African forest elephant social networks: fission–fusion dynamics, but fewer associations

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ABSTRACT: For animal species with dynamic interactions, understanding social patterns can be difficult. Social network analysis quantifies associations and their intensity between individuals within a population, revealing the overall patterns of the society. We used networks to test the hypothesis that the elusive African forest elephant *Loxodonta cyclotis* exhibits fission–fusion social dynamics, similar to other elephant species. We observed associations between individuals in savanna clearings in Lopé National Park, Gabon, in 2006, 2008, and 2010. When possible, dung was collected from individuals for genetic analyses using 10 microsatellite loci and the mitochondrial DNA control region. Using simple ratio association indices, networks were created for each year, wet and dry seasons, individuals detected at least twice, and for all females. We identified 118 unique adult females, for 40 of which we obtained genetic information. Networks had low densities, many disconnected components, short average path lengths, and high clustering coefficients. Within components, average relatedness was 0.093 ± 0.071 (SD) and females appeared to share mitochondrial haplotypes. We detected 1 large component consisting of 22 adult females, but there were few preferred associations (8 of 65, 12.3%). No seasonal or yearly differences were observed. Our results substantiate fission–fusion dynamics in forest elephants; however, the networks are more disconnected than those for other elephant species, possibly due to poaching and ecological constraints in the forest environment.

KEY WORDS: Social networks · Social structure · *Loxodonta cyclotis* · Fission–fusion · Elephants

INTRODUCTION

Individuals within a population rarely interact randomly. Ecological pressures such as competition influence individuals to develop strategies to maximize their fitness. The range of interactions varies from antagonistic, where individuals defend territories aggressively, to cooperative, in which conspecifics gain benefits such as predator defense through working together (Wrangham 1980, Krebs & Davies 1997). Social structure affects how individuals exploit habitats (Hoelzel 1993), transfer knowledge (Weimerskirch et al. 2010), transmit diseases (Hamede et al. 2009), and search for mates (Ortega et al. 2003,

Rossiter et al. 2012), and, therefore, has evolutionary consequences and implications for conservation.

Some species change group sizes over time and/or space, presenting a challenge to understanding interactions. Chimpanzees (*Pan troglodytes*; Lehmann & Boesch 2004), bats (Kerth & Konig 1999, Willis & Brigham 2005), African buffalo (*Synerus caffer*; Prins 1989), dolphins (Parra et al. 2011), and African savanna elephants (*Loxodonta africana*; Archie et al. 2006) have fission–fusion social systems, where group composition and structure can change monthly, daily, or hourly in response to resources or group dynamics. Social network analysis is an effective tool for studying and comparing social systems, as metrics

can be quantified and visualized (Croft et al. 2008, Wey et al. 2008, Sih et al. 2009, Croft et al. 2011). We used network analysis to elucidate the social structure of the African forest elephant *Loxodonta cyclotis*, an elusive species thought to have fission–fusion dynamics.

Two species of African elephant are recognized: savanna and forest (Rohland et al. 2010). In savanna elephants, related females form family groups that repeatedly join and separate from other groups (Moss 1988, Wittemyer et al. 2005, Archie et al. 2006). Family groups are important for fitness. Females rear young as a group (Lee 1987), and intact groups are more effective at forming defensive postures in response to playback calls from lions (McComb et al. 2011). The oldest member, the matriarch, retains knowledge about the landscape important for the group's survival (McComb et al. 2001). In poached populations, where social structure is disrupted, groups have lower reproductive output and higher stress levels (Gobush et al. 2008), with potentially long-term negative consequences for decision-making abilities (Shannon et al. 2013).

Less is known about forest elephant social structure, as their dense and remote habitat makes it difficult to conduct behavioral studies. Observational studies at forest clearings or in savanna patches within forested regions suggest that sociality is different; groups are typically composed of an adult female and her calves (White et al. 1993, Turkalo et al. 2013). This suggests that it may be disadvantageous for individuals to navigate the forest in groups, possibly because of increased difficulties in foraging and exploiting resources (Sukumar 2003). Forest elephant diet is largely composed of fruits (Campos-Arceiz & Blake 2011); fruiting trees may be depleted more rapidly when visited by large groups.

