The secret lives of African forest elephants: using genetics, networks, and telemetry to understand sociality.
The undersigned, appointed by the dean of the Graduate School, have examined the Dissertation entitled

THE SECRET LIVES OF AFRICAN FOREST ELEPHANTS: USING GENETICS, NETWORKS, AND TELEMETRY TO UNDERSTAND SOCIALITY.

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A candidate for the degree of
Doctor of Philosophy
And hereby certify that, in their opinion, it is worthy of acceptance.

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Professor Matthew Gompper
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ABSTRACT

Identifying the social structure of a species is critical for understanding the overall evolution and behavioral ecology of that species. An individual’s social relationships have consequences that impact the movements, habitat use, and mate choice of other individuals, and collectively influence spatial patterns and gene flow in the population or species. My dissertation research focuses on the social structure of African forest elephants (Loxodonta cyclotis) and tests for fission-fusion sociality, which has been detected in the other extant elephant species, the African savanna (L. africana) and Asian (Elephas maximus) elephants. Observational studies at forest clearings have shown that African forest elephants have the smallest group sizes of the extant elephants, and are typically composed of an adult female and her dependent calves. However, associations may be more extensive because it is difficult to detect individuals that may be obscured by the dense forest vegetation. I used satellite telemetry, behavioral observations, non-invasive genetic sampling, and social networks to look for evidence of multi-tiered fission fusion sociality, in which an adult female and her dependent calves (tier one) form a “family group” with related adult females (tier two), that fuse into larger “bond groups” (tier three), and larger “clans” (tier four) of up to hundreds of elephants.
First, I describe satellite telemetry results from six adult female forest elephants in Loango National Park, Gabon. As home range overlap can provide indirect information about the social interactions between individuals, this study found small home ranges with low volume of intersection indices between individuals, indicating that the probability of co-occurrence between dyads of individuals in the same area is also low. This suggests spatial avoidance among these adult females, which contrasts with the patterns of family groups overlapping in home ranges within sub-populations in African savanna elephants.

Second, I used non-invasive genetic approaches to infer sociality from African forest elephants in Lopé National Park (LNP), Gabon. I found evidence of fine-scale genetic structure with individuals being more closely related to each other than expected by chance at distances of five kilometers or less. Through network models created by genotyping dung samples collected together at the same time, location, and of the same freshness, I found larger group sizes of forest elephants compared to those from observations alone and that groups largely consisted of individuals of the same mitochondrial DNA matriline. These results support evidence of higher order social structure including family groups (representing second tier relationships), and possibly even bond groups (third tier).

Finally, I tracked the relationships of known individuals and created social networks of adult females within LNP. Social networks revealed evidence of kin-based fission-fusion sociality with one large component of twenty-two adult
females, followed by smaller ones of four. I observed many solitary females (females observed alone or only with dependent calves) throughout the study and few individuals had preferred associations. Although these results reveal that forest elephant females associate with other females in fission-fusion patterns, they frequently separate from them, and when preferred associations do form, it is typically with only one other individual.

When comparing these results with knowledge about the sociality of the other extant elephant species, they suggest that although there is evidence of kin-based fission-fusion sociality, African forest elephants differ from African and Asian elephants. Social networks from both African savanna and Asian elephants have more connected networks, and larger component sizes in networks. In contrast, forest elephant social networks and networks created from non-invasive genetic sampling had many small components and solitary individuals, few large components, and were disconnected.

Several ecological factors may contribute to the more limited sociality observed in forest elephants. Forest elephants have the most “closed” habitats of the three extant species, which may physically prevent larger aggregations. There also may be costs associated with foraging in larger groups, as patchily distributed resources such as fruits, on which forest elephants forage heavily, will quickly be depleted, resulting in increased travel for forage. Finally, large cooperatively hunting predators are currently absent in most locations throughout forest elephant range, negating the need for groups to form for defense against predators. Therefore, forest elephants may lack strong benefits
associated with group-living and suffer from costs which may drive the type of fission-fusion patterns observed.
CHAPTER 1
INTRODUCTION

The social structures of a species have profound effects on the overall evolution and behavioral ecology of that species. At a basic level, social structure is made up of individual behaviors, which form the basis of relationships between individuals. These then relationships become generalized over the population or species (Hinde 1976). Social systems vary from individuals living solitarily to incredibly complex systems, with some involving thousands of individuals each with a distinct role. An individual’s social rank, or relationship with conspecifics, has fitness consequences that ultimately affect movements (Perry et al. 2008), foraging or habitat use (Blake et al. 2007; Hoelzel 1993; Holekamp et al. 2012; Weimerskirch et al. 2010), and mate choice (Kays et al. 2000; Kulik et al. 2012; Ortega et al. 2003; Rossiter et al. 2012). Therefore, it is essential to understand social structure as it impacts spatial patterns and gene flow within a species.

