris found that younger males were more sociable and typically found in larger social groups than older males (Evans and Harris 2008), and Goldenberg and her colleagues found the

relationship between age and network centrality depended on sexual state: in a sexually inactive state, they found no relationship between EC or degree centrality (i.e., a measure of gregariousness similar to strength) and age, whereas in a sexually active state, they found a negative correlation between age and both EC and degree centrality (Goldenberg et al. 2014).

It has been argued that network centrality reflects an adaptive trait under selective pressure (Aplin et al. 2015) and some studies have found evidence for heritability of certain network centrality measures (Lea et al. 2010, Brent et al. 2013). Stability in social behavioral strategies within individuals may be expected to arise due to life-history trade-offs relating to the costs and benefits of maintaining more central positions in a network (Aplin et al. 2015), where more central individuals may benefit from greater access to social information (Aplin et al. 2012) and greater reproductive success (McDonald 2007; Formica et al. 2012), but may also experience greater levels of competition (Oh and Badyaev 2010) and exposure to disease (Hamede et al. 2009). Despite this, few studies have investigated consistency of social network position within individuals over time, although recent studies have found evidence for stable network positions within individuals in sharks (*Scyliorhinus canicula*, Jacoby et al. 2014) and great tits (*Parus major*, Aplin et al. 2015), suggesting that individuals maintain a stable "social phenotype," which has great importance for understanding the evolution and adaptive significance of social structure.

In this study, we examine the stability of social relationships and social network centrality in male elephants. Using a long-term (16 years) dataset on the spatial associations among adult male African elephants at the Associated Private Nature Reserves (APNR) in South Africa, firstly, we aim to determine whether there is evidence that male elephants maintain stable social relationships with other adult males over time. If so, it is possible that there are differences between older and younger males in both the temporal stability of their relationships and of their positions in the social network (as measured by the network centrality measures strength and EC). If this is the case, we expect that younger males, who are in the process of transitioning into male society (Lee and Moss 1999, Lee et al. 2011), will be less central in the social network of adult males, and will also show less stability than older males in both their social relationships and their network positions.

METHODS

Data collection

Data were collected at the Associated Private Nature Reserves (APNR) in the north-east of South Africa (24°18′S, 31°18′E). The APNR is a series of neighboring, privately owned nature reserves contiguous with the western boundary of Kruger National Park with no internal boundary fences among the reserves that make up the APNR, nor between the APNR and Kruger National Park. Data were collected between November 2002 and February 2018 inclusive.

Spatial association data were collected on average 2.3 days per week (mean calculated over the entire study period; see Supplementary Information for further information about sampling effort). During this time, between 1 and 20 adult male elephants had active GPS collars (Henley 2014). On each data collection day, field researchers located a lone elephant or group of elephants either by chance as they drove through the field site to or from pre-selected collared individuals or from within all the

associates found at the location of a collared individual if they were not solitary. Once the elephant or group was located, the researchers recorded the date, time and GPS coordinates and they took photographs of as many of the individuals present in the group as possible in order to confirm their identities later. They also noted the group composition (lone bull, bull group, mixed group, as well as groups composed of females and offspring, which are not included in this study) and the identity of any of the adult males that appeared to be in musth (Poole 1987). A "group" was defined as all individuals within sight of the researchers that appeared to be moving in the same direction and which typically were not more than 100 m from the center of the group (Wittemyer et al. 2005; Chiyo et al. 2011; Goldenberg et al. 2014). The range of vision of observers was typically limited to a 100 m radius, depending on the density of the vegetation. Where large groups of associating elephants arrived simultaneously at a waterhole and departed simultaneously in the same direction, they were considered part of the same group. On average, 1.8 groups were observed per sampling day with a mean of 1.6 individuals per group (SD = 1.2, min = 1, max = 11). Researchers also recorded the identities of any dead individuals they observed (N = 29 over the entire study period; see Supplementary Materials for further information), the cause of death (where known) and the date of the observation (which was taken as the confirmed date of death).

Data were divided into four sampling periods (SPs) of 4 years to replicate the length of SP used by Goldenberg et al. (2014) (SP1: November 2002 – October 2006; SP2: November 2006 – October 2010; SP3: November 2010 – October 2014; SP4: November 2014 – February 2018). Ages for each male were visually estimated based on a combination of characteristics related to the size, physical development, eruption of tusks, the length and circumference of the tusks, body shape proportions and behavioral characteristics (Poole 1987; Moss 1996; Henley 2012; Henley 2013) and averaged over each 4-year SP. Given that our measure of age was estimated and averaged, using a continuous scale in our analyses may have resulted in spurious accuracy and thus was not deemed suitable for this dataset. Instead, we grouped individuals to replicate the age groups previously used by Chiyo and colleagues (2011) to study age effects in male African elephant sociality. Individuals were thus categorized as "younger" adults (20–29 years old) or "older" adults (30+ years old) within each SP based on their mean age over the length of the SP. These age groups correspond to biologically meaningful age ranges, where males from 20 to 29 years are fully independent, experience their first musth, and become reproductively active (Lee et al. 2011), whereas from age 30 they are considered reproductively competitive (Poole 1982; Poole et al. 2011). Thus, the group we will call "younger" adults consist of both young and early adult males, whereas the group we will call "older" adults may be considered mature, prime breeding adults. By using the

mean age over the SP, we assigned individuals to the age group in which they spent the majority of each SP.

Network metrics

For the network computations, we included only sightings of males known to be independent of their family units (aged 20+) in male-only groups (lone bulls or bull groups). Furthermore, we excluded any male from an observation if it was observed to be in musth so that only associations between non-musth individuals were included in our network calculations, although we did not exclude individuals that were not overtly signaling sexual state as in the calculations for the sexually inactive network in Goldenberg et al. (2014). Finally, we excluded individuals from the network calculations for a given SP if they died less than 85% of the way through that SP. This resulted in a mean of 540 group observations included per SP and a mean of 3.2–5.0 observations per individual per SP (Table 1).

We made the assumption that all individuals in an observed group were associating with each other individual in the group (i.e., the Gambit-of-the-Group assumption; Franks et al. 2010) for our network computations. For each SP, we computed a symmetric matrix of weighted association indices (AIs) for each dyad using the simple ratio index as AI = $N_{AB}/(N_{AB} + N_A + N_B)$, where N_{AB} is the number of times individuals A and B were observed in the same group, N_A is the number of times individual A was observed without individual B, and N_B is the number of times individual B was observed without individual A (Cairns and Schwager 1987; Whitehead 2008). AIs give a measure of the strength of the relationship between two individuals, given the number of times each individual was observed together and separately (see Supplementary Materials for details of the mean AI values per SP). Next, we calculated two individual-level network centrality measures for each individual in each SP: strength (also known as weighted degree) and EC (Whitehead 2008). Strength and EC have been found to be robust measures of centrality even when the mean number of observations per individual is low (Silk et al. 2015; Davis et al. 2018). Network measures were calculated using the igraph package (Csárdi and Nepusz 2006) in R version 3.5.0 (R Core Team 2018).