Evidence suggests that forest elephants may have more extensive associations than indicated by group sizes alone and by fission–fusion dynamics (Fishlock & Lee 2013). Studies at natural clearings with mineral deposits that attract elephants show that females sometimes associate with other groups, and that individuals are not always in the same group or in groups of the same size (Turkalo & Fay 1996, Fishlock et al. 2008). A genetic network derived from non-invasive sampling of dung found in groups suggests that some elephants have larger associations than observed and that associations are largely based on matrilines (Schuttler et al. 2014).

Collectively, these studies suggest that individuals may have more associates than is indicated by observational studies and that group sizes vary. However, it is unknown how individuals are connected throughout the population and if associations are based on kinship. Using observations, genetic data, and network analyses, we tracked individual forest elephants to quantify the number of associates and the quality of relationships. We tested the hypotheses that forest elephants have a social structure with fission–fusion dynamics where kinship predicts associations, group sizes change over time and space, and associations are more extensive than observed within groups. We predicted that kin-based social structure exists, but group sizes and the number of associates would be smaller than for Asian elephants *Elephas maximus* and African savanna species due to ecological constraints in the forest.

MATERIALS AND METHODS

Field methods

Field research was conducted in northeastern Lopé National Park (LNP), Gabon, at the Station d'Etudes des Gorilles et Chimpanzees (SEGC; Fig. 1). LNP consists of mature forest, but the northeastern section contains a mosaic of diverse forest types and savannas that facilitate observations of elephants (White et al. 1993). Elephant (*Loxodonta cyclotis*) densities are estimated at approximately 3.0 elephants km^{-2} (White 1994). Two dry seasons (June to mid-September and December to January/February) and 2 wet seasons (September to November and February to May) are recognized, although inter-annual variation occurs (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/n025p165_suppl.pdf).

Observations were made in 2006 (1 March to 17 September), 2008 (8 August to 7 November) and 2010 (17 February to 12 May). Circuits were conducted by vehicle on roads (Fig. 1) at dusk and dawn and, opportunistically, after rainfall. Routes and circuits were changed daily to avoid spatio-temporal sampling biases. Individuals were considered to be in the same group if they were observed within 250 m of one another. This distance is a compromise between 50 m (Morgan & Lee 2007), which was too small for LNP, and those used in savanna elephant studies (500 m from center of aggregation; Wittemyer et al. 2005, Archie et al. 2006). Group differentiation was not difficult, as groups were usually at least several kilometers apart, and there were few groups (3%, 8 of 275) for which membership was uncertain.