How animals decide to associate with individuals can be explained by through the resource dispersion hypothesis (Carr & Macdonald 1986) and fitness costs and benefits, such that a species will become social when there are benefits from group living not outweighed by costs (Krebs & Davies 1993; Rubenstein & Wrangham 1986). Group-living animals may derive fitness benefits such as a lower risk of predation (Calvert et al. 1979; Hebblewhite & Pletscher 2002), aid in the rearing of young (Packer et al. 1990; Silk et al. 2003), cooperation in
accessing resources or defending territories (Baird & Dill 1996), and in the sharing of knowledge of important resources (Aplin et al. 2012; Weimerskirch et al. 2010). In social mammals, males typically disperse, while females are philopatric, which can lead to fine-scale spatial genetic structure, where the ranges of female kin are in close proximity (Arnaud et al. 2012; Meshriy et al. 2011). This increases the chances of amicable interactions between kin and if favored by selection, groups may form (Ross 2001). Sociality is often influenced by kinship because of inclusive fitness benefits from cooperation.

Alternatively, the resource dispersion hypothesis predicts that if resources are patchily distributed both spatially and temporally, group living may take place not because of any benefits that may be gained through cooperation between individuals, but because costs are low enough to tolerate groups (Johnson et al. 2002). When resources are heterogeneous, several individuals may be able to exploit these patches and share these resources without having to impose any costs of group-living. Costs of group living include competition for resources (Holekamp et al. 2012), interference with reproduction (Kappeler & Fichtel 2012), or exposure to disease and parasites (Bull et al. 2012; Hamede et al. 2009). If competition or other costs associated with group living are too great, natural selection should favor solitary living (Solomon 2003).

Some species overcome these challenges by living in flexible groups to minimize costs through changes in group size and structure in response to environmental or social conditions (Lehmann & Boesch 2004; Parra et al. 2011; Willis & Brigham 2005). Chimpanzees (Pan troglodytes, Lehmann and Boesch
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 societies,
in which group composition and structure can change monthly, daily, or even
hourly in response to resources or group dynamics.

This dissertation focuses on understanding the social structure of African
forest elephants (*Loxodonta cyclotis*) and testing for fission-fusion sociality,
which has been detected in the other extant elephant species, African savanna
and Asian (*Elephas maximus*). Observational studies at forest clearings or in
patches of savanna within forested regions show that forest elephants have the
smallest group sizes of the extant elephants, and are typically composed of an
adult female and her dependent calves (Turkalo & Fay 1996; White et al. 1993).
These small group sizes suggest there are costs associated with group living in the
forest environment or there are a lack of benefits to encourage group living. As
the diet of forest elephants is heavily composed of fruits (Campos-Arceiz & Blake
2011), some have suggested that it may be disadvantageous to forage with other
individuals as fruiting trees will become easily depleted when group sizes
increase, making it harder for individuals to exploit resources (Sukumar 2003).

However, group size data do not account for group composition, and small
groups may not be necessarily composed of the same individuals. In Asian
elephants, de Silva et al. (2011) found group sizes to be small during field
observations, but longitudinal results revealed larger social units with stable
relationships. Also, groups can be dynamic. African savanna elephants exhibit a
multi-tiered fission-fusion society based on kinship where an adult female and her dependent offspring (tier one) form a “family group” with related adult females (tier two), that fuse into larger “bond groups” (tier three), and even larger “clans” (tier four) of up to hundreds of elephants (Archie et al. 2006; Moss 1988; Wittemyer & Getz 2007). Group sizes change according to resources, and are largest in wet seasons when food and water are abundant (Western & Lindsay 1984). The oldest female in the group, the matriarch, has experience in resource acquisition and social interactions (McComb et al. 2001), and groups with older matriarchs have higher reproductive output, lower stress hormone levels, and respond to predator calls more quickly (McComb et al. 2011). Female savanna elephants cooperatively rear young, who benefit from exposure to more individuals and a larger repertoire of behaviors and situations (Sukumar 2003). Also, groups are more capable of defending young calves against cooperatively-hunting savanna predators (McComb et al. 2011).

There is some evidence to suggest that fission-fusion sociality may also occur in forest elephants, as seen in African savanna and Asian elephants. A study at Dzangha Bai, a large, natural forest clearing in the Central African Republic, found that some females frequently associate with the same groups, although this does not occur for most females that visit the bai (Turkalo & Fay 1996). At Mbeli Bai, Republic of Congo, individuals had preferred associates, but were not always observed in the same group, or found consistently in groups of the same size (Fishlock et al. 2008). In Lopé National Park, Gabon, preferred
relationships were observed between two to three adult females and their calves (Momont 2007).

Forest elephants may maintain associations with other individuals to receive benefits in the form of information about forest resources such as fruiting trees and mineral deposits. Forest elephants aggregate at *bais*, natural clearing in the forest that have mineral deposits, to acquire minerals, which are found in high concentrations in the soils of these clearings (Turkalo & Fay 1996). *Bais* are patchy throughout the forest zone and females may remain with mothers and other kin because they have greater knowledge of the locations of these important resources. Fruiting trees may have a similar influence on elephants. White *et al.* (1993) speculated that forest elephants may coordinate movements with infrasound [low frequency vocalizations, (Langbauer *et al.* 1991)] in response to availability of fruit. Even though trees appear to be evenly distributed throughout the forest, their fruits ripen at different times and in different intensities, making them ephemeral and patchy.