Statistical analyses

Temporal stability of relationships

To determine whether individuals maintained stable relationships over time, we compared the stability of dyads across each pair of consecutive SPs (i.e., SP1 and SP2, SP2 and SP3, SP3 and SP4). For each comparison, we included only those individuals that were observed at least five times in both SPs in the comparison (23 individuals in SPs 1 and 2, 25 in SPs 2 and 3, 22 in SPs 3 and 4). For each individual within each SP we ranked the AI of all dyads in which that individual appeared where 1 indicated the dyad with the largest AI (i.e., the dyad that included the individual of interest

Table 1
Descriptive statistics for each SP

SP	N, group sightings	N, unique individuals	Mean obs per ID	N, younger	Mean obs per ID (younger)	N, older	Mean obs per ID (older)
1	553	258	3.2	118	2.1	140	4.1
2	495	221	3.5	127	2.5	94	5
3	428	179	3.8	119	2.1	60	7.2
4	684	257	5.0	187	2.8	70	10.9

and their top associate within a given SP). Where dyads had equal AI values, we assigned each "tied" dyad the minimum rank (e.g., where two dyads were tied for rank position 3, both were assigned rank 3 rather than rank 4). We then counted the number of associates that were included in the top three dyads for each individual in the first SP in the comparison that also appeared in the top three for that individual in the second SP in the comparison. Note that because of the rank ties method described above, an individual may have more than three associates included in their top three dyads. A "stable relationship" was classed as any dyad that appeared in an individual's top three ranked dyads in two consecutive SPs. That is, if individual A's top three associates in SP1 were individuals B, C, and D, and in SP2 were B, D, and E, then A had two stable relationships from SP1 to SP2).

To determine whether there was a difference in the likelihood that older and younger individuals maintained stable relationships, we fit three generalized linear models (one for each pair of consecutive SPs) with a binomial distribution with age-class as a fixed effect and the outcome variable was the proportion of stable relationships maintained by an individual from one SP to the next out of the number of potential stable relationships for that individual over the same pair of SPs. Stable relationships were calculated as above. We included only individuals that appeared in the same age category in each pair of SPs in each comparison and only those individuals that were sighted at least five times within each SP (SPs1 – 2: 11 younger, 12 older; SPs2 – 3: 11 younger, 14 older; SPs3 – 4: 3 younger, 11 older).

Age and temporal stability in network centrality

First, we fit two linear mixed-effects models (LMMs) using the lme4 package (Bates et al. 2015) in R (R Core Team 2018) to model the relationship between age-class (a factor with two levels: older and younger adults) and each measure of network centrality (strength and EC, both continuous variables). In each model, we included SP and ID as random effects. We used a Bonferroni correction for multiple tests with the same dataset to determine the significance of both sets of model results, where two-tailed $\alpha = 0.025/2 = 0.0125$.

Next, to determine whether older males were more stable in their network centrality over time, first we ranked each individual's centrality values (strength and EC) within each SP and then standardized the ranks by dividing each rank by the maximum rank value within each SP so that each rank fell between 0 and 1. Then we calculated the coefficient of variation (CV) for both centrality measures for each individual as the standard deviation of an individual's standardized ranked centrality values divided by the mean standardized ranked centrality for that individual across all SPs in which the individual appeared. Greater values of CV indicate a lower degree of stability in network centrality. We included only individuals that appeared in the same age-class in at least three SPs (e.g., for a "younger" individual to be included, it would have to have been classed as "younger" in at least three consecutive SPs). Thus, 39 unique individuals were included in this set of analyses (13 younger, 26 older). We fit two linear models (LMs) with CV of strength and CV of EC as the outcome variable in each model, and age-class as a fixed-effect. We included the number of SPs an individual was observed in as a weight in the models. Again, we used a Bonferroni correction, where two-tailed $\alpha = 0.025/2 = 0.0125$.

Randomized null models

Network data are unsuitable for typical parametric statistical analyses as they are, by definition, not independent. Therefore, for all

analyses we used randomized null models by permuting the pre-network data to determine whether an observed effect was likely to have occurred by chance given the structure inherent in the data (Farine 2017). Randomized null models based on pre-network data are particularly useful combined with linear mixed models when comparing individual-level network metrics within a network as they can account for the uncertainty in these metrics that is expected due to the structure inherent in the data (Farine 2017). We generated 1000 randomized datasets, each one with 1000 "flips" between individuals observed in different groups on the same day, thus scrambling the social processes that might have given rise to the observed effect or value, while maintaining the structural properties of the data. We then calculated network metrics and test statistics for each randomized dataset as we did with the observed data and compared the distribution of resulting test statistics to the observed test statistic. If the observed value was greater than 97.5% or lower than 2.5% of the randomized values (i.e., two-tailed significance where $P < 0.025$), this was taken as evidence that the effect was significantly different than expected by chance and is reported alongside the test statistic as a P_{rand} value (where P_{rand} reflects the proportion of the 1000 randomized test statistics that were greater or less than the observed statistic). In our analyses, the relevant test statistics were the slope of the main effect in the case of LMs, LMMs, and GLMs, and the number of stable relationships maintained by individuals across pairs of SPs.

RESULTS

Temporal stability in relationships

To determine whether there was evidence that males maintained stable relationships over time, we compared the test statistic (in this case the total number of stable relationships observed between each pair of consecutive SPs) to the randomized distribution of the test statistic from the null models. We found no evidence that the number of stable relationships males maintained was any greater than chance between SP1 and SP2 ($n = 49$, $P_{rand} = 0.105$) and between SP2 and SP3 ($n = 47$, $P_{rand} = 0.143$). However, there was evidence that they maintained more stable relationships than expected between SP3 and SP4 ($n = 48$, $P_{rand} = 0.021$).

Using three binomial GLMs (one for each pair of consecutive SPs), we compared the test statistics (the slope of the effects for each model) to the appropriate distribution of test statistics from the randomized null models and found no evidence that older and younger males differed in their likelihood of maintaining stable relationships over time (SP1–2: $\beta = -0.322$, $P_{rand} = 0.064$; SP2–3: $\beta = -0.383$, $P_{rand} = 0.312$; SP3–4: $\beta = 0.788$, $P_{rand} = 0.208$; Table 2 and Figure 1).