All individuals were photographed and identified using morphological characteristics (ear tears and
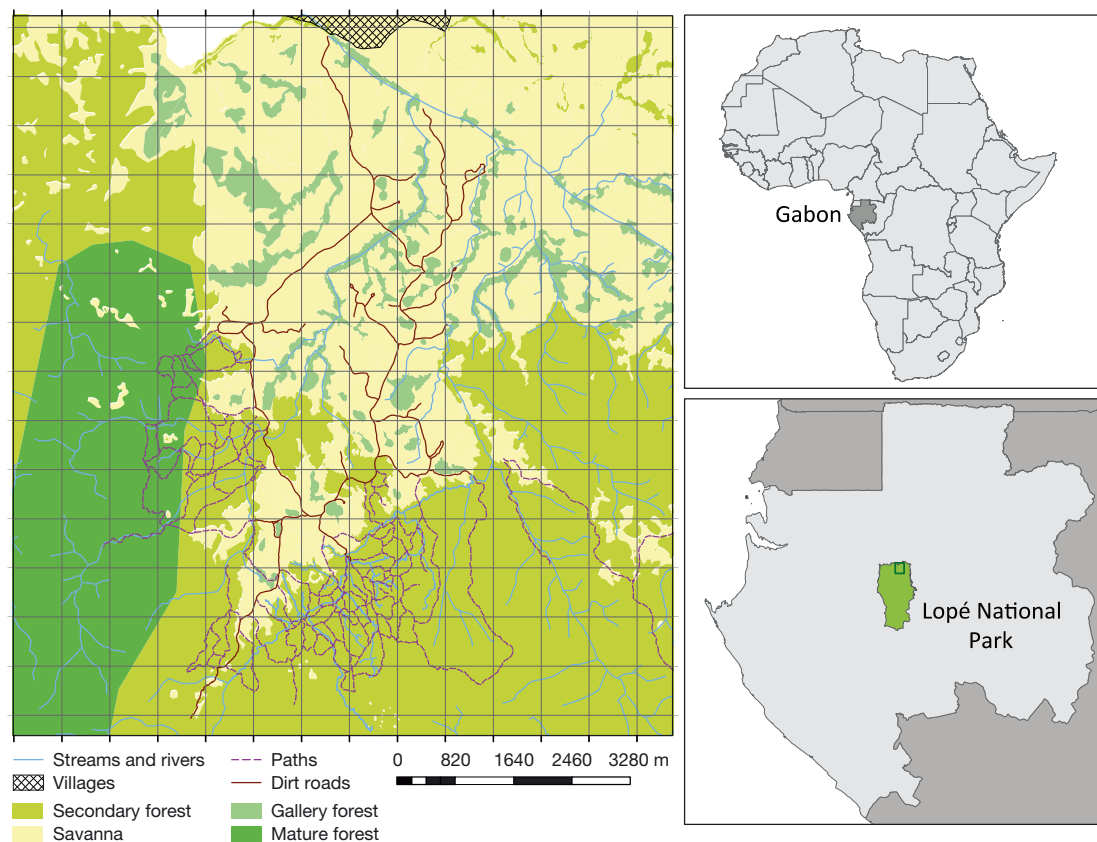
Fig. 1. Station d'Etudes des Gorilles et Chimpanzees (SEGC) study zone (left) from Schuttler et al. (2014). The green rectangle in Lopé National Park (LNP) represents the SEGC study zone area (bottom right)

vein patterns, tusks, and tail brushes) with reference to an existing database (Momont 2007). Groups were observed for 15 to 60 min, depending on visibility of individuals. Date, time, number of individuals, and sex were recorded. Age-classes were estimated following standard methods (Turkalo 2013), and 2 age-classes (juvenile, pre-reproductive; adult, reproductive) were used. Existing long-term data were used to confirm the ages of known adults >15 yr old (Momont 2007).

In 2008 and 2010, we collected fresh dung samples (≤24 h) for genetic analysis following Schuttler et al. (2014). Samples were imported into the United States under USDA (United States Department of Agriculture) Permit #48529. Dung searches were conducted immediately after elephants had left the observation area, except for groups observed at dusk, when searches were delayed until the following morning. Few individuals were observed defecating, so it was possible that some dung samples belonged to members of other groups. To address this, we categorized dung samples as: (1) definite — individual is seen defecating or sample is collected immediately after

elephant group has left; (2) probable — over time, the dung sample was collected repeatedly from the identified individual/group observed; (3) tentative — dung was collected after observations, but the individual was seen once or dung was collected from this individual once. We were confident most samples belonged to observed groups; there were usually fewer dung samples than observed group members; we used fresh tracks based on elephants' observation location to follow groups; and groups were usually separated by at least several kilometers. During observations, we rarely saw large groups or areas used by multiple groups; membership was uncertain in only a few groups (2.9%). We averaged circumferences of 3 dung boli to estimate 2 age-classes: juvenile (<30 cm, pre-reproductive) and adult (≥30 cm, reproductive; Schuttler et al. 2014).