The goal of this dissertation research was to elucidate the social patterns of forest elephants using three different methodologies: (1) analyzing space use patterns using data derived from satellite telemetry, (2) assessing fine-scale genetic structure, and (3) modeling associations between individuals using direct observations, individual identifications, and relatedness. I tested the broad hypothesis that African forest elephants have a fission-fusion social structure based on kinship where group sizes change over time and space, associations are more extensive than observed group sizes, and home ranges of associating
individuals overlap. Finally, I compare the social systems of the extant species of elephants in their ecological context to shed light on the evolutionary patterns of sociality in elephants.
LITERATURE CITED


CHAPTER 2
MOVEMENT PATTERNS AND SPATIAL RELATIONSHIPS AMONG AFRICAN FOREST ELEPHANTS

Stephanie G. Schuttler, Stephen Blake, and Lori S. Eggert

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ABSTRACT

African forest elephants (*Loxodonta cyclotis*) are of immediate conservation concern, yet are understudied due to inaccessible habitats. We analyzed the home range size and overlap of six adult females. Home ranges were among the smallest for all elephant species and individuals were positioned adjacent to one another with minimal overlap.

INTRODUCTION

African forest elephants (*Loxodonta cyclotis*) are in a state of crisis as population numbers and range are declining rapidly (Blake *et al.* 2007). The demand for ivory and bushmeat is unrelenting, while curbing and monitoring illegal activity is expensive and logistically difficult (Wasser *et al.* 2010), especially in the dense forests of the Congo Basin where the majority of forest elephants occur. Forest elephants are important seed dispersers, in part due to their rapid long-distance movements, and their conservation may be critical to the maintenance of ecosystem function (Campos-Arceiz & Blake 2011). Hunting
and loss of habitat can have dramatic negative impacts on forest elephant movements (Blake et al. 2008, Blake et al. 2009) and on social relationships in animals with complex societies (Caro 1998), including savanna elephants (L.africana, Archie & Chiyo 2012).

While little is known about the social and spatial relationships of forest elephants, long-term studies on savanna elephants have revealed their sociality to be a multi-tiered, fission-fusion society. Family groups consist of related females and their offspring, which unite and separate with other related groups over time and space (Archie et al. 2006, Wittemyer et al. 2007, Archie et al. 2008). In wet seasons, when competition is reduced and resources are abundant, spatial partitions between groups disappear and large aggregations form (Wittemyer et al. 2007).

In contrast, forest elephants are observed in smaller groups and most often only with dependent offspring (Turkalo & Fay 1996). Unlike most savanna habitats, tropical forests have reliable water sources, an abundance of fruiting trees, and concentrated mineral deposits in forest clearings. Forest elephants forage heavily on fruits, which may have a larger influence on movement patterns than water sources, as availability varies spatially and temporally.

METHODS

Here, we provide the first information on the spatial relationships among forest elephants. Our data come from a sample of six GPS-tagged female forest elephants from the coastal area of Loango National Park, Gabon (Figure 1). We...
quantify home range metrics and volume of intersection of home ranges to estimate spatial co-occurrence among individuals, and discuss our results in comparison to social relationships and space use observed in savanna elephants.

Loango National Park consists of closed and open-canopy forest, secondary forest, swamps, savannas, coastal scrub, and forests dominated by Sacoglottis gabonensis (Morgan 2007a). Seasonal rainfall is characterized by one long dry (May-September), short dry (December-January), long wet (February-April), and short wet season (October-November). Forest elephant density is high (Morgan 2007b), although Loango National Park has a low area of road-less wilderness compared to other major elephant strongholds in Central African forests (Blake et al. 2008).

In Nov-Dec. 2003, we fitted GPS collars (Africa Wildlife Tracking, Pretoria, SA) to six adult female elephants following the methods in Blake et al. (2001). Location error was not estimated prior to deployment. Individuals were captured at different locations and days in the northern region of the park. All but one elephant was found with one to two sub-adults or calves. Intervals between fixes were eight hours, and were changed periodically by one-hour increments throughout the study to capture variation within a 24-hour period. Elephant locations were converted into UTM coordinates and all data were retained to avoid losing behavioral information. Each individual had enough location points to generate an accurate fixed kernel home range estimate (Seaman et al. 1999). Fixed kernel bandwidths were produced using a plug-in smoothing method in Matlab (Mathworks Inc., Natick, MA) and the kernel density estimator.
Utilization distributions were transformed into rasters for ArcGIS 9.2 (ESRI, Redlands, CA) using inverse distance weighting point interpolation with spatial analyst tools on default settings and projected with the WGS 1984 datum. Home ranges were defined to isopleths using Hawth’s tools v3.2 (www.spatialecology.com/htools/) and converted into polygons.

We calculated home ranges at 10 – 100 percent isopleths for each elephant to determine if there was an inflection point that would characterize the area of core activity. We did not find an informative inflection, and therefore reported 95 percent and 50 percent home ranges as estimators of total home ranges and core areas of use respectively (Charif et al. 2005, Ntumi et al. 2005).