Age and temporal stability in network centrality

We used two LMMs to model the relationship between age-class and both measures of network centrality (strength and EC). We compared the observed test statistic (the slope of the fixed effect) to the distribution of test statistics from the randomized null models. We found no evidence that either strength ($\beta = 0.037$, $P_{rand} = 0.153$) or EC ($\beta = -0.008$, $P_{rand} = 0.116$) differed between age classes (Tables 3 and 4, and Figure 2).

Next, we used two LMs to determine whether older males showed greater stability in network centrality over time than younger males. We found no evidence that older males were more stable than younger males in EC ($\beta = 0.041$, $P_{rand} = 0.161$). However, older

males showed greater stability than younger males in strength (i.e., older males, aged 30+, had significantly lower values of CV for strength than younger males; $\beta = -0.185$, $P_{rand} = 0.01$; Table 5 and Figure 3). This result held after applying a Bonferroni correction for multiple tests with the same dataset, where two-tailed $\alpha = 0.025/2 = 0.0125$.

DISCUSSION

This is the first study to investigate the temporal stability of social relationships and social network centrality in male elephants, and also the first study to relate these to age effects. Our results suggest that adult male elephants maintain stable social relationships over time, but the likelihood that an individual maintains stable relationships with others does not vary with age. Similarly, we found no evidence that older and younger males differ in their network centrality, nor that they differ with regards to stability in EC over time. However, older males (30+ years) maintained greater stability in their position in the social network than younger males

Table 2

Model output with P_{rand} value from the binomial GLM describing the relationship between the likelihood of maintaining stable social relationships and age category across each pair of consecutive SPs

	Estimate	Standard error	P_{rand}
SP1–SP2			
Intercept	2.303	0.742	
Age category (older)	−0.322	0.913	0.064
SP2–SP3			
Intercept	1.299	0.461	
Age category (older)	−0.383	0.593	0.312
SP3–SP4			
Intercept	0.598	0.375	
Age category (younger)	0.788	0.875	0.208

Significant result, indicating that the estimated slope of the effect is greater (more positive or more negative, depending on the direction of the effect) than expected.

(20–29 years) as measured by the centrality measure strength. Since lack of stability in EC reflects the variability in the identity and behavior of an individual's social partners, whereas stability in strength suggests consistency in an individual's own behavioral strategy, older males appear to have more stability in their social behavioral strategies from one SP to the next, while younger males show more variability in the frequency with which they interact with others over time.

Previously, Goldenberg and her colleagues (2014) found that male elephants form stronger social bonds than previously expected when in a sexually inactive state. Our results further contribute to our knowledge of male elephant sociality, suggesting that males not only form strong social bonds, but they may also maintain stable social relationships over long periods of time. However, we only found evidence for stable relationships between two of our four SPs. The lack of evidence for stable relationships among the other SPs may simply reflect a lack of power to detect stable relationships due to our relatively small sample sizes, or that males maintain stable social relationships over different time-scales than the 4-year SPs we have examined here. Future studies with higher resolution data may find stability in social relationships from season to season or year to year, or even decade to decade, and thus shed light on the drivers of stability in male social relationships. It is also possible that stability in social relationships among male elephants may be driven by contingent behavioral responses to local conditions and motivational states, similar to the relationships of female baboons described by Barrett, Henzi and their colleagues (Henazi and Barrett 1999; Barrett and Henzi 2002; Henzi et al. 2009; McFarland et al. 2017). Indeed, it is interesting to note that the only period over which we found evidence for stable social relationships (2010–2018) coincided with a dramatic decline in estimated population size of elephants in Mozambique, which was likely due to an increase in ivory poaching (Chase et al. 2016). Our study area, the APNR, is part of an open system, contiguous with the Great Limpopo Transfrontier Conservation Area, which includes Kruger National Park in South Africa and Limpopo National Park in Mozambique. The management of these protected areas has changed over time both prior to and during the study period (Robson and van Aarde
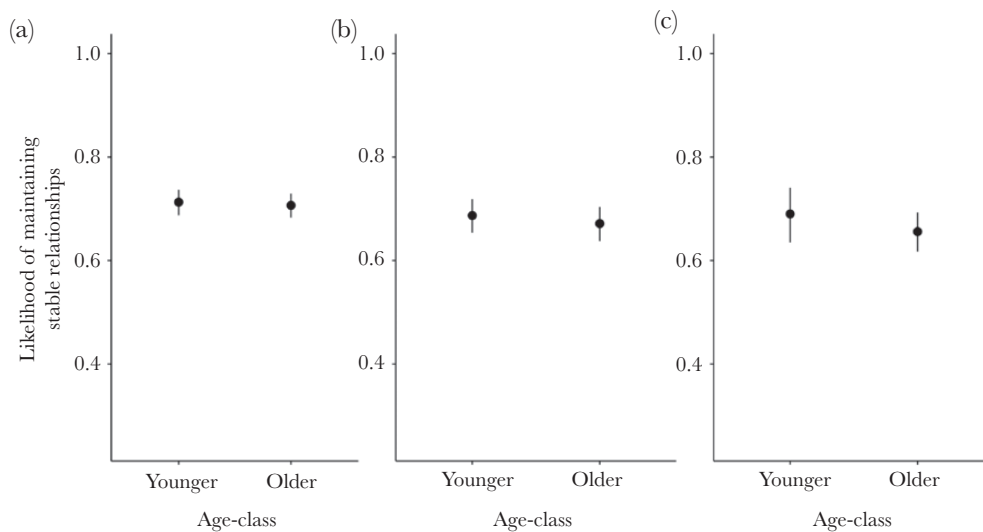

Figure 1
Model predicted likelihoods and confidence intervals for older and younger males to maintain stable social relationships from (a) SP1 to SP2, (b) SP2 to SP3, and (c) SP3 to SP4.

2018). Furthermore, sections of the fence separating the two parks have been removed since 2002 (Wray 2017). It is possible that the stability we found during this period reflects the spillover effects of increased poaching in Mozambique, as greater levels of social integration have been found among individuals during times of greater stress (Mitchell 1969; Henzi et al. 2009).

Table 3

Model output with P_{rand} value from the LMM describing the relationship between strength and age category (we do not report degrees of freedom or t-values as these are not appropriate for interpreting model results using randomized null models)

	Estimate	Standard error	P_{rand}
Fixed effects			
Intercept	0.495	0.092	
Age category (older)	0.037	0.037	0.153
Random effects	Variance	Standard deviation	
ID	0.07	0.264	
Sampling period	0.031	0.177	
Residual	0.192	0.439	

Significant result, indicating that the estimated slope of the fixed effect is greater (more positive or more negative, depending on the direction of the effect) than expected.