DNA extraction and genetic analysis

Methods for DNA extraction, microsatellite genotyping, molecular sexing, and sequencing of the

mitochondrial DNA (mtDNA) are fully described in Schuttler et al. (2014). In summary, individuals were genotyped at 10 microsatellites. Homozygous geno-types were amplified 3 times for confirmation, while heterozygous genotypes were amplified twice. Only samples with positive results for at least 6 loci were retained for analyses. A 627 bp fragment of the mtDNA control region was sequenced for unique individuals.

Social networks

From observational data, we computed simple ratio association indices (AI) as a measure of the strength of the relationships between dyads of adult females where $AI = N_{AB}/(N_A + N_B + N_{AB})$. N_{AB} represents the number of times individuals A and B were seen together, while N_A and N_B represent each time that individual was seen without the other individual (Ginsberg & Young 1992). We created networks to visualize associations using UCINET Version 6.415 (Borgatti et al. 2002) and NETDRAW Version 2.122 (Borgatti 2002). Individuals are represented as nodes, associations are represented as connections between nodes (edges), and nodes connected to one another, but not connected to the rest of the network, are com-ponents. Networks included only identified adult females, as offspring are dependent on mothers.

We created several types of social networks to highlight important associations: (1) global, (2) pre-ferred associates, (3) year, and (4) season. The global network represents all adult females and associations observed over all years to show the extent of social occurrences. The preferred associates network in-cluded individuals observed ≥2 times and therefore more representative of an individual's behavior (de Silva et al. 2011). Preferred associations are those for which an AI value is at least 2 times more than the mean (Whitehead 2008). Year networks represent 2006, 2008, and 2010, and include individuals found during those years. Season networks investigate dif-ferences in associations between wet and dry sea-sons and combine data across years. Rainfall data were collected and recorded daily at SEGC. Months with higher total rainfall than the 3 yr monthly aver-age were considered 'wet,' while those with less were considered 'dry.' As more observations were conducted in wet season months, to ensure equal sampling, we chose 3.5 mo worth of observational data from months occurring in the wet season (total rainfall = 703 mm, monthly average = 234 mm) to compare to data collected during the 3.5 mo of the

dry season (total rainfall = 74 mm, monthly average = 25 mm).

We conducted linear regressions in EXCEL 14.3.5. to test the hypothesis that the number of times an indi-vidual was seen influenced the number of associates and maximum AI value. We also investigated the relationship between the number of observations and number of edges, maximum component size, and the number of edges in the largest component in the global network.

For individuals where genetic data were success-fully generated, we estimated relatedness and added values to edges between dyads. Nodes were colored according to mitochondrial haplotype. Relatedness was calculated using the Queller-Goodnight moment estimator (Queller & Goodnight 1989) in RELATEDNESS Version 5.0.8 (Queller & Goodnight 1989) using bias correction (Schuttler et al. 2014).

We calculated the following network measures in UCINET: density, the ratio of edges that exist between nodes out of all that could exist; mean degree, the average number of edges a node is connected to; mean path length, the average shortest path for one node to connect to another (Croft et al. 2008); and clustering coefficient, i.e. the degree to which associ-ates of an individual are associated within the net-work (Whitehead 2008).

We tested for preferred/avoided associations in SOCPROG Version 2.4 (Whitehead 2009) using 7 d sampling periods to test the null hypothesis that there are no preferred or avoided associations for the global and preferred networks. We chose 7 d be-cause this was long enough to collect sufficient observations, but short enough to limit immigration/emigration into the sampling area (Whitehead 2008). We permuted groups within samples and used a 2-tailed significance level of 0.05 with 1000 trials per permutation and 20 000 permutations to determine the number of dyads preferred or avoided based on statistically significant high or low association in-dices. Twenty-thousand permutations were deter-mined to be a sufficient number, indicated by stabi-lizing p-values (Bejder et al. 1998).