Fixed kernel rasters were used to conduct volume of intersection (VI) analyses in ArcGIS 9.2, which measure the probability that individuals share space by comparing utilization distributions (Fieberg & Kochanny 2005). VI indices were calculated between (1) all individuals at 100 percent isopleths to show the maximum probability of co-occurrence, (2) 100 percent isopleths for individuals each calendar month to investigate the probability of co-occurrence at this temporal scale, and (3) 50 percent isopleths for all individuals throughout the study to estimate co-occurrence within core areas. Months were chosen as the time unit as they were the smallest standard temporal unit for which we could generate home range estimates, and only those elephant/month combinations in which at least 50 location points were obtained were included in the analysis (Seaman et al. 1999). Additionally, VI indices were calculated between 100 percent isopleths of the monthly home ranges of consecutive months from the
same individual to investigate the stability of home ranges for individual elephants.

To determine whether rainfall influenced home range size, we combined monthly home range estimates and the random effects individuals, months, year, and the fixed effect estimated rainfall in a linear mixed model in SAS version 9.2. We estimated rainfall from NASA’s Tropical Rainfall Measuring Mission (http://trmm.gsfc.nasa.gov/index.html) by averaging the amounts for each month between the two locations closest to the elephants’ home ranges. The model residuals were not distributed normally in quantile-quantile probability plots and the Shapiro-Wilks test run in SAS version 9.2; therefore, home range size was log-transformed. We calculated P-values using restricted maximum likelihood estimates.

RESULTS

GPS collars recorded 334 – 1421 location points per individual over 5-18 months with collar success rates ranging from 69.50 – 93.30 percent. All six elephants remained in the northern section of the park throughout the study (Fig. 1). Home range estimates ranged from 11.10 – 105.32 km² and 2.49 – 21.64 km² for 95 percent and 50 percent isopleths respectively (Table 1; Fig. 2a,b).

Between individuals, VI indices were low, ranging from 0.000 – 0.396 over the course of the study, and 0.000 (±0.000) - 0.274 (±0.102) for monthly comparisons (Table 2). Every elephant had a VI index greater than zero with at least one other individual. As expected, VIs at 50% isopleths were lower, ranging
from 0.000 – 0.155, and only six dyads had values above zero. The median isopleths size at which dyads reached a VI value of zero was 50 percent.

Within individuals, VI values for home ranges between consecutive months ranged from 0.340 (±0.194) to 0.521 (±0.109) (Table 1). Rainfall was weakly positively correlated with home range size in the mixed effects model ($F_{1,67}=3.48$, $P=0.066$), while individual was the most significant random effect ($\sigma_{\text{elephant}}=0.288$, 95% CI 0.108-1.961), followed by variation between months ($\sigma_{\text{months}}=0.02655$, 95% CI 0.007-0.791). Year had no effect on home range size.

These results indicate that female forest elephants in Loango National Park have small, adjacent home ranges with minimal overlap. Home ranges were relatively stable, with no evidence of migration or long-distance movements. Movements were subject to some seasonal differences, as home ranges increased slightly with rainfall and varied significantly with months, therefore reflecting some form of temporal variation outside of rainfall effects.

**DISCUSSION**

The home ranges we recorded are among the smallest recorded for any elephant species or population (Sukumar 2003, Charif *et al.* 2005, Fernando *et al.* 2008). Likely explanations for this include habitat characteristics and compression due to anthropogenic threats (Blake *et al.* 2008). Concerning habitat, Sukumar (1989) suggested that where water is not limited, food would be the primary determinant of home range size, and that increased habitat heterogeneity would lead to smaller home ranges in elephants, which has been
reported in African savanna (de Beer & van Aarde 2008) and Asian elephants (*Elephas maximus*, Fernando et al. 2008).

Loango National Park has a dense mosaic of habitats, likely providing a high diversity of resources that may supply elephants with high quality food sources throughout the year, resulting in little ecological need to travel more extensively. There is an abundance of *Sacoglottis gabonensis*, a species whose fruit is preferred by forest elephants (Morgan 2007a), and ripen during the dry season when forage is typically limited. Large mineral deposits, which are also favored by forest elephants, are absent in Loango, but observational studies have suggested that individuals may obtain minerals from saltwater residue on vegetation along the coastline instead (Morgan & Lee 2007). There is also strong evidence that the human footprint, particularly road development, has severely restricted the ranging behavior of Loango elephants, at least compared to other populations of forest elephants (Blake *et al.* 2008).