Table 4

Model output with P_{rand} value from the LMM describing the relationship between EC and age category

	Estimate	Standard error	P_{rand}
Fixed effects			
Intercept	0.016	0.004	
Age category (older)	−0.008	0.004	0.116
Random effects	Variance	Standard deviation	
ID	<0.001	0.00	
Sampling period	<0.001	0.004	
Residual	0.004	0.065	

Significant result, indicating that the estimated slope of the fixed effect is greater (more positive or more negative, depending on the direction of the effect) than expected.

Our results complement what is known about the stability of female elephant social relationships, where females maintain strong, temporally stable bonds (Wittemyer et al. 2005). However, it is somewhat unexpected, given that male elephants are often solitary (Chiyo et al. 2011) and range over large distances (Roux and Bernard 2009) and thus may not encounter the same social partners for long periods of time. In terms of other species, there are similarities in the social structure of female African elephants and female sperm whales (*Physeter macrocephalus*). However, Lettevall and colleagues (2002) found no evidence for social structure or stable relationships among groups of male sperm whales. Stable social relationships among (nonhuman) male mammals are not as common as those among females (Van Hooff and Van Schaik 1994), and are typically found among kin (e.g., bottlenose dolphins, Parsons et al. 2003; lions (*Panthera leo*), Packer et al. 1991) in species where males are philopatric (e.g., chimpanzees, Mitani 2009). The stable relationships we found may indeed be driven by genetic relatedness, as social bonds among male elephants were found to be stronger among kin (Chiyo et al. 2011). Stable social bonds among male mammals are often linked to the formation of coalitions to secure mating opportunities, and fitness benefits of male coalitions have been found lions (Packer et al. 1991), horses (*Equus caballus*, Feh 1999), primates (Schülke et al. 2010), and birds (Ryder et al. 2009). There may also be fitness implications for male elephants that maintain stable social bonds with others over time, and if so, the benefits derived from such relationships may vary with age, and this may be a worthwhile avenue for future research

Network centrality has been found to vary with age in a number of species. In sperm whales, for example, young calves occupy the most central positions in their social networks as they receive allomothering care from many adult females (Gero et al. 2013). In contrast, older female African elephants have been found to be more central in their networks, acting as social hubs and repositories of fitness-relevant information (McComb et al. 2001; Wittemyer et al. 2005). Among female elephants, this age effect seems to be relative; social roles are passed from a mother to her daughters when she dies, and within 'highly disrupted' families, the oldest surviving female has been observed to act as a social hub for the surviving members of the group, even if she was a juvenile.

(a)

(b)
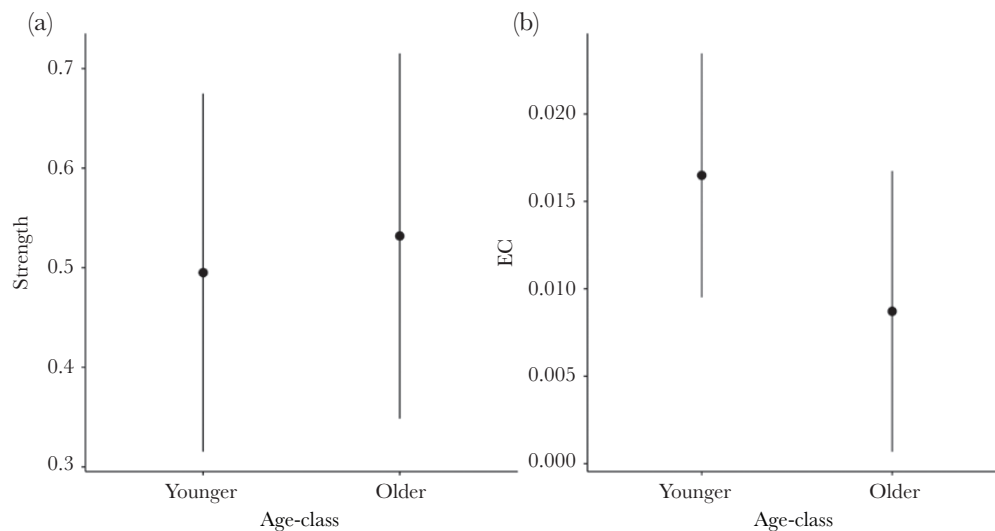
Figure 2
Predicted values and confidence intervals from the LMMs showing the nonsignificant difference between older and younger males in (a) strength and (b) EC.

(Goldenberg et al. 2016). Previous studies found conflicting results regarding the centrality of older male elephants within their social networks. Evans and Harris (2008) found that younger males were more sociable than older males and were typically found in larger groups, whereas Chiyo and his colleagues (2011) found that older males had greater strength and EC than younger males. Goldenberg and her colleagues (2014) found that the relationship between network centrality and age varied with sexual state. In a network of individuals in a sexually active state, they found a negative correlation between age and network centrality as measured by degree centrality and EC. In their sexually inactive network, they found no relationship between degree centrality or EC and age. Similarly, we found no evidence for a difference between older and younger males in a sexually inactive state in network centrality as measured by strength and EC within a given SP.

There were a number of methodological and analytical differences among our study and previous studies, which may explain these divergent results. Firstly, it is important to account for sexual state when examining the social networks of adult male elephants as failing to do this may lead to spuriously low estimates

of association rates where periods of restricted social behavior are treated as missed opportunities to associate (Goldenberg et al. 2014). We accounted for this in our study by including only associations among individuals in a sexually inactive state in our network calculations (something Goldenberg and colleagues' (2014) did using a different method of "sexually inactive network" calculations) but the other two studies did not (Evans and Harris 2008; Chiyo et al. 2011). Secondly, we used randomized null models by permuting the pre-network data to determine the likelihood that our results might simply reflect the structure inherent in our dataset, as network data are not suitable for typical parametric tests (Farine 2017). The previous studies differed with regard to their use of randomization tests. Evans and Harris (2008) did not use randomization tests, whereas Chiyo and colleagues (2011) used randomization tests in which the connections between individuals in the network but not the pre-network data were randomized, which may give less robust results (Farine 2017). Goldenberg and her colleagues (2014) used two kinds of randomization tests in their analyses: one similar to the pre-network randomizations described in this article, and another where the sexual state of individuals were randomly assigned to determine whether network centrality measures differed in sexually active and sexually inactive networks. Such "node-based" randomizations are often used to test for differences in network measures between individuals with different attributes, but they are based on the assumption that the observed data are highly representative of the "true" underlying network, and thus may result in higher rates of both Type I and Type II errors than using pre-network randomizations (Croft et al. 2011; Farine and Whitehead 2015; Farine 2017).