RESULTS

We identified 118 adult females, seen an average of 3.0 times (range: 1 to 34, mode: 2). The number of new individuals increased as the number of identifi-cations increased (Fig. S2 in the Supplement at www. int-res.com/articles/suppl/n025p165_supp.pdf). We were able to assign unique genotypes from dung

samples to 40 individuals as definite (n = 20), proba- ble (n = 4), or tentative (n = 16), and 7 mtDNA haplo- types were identified (Schuttler et al. 2014).

Average observed group sizes ranged from 2.7 to 3.3 for all individuals and 1.3 to 1.6 when excluding dependent calves (Table 1). There was a bimodal pattern in association indices between dyads, with a large number of individuals having low and high AI values. When excluding individuals seen once, this pattern disappeared, with values being more equally represented (Fig. 2).

There was a weak, but statistically significant, correlation between the number of times an indi- vidual was seen and the number of associates it had (R^2 = 0.104, p < 0.001). This did not influence the maximum AI value for an individual (R^2 = 0.010, p = 0.295). Therefore, individuals observed more often were more likely to have more associ- ates, but not stronger associations. After removing individuals seen once (n = 55), there was no signif- icant relationship between the number of times an individual was seen and the number of associates it had (R^2 = 0.030, p = 0.200). However, there was a weak, but significant, correlation between the number of sightings and the maximum AI of an individual (R^2 = 0.076, p = 0.036). We found a
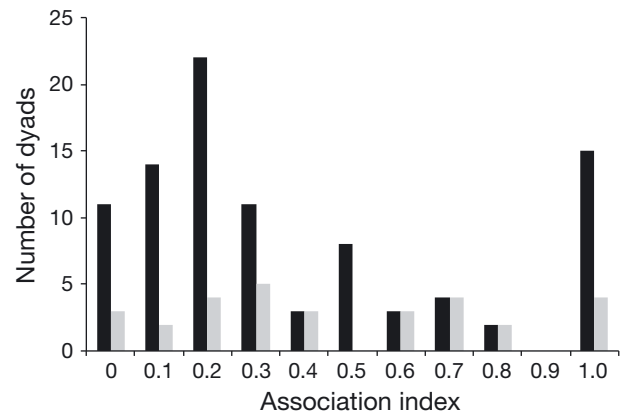

Fig. 2. *Loxodonta cyclotis*. Association index values in all adult female dyads observed (black bars) and dyads in which the adult females were observed 2 or more times (grey bars)

strong linear relationship between the number of observations and the number of edges added (R^2 = 0.960, p < 0.001) and between the number of observations and the maximum component size (R^2 = 0.719, p < 0.001), and the maximum number of edges within the largest component (R^2 = 0.500, p < 0.001).

Approximately one-quarter of the global network (25.4%) was made up of solitary individuals (Table 2, Fig. 3a). There was 1 large compo- nent of 22 adult females of which all but 1 individual with genetic informa- tion shared the same haplotype. The next largest component was 4 indi- viduals; 5 components of this size were detected in the network. The average relatedness of adult females within a component was 0.105 ± 0.078

Table 1. *Loxodonta cyclotis*. Group sizes (±SD) of forest elephants observed in Lopé National Park, including all age-classes and sexes. Excl.: excluding; ind.: individuals

	No. of groups observed	No. of solitary ind. observed	All	Excl. solitary ind.	Excl. dependent calves
				Mean group size	
All years	275	65	3.13 ± 2.00	3.68 ± 1.89	1.48 ± 0.80
2006	142	31	3.19 ± 1.94	3.80 ± 1.77	1.34 ± 0.76
2008	92	40	2.73 ± 1.66	3.44 ± 1.46	1.29 ± 0.60
2010	112	25	3.33 ± 2.38	3.84 ± 2.33	1.63 ± 0.97

Table 2. *Loxodonta cyclotis*. Network metrics from different observation periods of forest elephants in Lopé National Park. Definitions of metrics are given in 'Materials and methods: Social networks'