Elephant density at Loango National Park, estimated at 2.57 elephants/km² (Morgan 2007b), is high compared to most forest elephant populations (Eggert *et al.* 2003). High population density may contribute to the small home ranges observed, since reduction in home range size is a common response as a strategy to reduce intraspecific competition (Schradin *et al.* 2010). In a study of forest elephants in the Ndoki Forest, Republic of Congo, elephant densities were lower (0.66 elephants/km²) and much larger home ranges were observed (up to 2,402.1 km², Blake *et al.* 2009), although no clear relationships have been observed overall between forest elephant density and home range size.
Home range overlap can provide indirect information about the social interactions between individuals (Clutton-Brock 1989). For overlap indices that use utilization distributions, estimates of 0.6 and greater reflect high degrees of overlap between home ranges (Fieberg & Kochanny 2005). Our study found lower estimates and for core areas of use; only six dyads had non-zero values and the highest volume of intersection was 0.155. By this criterion, our data indicate strong spatial avoidance among Loango female forest elephants, which contrasts with patterns seen in savanna elephants. The home ranges of family groups of savanna elephants have been found to be largely overlapping within sub-populations (Charif et al. 2005, Galanti et al. 2006). Female forest elephants at Loango appear to maintain separate home ranges throughout the year, though more research is needed to determine if this is a peculiarity of this site or a consistent trait among forest elephant populations.

Our research provides the first insight into the spatial relationships of African forest elephants. Our results suggest that forest elephants can sustain small home ranges, and we found that individuals in this study share only minimal portions of their range with conspecific adults. These preliminary results underscore the paucity of knowledge we have of forest elephant social and spatial relationships compared to savanna elephants, and highlight the importance of deepening our understanding for conservation and management of this threatened species.
ACKNOWLEDGMENTS

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LITERATURE CITED


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Table 1. Summary of collaring information, home range estimates, and VI indices for individual elephants.

<table>
<thead>
<tr>
<th>elephant ID</th>
<th>estimated age (years)</th>
<th>start date</th>
<th>end date</th>
<th>location points</th>
<th>collar success rate (%)</th>
<th>95% isopleth (km²)</th>
<th>50% isopleth (km²)</th>
<th>mean VI between consecutive months (±SD)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Loango1</td>
<td>20-25</td>
<td>11/27/03</td>
<td>3/27/04</td>
<td>334</td>
<td>93.3</td>
<td>20.49</td>
<td>4.44</td>
<td>0.521 ± 0.109</td>
</tr>
<tr>
<td>Loango2</td>
<td>15-20</td>
<td>12/3/03</td>
<td>5/2/05</td>
<td>932</td>
<td>90.22</td>
<td>90.52</td>
<td>18.36</td>
<td>0.396 ± 0.134</td>
</tr>
<tr>
<td>Loango3</td>
<td>15-20</td>
<td>11/30/03</td>
<td>6/10/05</td>
<td>1407</td>
<td>89.33</td>
<td>43.33</td>
<td>10.13</td>
<td>0.34 ± 0.194</td>
</tr>
<tr>
<td>Loango4</td>
<td>20</td>
<td>12/1/03</td>
<td>5/24/05</td>
<td>1421</td>
<td>69.5</td>
<td>11.10</td>
<td>2.49</td>
<td>0.389 ± 0.168</td>
</tr>
<tr>
<td>Loango5</td>
<td>45</td>
<td>12/2/03</td>
<td>11/27/04</td>
<td>629</td>
<td>80.97</td>
<td>39.56</td>
<td>10.37</td>
<td>0.454 ± 0.124</td>
</tr>
<tr>
<td>Loango6</td>
<td>20-25</td>
<td>12/3/03</td>
<td>7/12/05</td>
<td>985</td>
<td>87.57</td>
<td>105.32</td>
<td>21.64</td>
<td>0.481 ± 0.195</td>
</tr>
</tbody>
</table>
Table 2. Mean VI indices (± SD) between individuals at months, for all data at 100% isopleths, and 50% isopleths.

<table>
<thead>
<tr>
<th>dyad</th>
<th>mean month VI (±SD)</th>
<th>100% VI</th>
<th>50% VI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Loango1 - Loango2</td>
<td>0.274 ± 0.102</td>
<td>0.204</td>
<td>0.029</td>
</tr>
<tr>
<td>Loango1 - Loango3</td>
<td>0.000 ± 0.000</td>
<td>0.000</td>
<td>0.000</td>
</tr>
<tr>
<td>Loango1 - Loango4</td>
<td>0.000 ± 0.000</td>
<td>0.000</td>
<td>0.000</td>
</tr>
<tr>
<td>Loango1 - Loango5</td>
<td>0.240 ± 0.146</td>
<td>0.122</td>
<td>0.100</td>
</tr>
<tr>
<td>Loango1 - Loango6</td>
<td>0.058 ± 0.048</td>
<td>0.102</td>
<td>0.046</td>
</tr>
<tr>
<td>Loango2 - Loango3</td>
<td>0.000 ± 0.000</td>
<td>0.001</td>
<td>0.000</td>
</tr>
<tr>
<td>Loango2 - Loango4</td>
<td>0.000 ± 0.000</td>
<td>0.000</td>
<td>0.000</td>
</tr>
<tr>
<td>Loango2 - Loango5</td>
<td>0.067 ± 0.081</td>
<td>0.115</td>
<td>0.023</td>
</tr>
<tr>
<td>Loango2 - Loango6</td>
<td>0.060 ± 0.084</td>
<td>0.079</td>
<td>0.000</td>
</tr>
<tr>
<td>Loango3 - Loango4</td>
<td>0.069 ± 0.138</td>
<td>0.074</td>
<td>0.000</td>
</tr>
<tr>
<td>Loango3 - Loango5</td>
<td>0.097 ± 0.098</td>
<td>0.101</td>
<td>0.052</td>
</tr>
<tr>
<td>Loango3 - Loango6</td>
<td>0.034 ± 0.050</td>
<td>0.047</td>
<td>0.000</td>
</tr>
<tr>
<td>Loango4 - Loango5</td>
<td>0.081 ± 0.100</td>
<td>0.092</td>
<td>0.000</td>
</tr>
<tr>
<td>Loango4 - Loango6</td>
<td>0.009 ± 0.025</td>
<td>0.027</td>
<td>0.000</td>
</tr>
<tr>
<td>Loango5 - Loango6</td>
<td>0.202 ± 0.144</td>
<td>0.396</td>
<td>0.155</td>
</tr>
</tbody>
</table>
Figure 1. Map of Gabon with Loango National Park encircled.
Figure 2. 95% (A) and 50% (B) isopleths of each individual using all location data. Color gradient reflects areas of high (white) and low (color) use according to the utilization distribution.
CHAPTER 3
THE SECRET LIVES OF FOREST ELEPHANTS:
REVEALING SOCIAL STRUCTURE USING GENETIC
NETWORKS AND SPATIAL AUTOCORRELATION