Our network calculations were based on a relatively small mean number of observations per individual compared to similar studies (3.9 in our study, cf. a minimum of 20 observations per individual (median 42–45 observations) in Goldenberg and colleagues' (2014) study, and a minimum of 15 observations per individual (mean 45 observations) in Chiyo and colleagues' (2011) study. Small samples are a common issue in network studies with wild animals (Franks
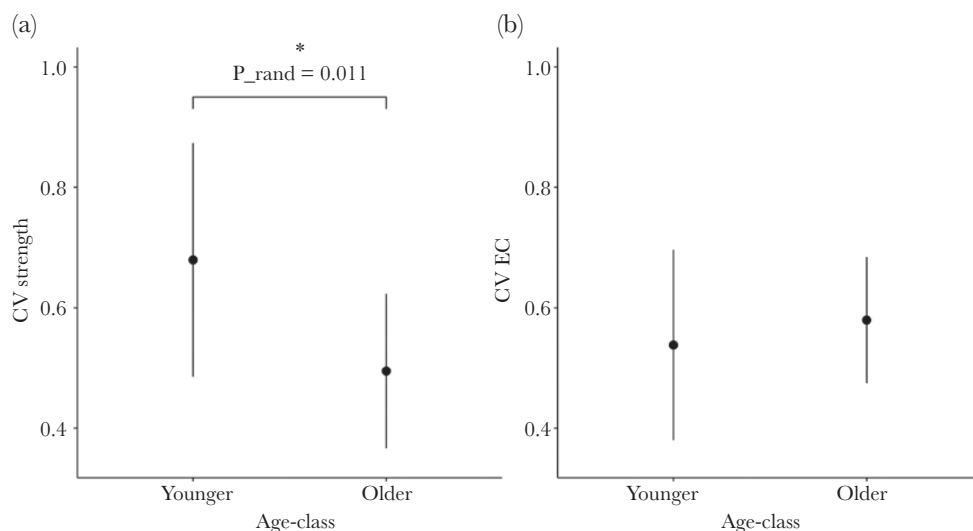
Table 5

Model output with P_{rand} value from the LM describing the relationship between stability in strength (CV of standardized, ranked strength scores) and age category and between stability in EC (CV of standardized, ranked EC scores) and age category

	Estimate	Standard error	P_{rand}
Strength			
Intercept	0.679	0.096	
Age category (older)	−0.185	0.115	0.011*
EC			
Intercept	0.538	0.078	
Age category (older)	0.041	0.094	0.161

*Significant result, indicating that the estimated slope of the effect is greater (more positive or more negative, depending on the direction of the effect) than expected.

Figure 3
Predicted values and confidence intervals from the LMs showing (a) that older males have significantly lower values of CV for strength (i.e., have greater stability in strength) than younger males and (b) no significant difference between older and younger males in CV values for EC. The P_{rand} value reflects the proportion of randomized null models where the slope of the effect was greater (in this case, more negative) than the slope of the model using the observed data.

et al. 2010, Silk et al. 2015, Garamszegi 2016, Davis et al. 2018, Hoppitt and Farine 2018), particularly those that range over large areas (Murphy et al. in preparation), and in the worst cases may lead to values of network centrality measures that do not accurately represent underlying social behavior and structure (James et al. 2009, Farine and Whitehead 2015). To make our analyses as robust as possible, we used only strength and EC as our network measures of interest, as these have been shown to be relatively accurate even when calculated with few observations per individual, although greater numbers of observations lead to greater levels of accuracy (Davis et al. 2018). Furthermore, by using randomized null models, we can be confident that any significant effects that we found are unlikely to be due to bias inherent in our dataset (Farine 2017), although the lack of an effect may simply reflect a lack of power to detect an effect due to insufficient sampling. Future studies with greater numbers of samples per individual over a similar time-scale as in this study may indeed find temporal stability in EC and other network measures where we failed to find such an effect.

In terms of the age differences we found, given the uncertain, novel social environment that young males face, it is unsurprising that they show less stability in their behavioral responses to others. In contrast, older males may have learned to better navigate their social environment. Although males are thought to make the transition from life in their natal group to independence between 10 and 19 years of age (Lee et al. 2011), the lower level of stability in network centrality we found for males between 20 and 30 years suggest that males continue to adapt their behavior well after this period. Although we did not include males younger than 20 years in our study, Evans and Harris (2008) and Chiyo et al. (2011) included younger individuals (estimated to be at least 10 years old) in their analyses. We excluded males younger than 20 years old from our analyses for both biological and practical reasons: these males are typically more difficult to identify as they are observed infrequently when they begin to disperse and tend to lack distinctive ear markings. Furthermore, males under 20 years old are typically still dependent on their maternal family units and spend a significant proportion of their time in mixed-sex groups (Lee et al. 2011). Indeed, Chiyo et al. (2011) found that males aged 10–19 years showed a random association pattern with older males, which they suggest was due to the younger males spending less time in all-male groups and more time with their natal groups.

It is possible that the greater stability in network strength of older males also reflects a greater consistency in (non-musth) spatial range use by older males, whereas younger males have not yet established a core "home range." Consistency in spatial range use, or spatial philopatry, is thought to allow individuals to exploit areas more effectively due to having a greater level of spatial and ecological information (Piper 2011; Spencer 2012). Goldenberg and her colleagues (2018) recently found that the loss of mature individuals was an important predictor of spatial range shifts among female elephant groups, where there was often a trade-off between resource availability and safety. Understanding how male elephant spatial behavior changes with age and how population-level spatial ranges may be influenced by the loss of older males in a changing landscape may be of particular importance to future conservation efforts (Goldenberg et al. 2018). Future studies using long-term data gathered from geotagged animals may be able to illuminate the relationship between age and spatial behavior among males.

Our results contribute to the growing body of evidence suggesting that older male elephants are of particular importance to elephant conservation efforts (Chiyo et al. 2011; Archie and Chiyo 2012). Older males are at greater risk from poaching or hunting (Chiyo et al. 2015) as they are typically larger, with bigger tusks, and maybe more likely to be alone (Poole 1994). Previous studies have shown that the loss of older males increases reproductive skew (Ishengoma et al. 2008), decreasing genetic diversity in wild populations (Archie and Chiyo 2012). Older males are also important repositories of fitness-relevant social and ecological information that younger males rely on (Evans and Harris 2008), similar to the role of matriarchs in breeding herds (McComb et al. 2001). Furthermore, our results suggest that younger males may continue to learn new social behavioral strategies from older males until at least 30 years of age—long after they have become independent from their natal groups. Our results further suggest that the loss of older males, who maintain more stable positions in their social network positions than younger males, may lead to instability in population-level social structure and spatial range use. Higher resolution data may allow us greater insight into the impacts of the loss of older males on network structure, however such data are difficult to collect on large, wide-ranging animals (Murphy et al., in preparation).