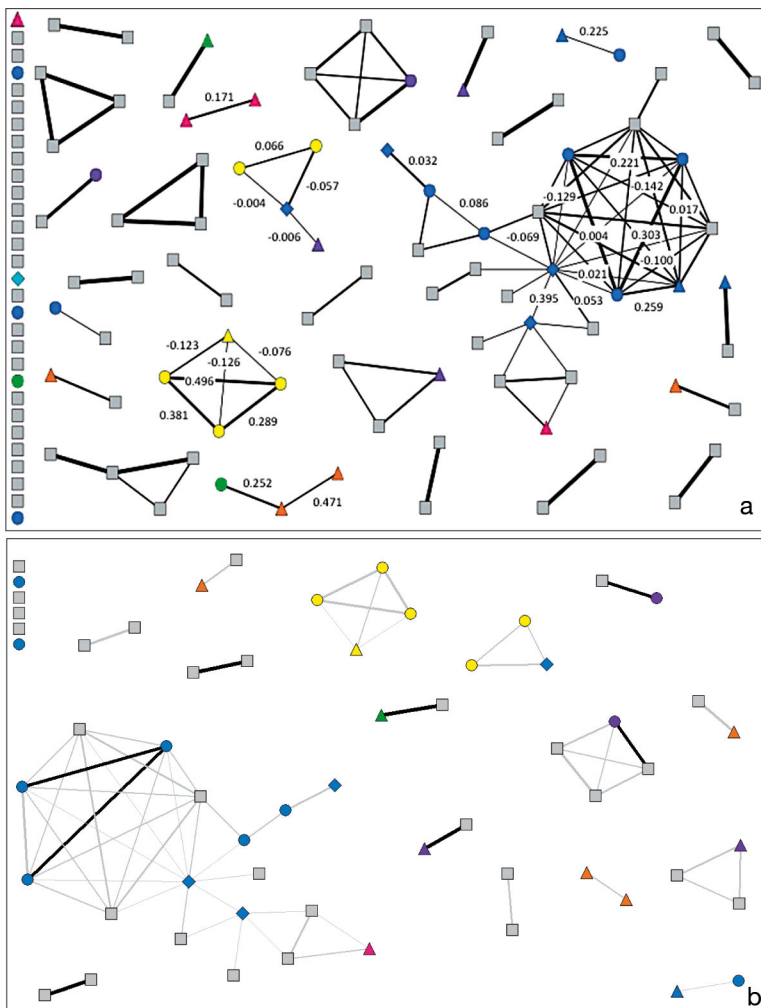| Social network	Nodes	Edges	Solitary individuals	Connected components	Largest connected component	Density	Mean degree	Mean path length	Clustering coefficient
Global	118	97	30	27	22	0.014	1.664	2.275	0.804
Preferred associates	63	65	8	17	17	0.033	2.063	2.157	0.857
Year 2006	43	19	6	14	5	0.034	1.442	1.167	0.870
Year 2008	58	28	21	15	4	0.018	1.000	1.125	0.822
Year 2010	68	59	20	16	14	0.026	1.735	1.836	0.832
Wet season	52	56	15	15	4	0.021	1.077	1.125	0.897
Dry season	29	24	8	10	3	0.049	1.379	1.091	0.933

Fig. 3. *Loxodonta cyclotis*. (a) Global social network for adult females observed throughout the study. Edge width is associated with the simple ratio association index between dyads. Dyads with thicker edges have a higher association index. (b) Preferred associates social network, including only adult females seen 2 times or more. All associations are shown (grey), and black edges represent preferred associations, defined as those dyads with a simple ration association index at least 2 times the mean. For both networks, the shape of the node designates the certainty of the genetic sample collected for the individual — □: no genetic data available; ○: definite; ◇: probable; △: tentative. The color of the node indicates the mitochondrial haplotype associated with the sample — grey: haplotype is absent; pink: Lope1; orange: Lope3; yellow: Lope4; green: Lope5; aqua: Lope6; blue: Lope7; purple: Lope9

The preferred associates network included a large component of 17 adult females, including adult females not present in the global group of 22 individuals (Table 2, Fig. 3). Fifty-five individuals were seen once during the study and were removed from the preferred associates network (Table 2, Fig. 3). Almost half of these females (n = 23) were solitary, accompanied only by juveniles. The mean AI for dyads in the preferred association network was 0.339 ± 0.270 (SD), and few preferred associations (those ≥0.679) were identified (8 of 65 associations, 12.3%) overall (Fig. 3b).