ABSTRACT
Social structure is important to understanding the evolution, behavioral
ecology, and conservation of a species as it impacts movements and gene flow.
We used genetic analyses to elucidate social structure in a species difficult to
observe, the African forest elephant (Loxodonta cyclotis). We tested the
hypothesis that geographic distance predicts genetic relatedness, looked for
evidence of fission-fusion sociality, and inferred patterns of dispersal. Dung
samples were collected in Lopé National Park, Gabon in 2008 and 2010 and were
genotyped at 10 microsatellite loci, genetically sexed, and sequenced at the
control region of mitochondrial DNA. We conducted spatial autocorrelation
analyses, Mantel, and Tau K_r tests on samples collected within a day, in four,
week sampling sessions, and for each year. We used permutation tests and social
networks to investigate group structure, and compared adult males with females
to infer dispersal. Spatial autocorrelation analyses revealed significant positive
genetic structure in two sampling sessions and for both years in the distance class
0.0–5.0 km. Mantel and Tau K_r tests were significant in three cases. The single
day analysis was significant for all tests. Patterns for adult males were consistent
with male-biased dispersal. Individuals within groups were significantly more
related to each other than to individuals between groups. The results of the social networks suggest more extensive matrilineal groups than detected from observational studies. Our results do not violate the assumptions of a fission-fusion model, but suggest that African forest elephants are the least social of the extant elephant species.

**INTRODUCTION**

Knowledge of social structure is important to understanding the overall evolution and behavioral ecology of a species. Patterns of interactions between individuals form the basis of relationships, and relationships are generalized over the population or species (Hinde 1976). An individual’s social rank, or relationship with conspecifics, has fitness consequences that affect movements, habitat use, and mate choice, which influence spatial patterns and gene flow. Major factors in the variation of mammalian social structure are ecological, and are mostly attributed to resource distribution and predation risk (Rubenstein & Wrangham 1986).

For some species, social structure is difficult to ascertain because habitat characteristics prevent observations, behaviors are cryptic, or individuals range over large areas. Under these circumstances, inferences can be made using indirect methods such as genetic sampling. Genetic analyses have revealed atypical male-based kin groups in southern hairy-nosed wombats, *Lasiorhinus latifrons* (Walker et al. 2008), kinship associations in the solitary rodent *Dipodymys ingens* at high densities (Meshriy et al. 2011), and even recognition of
and preferences for more closely related individuals in *Dictyostelium purpureum*, a social amoeba (Mehdiabadi *et al.* 2009).

African forest elephants (*Loxodonta cyclotis*) fit these criteria because they can range over large areas and live in rainforest habitats that obscure individuals from sight. Observational research at natural clearings and in savanna-forest habitats suggest small groups, most commonly composed of an adult female and her calves (Turkalo & Fay 1996; White *et al.* 1993), while a study based on dung samples inferred that individuals from the same groups were kin (Munshi-South 2011). In one population, the home ranges of six adult females were found to be small with minimal overlap between individuals, but adjacent in position, suggesting limited social interactions (Schuttler *et al.* 2012). Forest elephants may have evolved to live in smaller groups because forest habitat constricts group size and there may be competition costs associated with foraging in groups.

However, group size data do not account for group composition, and small groups may not always be composed of the same individuals. In Asian elephants (*Elephas maximus*), de Silva *et al.* (2011) found group sizes to be small during field observations, but longitudinal results revealed larger social units with stable relationships. Also, social structure can be dynamic. African savanna elephants (*Loxondonta africana*) exhibit a multi-tiered fission-fusion society based on kinship where an adult female and her dependent offspring (tier one) form a “family group” with related adult females (tier two), that fuse into larger “bond groups” (tier three), and even larger “clans” (tier four) of up to hundreds of
elephants (Archie et al. 2006; Moss 1988; Wittemyer & Getz 2007). Group sizes change according to resources, and are largest in wet seasons when food and water are abundant (Western & Lindsay 1984). The oldest female in the group, the matriarch, has experience in resource acquisition and social interactions (McComb et al. 2001), and groups with older matriarchs have higher reproductive output, lower stress hormone levels, and respond to predator calls more quickly (McComb et al. 2011).