Given the temporal variability in sociality that we found, future studies should consider the temporal dynamics of social behavior and the age structure of a population when quantifying the structure of male social groups. Our findings may have important implications for understanding how male animals integrate into adult male societies in other species where males emigrate from their natal groups and form male groups (e.g., horses, McDonnell and Murray 1995; giraffes, Bercovitch and Berry 2014; dolphins, Fury et al. 2013, Cape ground squirrels (*Xerus inauris*), Waterman 1997), an area which has received very little research attention.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at *Behavioral Ecology* online.

REFERENCES

Apicella CL, Marlowe FW, Fowler JH, Christakis NA. 2012. Social networks and cooperation in hunter-gatherers. Nature. 481:497–501.
Aplin LM, Farine DR, Morand-Ferron J, Sheldon BC. 2012. Social networks predict patch discovery in a wild population of songbirds. Proc Biol Sci. 279:4199–4205.

Aplin LM, Firth JA, Farine DR, Voelkl B, Crates RA, Culina A, Garroway CJ, Hinde CA, Kidd LR, Psorakis I, et al. 2015. Consistent individual differences in the social phenotypes of wild great tits, Parus major. Anim Behav. 108:117–127.

Archie EA, Chiyo PI. 2012. Elephant behaviour and conservation: social relationships, the effects of poaching, and genetic tools for management. Mol Ecol. 21:765–778.

Barrett L, Henzi SP. 2002. Constraints on relationship formation among female primates. Behaviour. 139(2):263–289.

Barrett L, Henzi SP, Lusseau D. 2012. Taking sociality seriously: the structure of multi-dimensional social networks as a source of information for individuals. Philos Trans R Soc Lond B Biol Sci. 367:2108–2118.

Bates D, Maechler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using lme4. J Stat Soft. 67(1):1–48.

Bercovitch FB, Berry PSM. 2014. The composition and function of all-male herds of Thornicroft's giraffe, Giraffa camelopardalis Thornicrofti, in Zambia. Afr J Ecol. 53(2):167–174.

Blonder B, Wey TW, Dornhaus A, James R, Sih A. 2012. Temporal dynamics and network analysis. Methods Ecol Evol. 3(6):958–972.

Böhm M, Hutchings MR, White PC. 2009. Contact networks in a wildlife-livestock host community: identifying high-risk individuals in the transmission of bovine TB among badgers and cattle. PLoS One. 4:e5016.

Brent LJ, Heilbronner SR, Horvath JE, Gonzalez-Martinez J, Ruiz-Lambides A, Robinson AG, Skene JH, Platt ML. 2013. Genetic origins of social networks in rhesus macaques. Sci Rep. 3:1042.

Cairns SJ, Schwager SJ. 1987. A comparison of association indices. Anim Behav. 35(5):1454–1469.

Cameron EZ, Setsaas TH, Linklater WL. 2009. Social bonds between unrelated females increase reproductive success in feral horses. Proc Natl Acad Sci U S A. 106:13850–13853.

Carter KD, Brand R, Carter JK, Shorrocks B, Goldizen AW. 2013. Social networks, long-term associations and age-related sociability of wild giraffes. Anim Behav. 86(5):901–910.

Chase MJ, Schlossberg S, Griffin CR, Bouché PJ, Djene SW, Elkan PW, Ferreira S, Grossman F, Kohi EM, Landen K, et al. 2016. Continent-wide survey reveals massive decline in African savannah elephants. PeerJ. 4:e2354.

Cheney D, Seyfarth R, Smuts B. 1986. Social relationships and social cognition in nonhuman primates. Science. 234:1361–1366.

Cheney DL, Silk JB, Seyfarth RM. 2016. Network connections, dyadic bonds and fitness in wild female baboons. R Soc Open Sci. 3:160255.

Chiyo PI, Archie EA, Hollister-Smith JA, Lee PC, Poole JH, Moss CJ, Alberts SC. 2011. Association patterns of African elephants in all-male groups: the role of age and genetic relatedness. Anim Behav. 81(6):1093–1099.

Chiyo PI, Obanda V, Korir DK. 2015. Illegal tusk harvest and the decline of tusk size in the African elephant. Ecol Evol. 5:5216–5229.

Connor RC, Krützen M. 2015. Male dolphin alliances in Shark Bay: changing perspectives in a 30-year study. Anim Behav. 103:223–235.

Croft DP, Madden JR, Franks DW, James R. 2011. Hypothesis testing in animal social networks. Trends Ecol Evol. 26:502–507.

Csárdi G, Nepusz T. 2006. The igraph software package for complex network research. InterJournal Complex Systems. 6: 1695.

Davis GH, Crofoot MC, Farine DR. 2018. Estimating the robustness and uncertainty of animal social networks using different observational methods. Anim Behav. 141:29–44.

Ellis S, Franks DW, Nattrass S, Cant MA, Weiss MN, Giles D, Balcomb KC, Croft D. 2017. Mortality risk and social network position in resident killer whales: sex differences and the importance of resource abundance. Proc R Soc B. 284:20171313.

Evans KE, Harris S. 2008. Adolescence in male African elephants, Loxodonta africana, and the importance of sociality. Anim Behav. 76(3):779–787.

Farine DR. 2017. A guide to null models for animal social network analysis. Methods Ecol Evol. 8:1309–1320.

Farine DR. 2018. When to choose dynamic vs. static social network analysis. J Anim Ecol. 87:128–138.

Farine DR, Whitehead H. 2015. Constructing, conducting and interpreting animal social network analysis. J Anim Ecol. 84:1144–1163.

Feh C. 1999. Alliances and reproductive success in Camargue stallions. Anim Behav. 57:705–713.

Flack JC, Girvan M, de Waal FB, Krakauer DC. 2006. Policing stabilizes construction of social niches in primates. Nature. 439:426–429.

Flack JC, Krakauer DC, de Waal FB. 2005. Robustness mechanisms in primate societies: a perturbation study. Proc Biol Sci. 272:1091–1099.

Formica VA, Wood CW, Larsen WB, Butterfield RE, Augat ME, Hougen HY, Brodie ED. 2012. Fitness consequences of social network position in a wild population of forked fungus beetles (Bolitotherus cornutus). J Evol Biol. 25(1):130–137.

Franks DW, Ruxton GD, James R. 2010. Sampling animal association networks with the gambit of the group. Behav Ecol Sociobiol. 64(3):493–503.

Fury CA, Ruckstuhl KE, Harrison PL. 2013. Spatial and social sexual segregation patterns in indo-pacific bottlenose dolphins (Tursiops aduncus). PLoS One. 8:e52987.