Rainfall data from SEGC are shown in Fig. S1 in the Supplement. There were no clear differences between dry and wet season networks (Table 2). The wet season network included more individuals, but not larger components. The largest component in both networks consisted of 4 females. The wet season network had a larger number of solitary individuals (15 versus 8), but also had more individuals overall.

All networks had low densities (range: 0.014 to 0.049) and short average path lengths (1.091 to 2.275) due to many disconnected components (Table 2). Mean degrees, reflecting the number of associates an individual has, were also low (1.000 to 2.063), but clustering coefficients were high (0.804 to 0.933; Table 2).

Global and preferred networks showed mean levels of association that were significantly different from those expected by chance (Table 3). The standard deviation (SD) and coefficient of variation (CV) of the AIs were also significantly higher than expected values, indicating that individuals preferentially associate across sampling periods. However, only a few dyads were non-randomly associated (global: 23 of 345 expected, 6.7%; preferred: 19 of 104 expected, 18.3%) as indicated by the low number of significant dyads with preferred associations (p > 0.975). There was no evidence that certain dyads were avoided (p < 0.025), but the proportion of nonzero association indices was lower in the observed data than in the expected data, suggesting that some individuals avoid others (Table 3).

(SD), with a range of 0.031 to 0.180 (SD). Average relatedness of dyads was 0.104 ± 0.190 (SD).

The networks for each year included solitary individuals. The largest components for 2006 and 2008 contained 5 and 4 individuals, respectively, while 2010 contained 1 large component of 14 individuals (Table 2). This component was largely due to an observation of the largest group, containing 22 individuals (8 adult females).

Table 3. *Loxodonta cyclotis*. Observed and expected association indices (simple ratio association index, AI) for all adult females sighted (global) and for adult females observed 2 times or more (preferred). Values in **bold** are significant at p < 0.05

| | —— Simple ratio AI —— | | p |
	Observed	Expected	
Global			
Mean	0.007	0.005	**0.998**
SD	0.068	0.049	**1.000**
CV	10.020	9.340	**0.998**
Nonzero	0.014	0.024	**0.001**
Preferred			
Mean	0.013	0.010	**1.000**
SD	0.086	0.048	**1.000**
CV	6.576	4.843	**1.000**
Nonzero	0.033	0.067	**0.001**

DISCUSSION

Our study presents the first inference of African forest elephant social networks from observational data. The networks exhibit fission–fusion dynamics, but are different in structure from African savanna and Asian species. We detected a component (n = 22 adult females) larger in size than any forest elephant group observed in any population (White et al. 1993, Morgan & Lee 2007, Turkalo et al. 2013). Overall, though, networks were disconnected, with many small components, including many solitary females with no differences in structure between seasons. Few individuals had preferred associations, and those that existed were mostly between dyads, and were not interconnected as larger components. Components and associations appeared to be based on matrilines and kinship, consistent with previous studies (Munshi-South 2011, Schuttler et al. 2014), although average component relatedness (0.105 ± 0.078, SD) was lower than the mean group relatedness in savanna elephants *Loxodonta africana* (0.150: Archie et al. 2006; 0.234: Wittemyer et al. 2009).

The global network for forest elephants differs greatly from those for African savanna and Asian elephant populations. The savanna elephant population was connected as a single component of 89 females (Archie & Chiyo 2012). Even when filtering associations and including only individuals spending >10% of their time together, large components still exist (5 to 13 adult females). In the Asian elephant population, despite observed smaller group sizes (2.8 to 3.0 adult females), population-level networks consisted of 5 to 10 components, plus solitary individuals (de Silva et al. 2011), which was more disconnected than the savanna elephant population, but more connected than our global network of 27 components and 30 solitary individuals.