There is some evidence to suggest that fission-fusion sociality may occur in forest elephants. Momont (2007) found adult females repeatedly observed to have associations with up to two other females, but were not always seen together. Fishlock et al. (2008) found that individuals had preferred associates, but were not always found in the same group, or in groups of the same size, while Turkalo & Fay (1996) observed greeting ceremonies between groups in a large natural clearing.

The goal of our study was to further elucidate the social patterns of forest elephants by examining fine-scale genetic structure. Genetic methods have the capability to reveal kin structure by overcoming obstacles to direct observations in the forest environment. If female forest elephants maintain relationships with more closely related kin, related individuals should be in closer spatial proximity. We tested the hypothesis that geographic distance predicts genetic relatedness, as kin will be located closer to one another. We also looked for evidence of fission-fusion sociality by examining patterns of relatedness within and between groups, as well as patterns of dispersal for males and females. Finally, we compare the

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social systems of the extant elephant species in their ecological context to shed light on the evolutionary patterns of sociality.

**METHODS AND MATERIALS**

**Study Area and Sample Collection**

Field research was conducted in the Station d’Etudes des Gorilles et Chimpanzees (SEGC) study zone of Lopé National Park (LNP), Gabon (Fig. 1). LNP consists of mature forest, but the northeastern section contains a mosaic of secondary forests and savannas (White *et al.* 1993). The SEGC study zone (approximately 200 km²) makes up about 3% of the park (4,910 km²), but has higher elephant densities at approximately 3.0 elephants/km² (White 1994a), and higher encounter rates than other areas (Maisels *et al.* 2006). This study was conducted concurrently with an observational study in which individuals were identified, and dung was collected for genetic analyses when possible.

The SEGC study zone was divided into 1.0 km² sections (n=196) according to UTM gridlines. Sampling sessions were chosen to capture the range of seasonality. There are two dry seasons, one from June until August, and a less defined one from December to February. Wet seasons occur in October/November and in March/April, although variation occurs between years. Our study included four, five-to-six-day sampling sessions; session 1: September 23rd-26th, 2008 (end of dry season); session 2: October 20th-24th, 2008 (wet season); session 3: March 21st-27th, 2010 (beginning of wet season); and session 4: May 10th-15th, 2010 (end of short wet season, beginning of dry season). Rainfall data were collected daily at SEGC. Our intentions were to conduct short
sampling sessions to reduce the possibility that individuals would move large
distances; thus dung sample locations would represent elephant positions in time
and space.

Within each sampling session, between 47-61 1.0 km² sections were
searched for fresh (≤24 hours) elephant dung. Sections were chosen randomly
each morning and multiple teams searched simultaneously in different sections
of the study zone. Sections were chosen to cover habitat types and the largest
spatial extent possible. The same sections were not necessarily searched between
sampling sessions due to access inside LNP.

In forests, teams searched on and around known elephant trails. In
savannas, teams searched for recent elephant tracks and paths. Fresh paths can
be distinguished from older paths by footprints in marsh or muddy areas, and
from vegetation that is freshly broken from elephant activity. If no or old signs
were observed, the section was abandoned. Each team included at least one
experienced Gabonese field assistant.

Although elephant dung can remain visible for months after defecation
(White 1995), the appearance and odor changes, making it possible to discern
fresh dung. When fresh dung was encountered, it was first determined if the
sample appeared to be less than 24 hours old. Samples older than 24 hours often
lose the circular shape of the bolus due to insects, animals, or rain, which flatten
the sample, and have lost their odor and sheen (personal obs.). Elephants act as
seed dispersers for plants, and therefore old dung piles have plants or fungus
growing from the bolus.
When a sample appeared to be ≤24 hours in age, it was assigned a freshness category; (1) fresh: up to two hours old, sample has sheen, boli are intact (unless they are crushed by elephants), smell is strong, (2) hours: two to eighteen hours old, sample has sheen (depending on sun exposure sheen may only be seen when a bolus is turned over), odor is present, boli are intact or disturbed due to insects or other animals, and (3) day: eighteen to twenty-four hours, samples have odor, but not as strong, boli may not be intact, sheen may be present, but little is left. Approximately 10 grams were collected in polypropylene tubes for genetic analyses and GPS coordinates were recorded. If dung piles were intact, up to three bolus circumferences were recorded for each sample and averaged to infer the age class of the individual (Eggert et al. 2003). Samples were boiled for 15 minutes to destroy pathogens and preserved with Queen’s College buffer (20% DMSO, 100 mM Tris pH 7.5, 0.25 EDTA, saturated with NaCL; Amos et al. 1992). Samples were stored in the dark in the field and were imported into the US under USDA permit #48529. In the laboratory, they were stored at 4°C.