Garamszegi LZ. 2016. A simple statistical guide for the analysis of behaviour when data are constrained due to practical or ethical reasons. Anim Behav. 120:223–234.

Gero S, Gordon J, Whitehead H. 2013. Calves as social hubs: dynamics of the social network within sperm whale units. Proc Biol Sci. 280:20131113.

Goldenberg SZ, Douglas-Hamilton I, Wittemyer G. 2016. Vertical transmission of social roles drives resilience to poaching in elephant networks. Curr Biol. 26:75–79.

Goldenberg SZ, Douglas-Hamilton I, Wittemyer G. 2018. Intergenerational change in African elephant range use is associated with poaching risk, primary productivity and adult mortality. Proc R Soc B. 285(1879):20180286.

Goldenberg SZ, de Silva S, Rasmussen HB, Douglas-Hamilton I, Wittemyer G. 2014. Controlling for behavioural state reveals social dynamics among male African elephants, Loxodonta africana. Anim Behav. 95:111–119.

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. 12:1147–1157.

Haulsee DE, Fox DA, Breece MW, Brown LM, Kneebone J, Skomal GB, Oliver MJ. 2016. Social network analysis reveals potential fission-fusion behavior in a shark. Sci Rep. 6:34087.

Henley MD. 2012. Aging elephants – a practical guide. In: Unpublished manual to the Associated Private Nature Reserves. p. 17.

Henley MD. 2013. Report on the demographics of the bull population of the Associated Private Nature Reserves. Available from: http://elephantsalive.org/wp-content/uploads/2019/04/ID-Study_Report_2013.pdf

Henley MD. 2014. Report on elephant movements in relation to water and the effect of the 2012 floods within the Associated Private Nature Reserves. Unpublished report to the Associated Private Nature Reserves. 32. Available from: http://elephantsalive.org/wp-content/uploads/2015/01/2014.pdf.

Henzi SP, Barrett L. 1999. The value of grooming to female primates. Primates. 40:47–59.

Henzi SP, Lusseau D, Weingrill T, van Schaik CP, Barrett L. 2009. Cyclicity in the structure of female baboon social networks. Behav Ecol Sociobiol. 63(7):1015–1021.

Hobaiter C, Poisot T, Zuberbühler K, Hoppitt W, Gruber T. 2014. Social network analysis shows direct evidence for social transmission of tool use in wild chimpanzees. PLoS Biol. 12:e1001960.

Hobson EA, Avery ML, Wright TF. 2013. An analytical framework for quantifying and testing patterns of temporal dynamics in social networks. Anim Behav. 85(1):83–96.

Hoppitt WJE, Farine DR. 2018. Association indices for quantifying social relationships: how to deal with missing observations of individuals or groups. Anim Behav. 136:227–238.

Ilany A, Booms AS, Holekamp KE. 2015. Topological effects of network structure on long-term social network dynamics in a wild mammal. Ecol Lett. 18:687–695.

Ishengoma DRS, Shedlock AM, Foley CAH, Foley LJ, Wasser SK, Balthazary ST, Mutayoba BM. 2008. Effects of poaching on bull mating success in a free ranging African elephant (Loxodonta africana) population in Tarangire National Park, Tanzania. Conserv Genet. 9(2):247–255.

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.

James R, Croft DP, Krause J. 2009. Potential banana skins in animal social network analysis. Behav Ecol Sociobiol. 63(7):989–997.

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.

Kramer AD, Guillory JE, Hancock JT. 2014. Experimental evidence of massive-scale emotional contagion through social networks. Proc Natl Acad Sci U S A. 111:8788–8790.

Lea AJ, Blumstein DT, Wey TW, Martin JG. 2010. Heritable victimization and the benefits of agonistic relationships. Proc Natl Acad Sci U S A. 107:21587–21592.

Lee PC, Moss CJ. 1999. The social context for learning and behavioural development among wild African elephants. In: Box HO, Gibson KR, editors. Mammalian social learning: comparative and ecological perspectives. Cambridge (UK): Cambridge University Press. p. 102–125.

Lee PC, Poole JH, Njiraini N, Sayialel SN, Moss CJ. 2011. Male social dynamics: independence and beyond. In: Moss C, Croze HJ, Lee PC, editors. The Amboseli elephants: A long-term perspective on a long-lived mammal. Chicago: University of Chicago Press. p. 260–271.

Lettevall E, Richter C, Jaquet N, Slooten E, Dawson S, Whitehead H, Christal J, McCall Howard P. 2002. Social structure and residency in aggregations of male sperm whales. Can J Zool. 80(7):1189–1196.

Leu ST, Farine DR, Wey TW, Sih A, Bull CM. 2016. Environment modulates population social structure: experimental evidence from replicated social networks of wild lizards. Anim Behav. 111:23–31.

Lusseau D. 2007. Why are male social relationships complex in the Doubtful Sound bottlenose dolphin population? PLoS One. 2:e348.

Lusseau D, Newman ME. 2004. Identifying the role that animals play in their social networks. Proc Biol Sci. 271(Suppl 6):S477–S481.

McComb K, Moss C, Durant SM, Baker L, Sayialel S. 2001. Matriarchs as repositories of social knowledge in African elephants. Science. 292:491–494.

McDonald DB. 2007. Predicting fate from early connectivity in a social network. Proc Natl Acad Sci U S A. 104:10910–10914.

McDonnell SM, Murray SC. 1995. Bachelor and Harem Stallion Behavior and Endocrinology. Biol Reprod. 52(monograph series1):577–590.

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. 154:357–364.

McFarland R, Murphy D, Lusseau D, Henzi SP, Parker JL, Pollet TV, Barrett L. 2017. The 'strength of weak ties' among female baboons: fitness-related benefits of social bonds. Animal Behaviour. 126:101–106.

Mitani JC. 2009. Male chimpanzees form enduring and equitable social bonds. Anim Behav. 77(3):633–640.

Mitchell J. 1969. The concept and use of social networks. In Mitchell J, editor. Social networks in urban situations. Manchester (UK): Manchester University Press. p. 1–50.

Moss CJ. 1996. Getting to know a population. In: Kangwana K, editor. Studying Elephants, AWF Technical Handbook Series 7. Nairobi (Kenya): African Wildlife Foundation. p. 58–74.

Murphy D, Mumby HS, Henley MD. 2019. Data from: age differences in the temporal stability of a male African elephant (*Loxodonta africana*) social network. Dryad Digital Repository. https://doi.org/10.5061/dryad.1j43g7r.

Nandini S, Keerthipriya P, Vidya TNC. 2017. Seasonal variation in female Asian elephant social structure in Nagarahole-Bandipur, southern India. Anim Behav. 134:135–145.