The networks also vary in sampling and the number of times individuals were seen, which can impact structure and present a source for the differences detected. Savanna elephants were observed for 36 mo (recapture values not included); Asian elephants for 20 mo, with 9 as the mode recapture rate; and forest elephants for approximately 15 mo, with a low recapture rate (mode of 2). The preferred associates network included higher recaptures and likely better characterization of forest elephant sociality. One large component was still present in this network (n = 17), and there were fewer solitary individuals. However, this network had fewer females compared to other studies (n = 63, this study; n = 89, savanna elephants; n = 154 to 201, Asian elephants). Adding more observations may alter network structure; the number of associates increased with the number of observations, and significant correlation was found between the number of observations and the edges added. New individuals were identified throughout the study and possibly confounded these relationships. However, an increasing number of observations added new individuals to the network, but did not heighten network complexity. More components containing dyads were added than edges between existing individuals. Furthermore, there was no influence on the number of times an individual was seen on its maximum AI value. Further research is needed to evaluate these relationships.

The largest component observed in the network may result from sampling in the savannas, possibly representing a more complete group of individuals, while smaller components may represent subsets of groups at the edges of their range. Telemetry studies in LNP and the ecologically similar Loango NP, Gabon, found home ranges to be small, 9 to 343 km^2 (Momont 2007) and 11 to 105 km^2 (Schuttler et al. 2012), respectively, and, in LNP, 1 'resident' elephant remained in a small, northeastern section of the park. Additionally, Fishlock & Lee (2013) found that forest elephants maximize social opportunities at mineral resources, staying longer and joining larger groups. Increasing the sampling area, in addition to recapturing individuals, may increase connections between those individuals at range edges and more large components may be detected.

Perhaps the greatest influence on network structure is poaching, which has reached crisis levels in Central Africa (Blake et al. 2007, Maisels et al. 2013).

Gobush et al. (2009) found smaller savanna elephant groups (means of 2 adult females) and a large presence of solitary females (30%) in the heavily poached population of Mikumi National Park, Tanzania. Poaching may have disrupted forest elephant social structure by removing individuals, thus reducing associations. However, individuals in the Mikumi population grouped with non-kin, which was not strongly observed in this study or in that of Schuttler et al. (2014).

Finally, ecological and environmental factors also likely have a large influence on forest elephant social structure and the differences observed between the species. Even with additional observations, it is unlikely that forest elephant networks will reach the level of complexity of savanna elephants over the same time period. In chimpanzees, the advantages of fission–fusion sociality lie in reducing the costs of moving; by splitting into smaller parties during foraging, individuals are able to reduce moving time, which reduces energy demand and feeding time (Lehmann et al. 2007). As the diets of forest elephants and chimpanzees overlap substantially (White et al. 1994), the spatial patchiness of and ephemeral nature of forest fruits may have similar influences on forest elephants, favoring small groups. Smaller group sizes and fewer permanent associations have also been observed in the savanna elephants of Namibia, which may be a result of another environmental constraint, an extreme desert environment (Leggett et al. 2003). Further research is needed to fully evaluate the influence of habitat on social structure in elephants.

CONCLUSIONS

We found that forest elephants have fission–fusion patterns of sociality, but, as a population, individuals are largely disconnected from one another; this differs from the social structure in Asian and African savanna species. Great variation occurs within the population, with some elephants having many associates, while others remain solitary. Although genetic data were sparse, they suggest most associations are based on matrilineal kinship, consistent with savanna elephant populations and previous studies on forest elephants. Forest elephants, therefore, appear to differ from the other elephant species, overall with more fragmented networks, fewer associations, and more solitary individuals. However, due to low re-sightings of individuals within this population, we recommend further research for future comparisons.

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