O'Connell-Rodwell CE, Wood JD, Kinzley C, Rodwell TC, Alarcon C, Wasser SK, Sapolsky R. 2011. Male African elephants (Loxodonta africana) queue when the stakes are high. Ethol Ecol Evol. 23(4):388–397.

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.

Packer C, Gilbert DA, Pusey AE, O'Brien SJ. 1991. A molecular genetic analysis of kinship and cooperation in African lions. Nature. 351(6327):562–565.

Parsons KM, Durban JW, Claridge DE, Balcomb KC, Noble LR, Thompson PM. 2003. Kinship as a basis for alliance formation between male bottlenose dolphins, Tursiops truncatus, in the Bahamas. Anim Behav. 66(1):185–194.

Pinter-Wollman N, Hobson EA, Smith JE, Edelman AJ, Shizuka D, De Silva S, Waters JS, Prager SD, Sasaki T, Wittemyer G, et al. 2014. The dynamics of animal social networks: analytical, conceptual, and theoretical advances. Behav Ecol. 25(2):242–255.

Piper WH. 2011. Making habitat selection more "familiar": a review. Behav Ecol Sociobiol. 65(7):1329–1351.

Poole JH. 1982. Musth and male-male competition in the African Elephant. PhD Thesis. University of Cambridge.

Poole JH. 1987. Rutting behavior in African elephants: the phenomenon of musth. Behaviour. 102(3):283–316.

Poole JH. 1994. Sex differences in the behaviour of African elephants. In: Short RV, Balaban E, editors. The differences between the sexes. Cambridge (UK). Cambridge University Press. p. 331–346.

Poole JH, Lee PC, Njiraini N, Moss CJ. 2011. Longevity, competition and musth: a long-term perspective on male reproductive strategies. In: Moss CJ, Croze HJ, Lee PC, editors. The amboseli elephants: a long-term perspective on a long-lived mammal. Chicago: University of Chicago Press. p. 272–286.

Poole JH, Moss CJ. 2008. Elephant sociality and complexity: the scientific evidence. In: Wemmer C, Christen K, editors. Elephants and ethics: Toward a morality of co-existence. Baltimore (MD): John Hopkins University Press. p. 69–98.

R Core Team. 2018. R: A language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing. Available from: https://www.R-project.org/.

Rand DG, Arbesman S, Christakis NA. 2011. Dynamic social networks promote cooperation in experiments with humans. Proc Natl Acad Sci U S A. 108:19193–19198.

Riehl C, Strong MJ. 2018. Stable social relationships between unrelated females increase individual fitness in a cooperative bird. Proc R Soc B. 285(1876):20180130.

Robson AS, Van Aarde RJ. 2018. Changes in elephant conservation management promote density-dependent habitat selection in the Kruger National Park. Anim Conserv. 21:302–312.

Roux C, Bernard RTF. 2009. Home range size, spatial distribution and habitat use of elephants in two enclosed game reserves in the Eastern Cape Province, South Africa. Afr J Ecol. 47(2):146–153.

Ryder TB, Parker PG, Blake JG, Loiselle BA. 2009. It takes two to tango: reproductive skew and social correlates of male mating success in a lek-breeding bird. Proc Biol Sci. 276:2377–2384.

Schülke O, Bhagavatula J, Vigilant L, Ostner J. 2010. Social bonds enhance reproductive success in male macaques. Curr Biol. 20:2207–2210.

Shizuka D, Chaine AS, Anderson J, Johnson O, Laursen IM, Lyon BE. 2014. Across-year social stability shapes network structure in wintering migrant sparrows. Ecol Lett. 17:998–1007.

Silk JB. 2007. The adaptive value of sociality in mammalian groups. Philos Trans R Soc Lond B Biol Sci. 362:539–559.

Silk JB, Alberts SC, Altmann J. 2006. Social relationships among adult female baboons (*Papio cynocephalus*) II. Variation in the quality and stability of social bonds. Behav Ecol Sociobiol. 61(2):197–204.

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 Biol Sci. 276:3099–3104.

Silk JB, Beehner JC, Bergman TJ, Crockford C, Engh AL, Moscovice LR, Wittig RM, Seyfarth RM, Cheney DL. 2010a. Female chacma baboons form strong, equitable, and enduring social bonds. Behav Ecol Sociobiol. 64:1733–1747.

Silk JB, Beehner JC, Bergman TJ, Crockford C, Engh AL, Moscovice LR, Wittig RM, Seyfarth RM, Cheney DL. 2010b. Strong and consistent social bonds enhance the longevity of female baboons. Curr Biol. 20:1359–1361.

Silk MJ, Croft DP, Delahay RJ, Hodgson DJ, Boots M, Weber N, McDonald RA. 2017. Using social network measures in wildlife disease ecology, epidemiology, and management. Bioscience. 67:245–257.

Silk MJ, Jackson AL, Croft DP, Colhoun K, Bearhop S. 2015. The consequences of unidentifiable individuals for the analysis of an animal social network. Anim Behav. 104:1–11.

Spencer WD. 2012. Home ranges and the value of spatial information. J Mammal. 93(4):929–947.

Stanton MA, Mann J. 2012. Early social networks predict survival in wild bottlenose dolphins. PLoS One. 7:e47508.

Sueur C, Maire A. 2014. Modelling animal group fission using social network dynamics. PLoS One. 9:e97813.

Tranmer M, Marcum CS, Morton FB, Croft DP, de Kort SR. 2015. Using the relational event model (REM) to investigate the temporal dynamics of animal social networks. Anim Behav. 101:99–105.

Van Hooff JARAM, Van Schaik CP. 1994. Male bonds: afiliative relationships among nonhuman primate males. Behaviour. 130(3–4):309–337.

Waterman JM. 1997. Why do male cape ground squirrels live in groups? Anim Behav. 53(4):809–817.

Whitehead H. 2008. Analyzing animal societies. Chicago: University of Chicago Press.

Whitehead H, Antunes R, Gero S, Wong SNP, Engelhaupt D, Rendell L. 2012. Multilevel societies of female sperm whales (*Physeter macrocephalus*) in the Atlantic and Pacific: why are they so different? Int J Primatol. 33(5):1142–1164.

Wittemyer G, Douglas-Hamilton I, Getz WM. 2005. The socioecology of elephants: analysis of the processes creating multitiered social structures. Anim Behav. 69(6):1357–1371.

Wray M. [Internet]. 2017. Fence between the park and Limpopo Nature Reserve [Retrieved 9 April 2019]. Available from http://www.krugerpark. co.za/krugerpark-times-3-1-kruger-fence-21861.html.