**Laboratory Methods**

DNA was extracted either using the QIAamp Mini Stool Kit (QIAGEN) with the modifications of Archie et al. (2003) or following the Guanadine Thiocyanate method of Eggert et al. (2005). Extractions took place in a separate room designated exclusively for the extraction of DNA from non-invasive samples to reduce the possibility of contamination.
**Microsatellites**

We genotyped all samples using 12 polymorphic microsatellite loci: FH60R, FH94R, FH48R, FH19R, LA6R, LafMS02R (Eggert et al. 2008), FH67, FH126, FH103R (Comstock et al. 2000) FH129 (5’-3’ F-TGGCTAAATGCCTATCACTCA, R-CCAGCTAAACTAAGTCTGCTTTT, Gobush et al. 2009), LaT05, (Archie et al. 2003), and LaT13R (Ahlering et al. 2012). We redesigned primers FH103R (5’-3’ F-GCTGCCACTTCCCTACACCTT, R-CCTTTGCTTTTCTAATGAGTCC) and LafMS02R (5’-3’ F-GTCTATCTCCACCCCTGCT, R-TGTCTGTTTGTAAAAATCGCTTG) to shorten the fragments. All polymerase chain reaction amplifications (PCRs) were performed in a PCR Workstation (Fisher Scientific) with ultraviolet light used between PCRs to decontaminate surfaces.

Samples were amplified in single locus reactions or in four different multiplex reactions. Single locus reactions contained 0.5 U AmpliTaq Gold Polymerase (Applied Biosystems), 1X PCR Gold Buffer (Applied Biosystems), 0.4 \( \mu \)M fluorescently labeled forward primer, 0.4 \( \mu \)M unlabeled reverse primer, 2 mM MgCl2, 0.2 mM each dNTP, 1.5 \( \mu \)l 20X BSA, and 3 \( \mu \)l of the DNA extract in 25 \( \mu \)l reactions. The profile consisted of 95°C for 10 minutes, 45 cycles of denaturation at 95°C for 1 minute, primer annealing at locus specific temperatures for 1 minute, and primer extension at 72°C for 1 minute, followed by a final extension of 72°C for 10 minutes. Samples amplified well at either 58°C or 60°C and were arranged into four multiplex reactions (Table 1). Loci LaT05 and LaT13R were included in all multiplexes as they have larger fragment sizes.
and yielded the same genotypes at 58°C and 60°C. Loci LA6R and FH126 had different annealing temperatures from the single to the multiplex reactions (from 54°C to 58°C, and 58°C to 60°C). These loci were tested on two different positive controls and 16 samples to confirm that amplification at different temperatures resulted in the same genotypes. Multiplex reactions were performed in 8.0 μL volumes containing 4.0 μL Master multiplex mix (QIAGEN), 0.2 μM diluted primer mix, 0.8x BSA, and 1.0-2.5 μL fecal DNA extract. Amplifications were performed with an initial cycle of 95°C for 15 minutes, followed by 40-45 cycles of denaturation at 94°C for 0.5 minutes, primer annealing at 58°C or 60°C for 1.5 minutes, primer extension at 72°C for 1 minute, and a final extension cycle at 60°C for 30 minutes. Each reaction included a positive control to standardize allele scoring and a negative control to detect reagent contamination. PCR products were visualized in 2% agarose gels containing Gel Star (Lonza) to verify amplification.

Fragment analysis was performed using an ABI 3730 DNA Analyzer with Liz 600 size standard (Applied Biosystems) and genotypes were scored in GENEMARKER v1.6 (Soft Genetics LLC). Matching heterozygotes from the same sample were scored at least twice and matching homozygotes were scored at least three times to obtain a consensus genotype (Frantz et al. 2003; Hansen et al. 2008).

We calculated PID_{sib}, the power to differentiate between siblings (Waits et al. 2001), using a subset of 20 genotyped individuals in GENALEX version 6.41 (Peakall & Smouse 2006). We chose the PID_{sib} test over the PID_{random} test.
because it is more conservative and elephants may be found in groups of related individuals (Archie et al. 2006). Based on the results, only genotypes that included at least six loci (PID_{sib} = 0.002, (Waits et al. 2001) were included in the analyses. PID_{sib} was calculated again once all samples were genotyped, and the results did not change. Locus LafMS02R did not amplify reliably and was removed from the study.

Genotyping error rate was calculated using 25 randomly selected samples in RELIOTYPE (Miller et al. 2002). We used default settings and 10,000 bootstrap replicates.

We used DROUPOUT (McKelvey & Schwartz 2005) to identify genotypes that differed at two or less loci, and those genotypes were checked manually. We considered genotypes to represent the same individual if they met the following criteria: (1) at least six matching loci (2) the other loci either did not amplify, or mismatches could be explained by allelic dropout, and (3) one mismatch was allowed if the alleles were difficult to score. If samples were identified as the same individual, molecular sexing, haplotypes, and bolus circumferences were compared to ensure they were in accordance. For matches that differed in bolus circumferences, field notes were checked to determine if differences could be explained by field conditions.

**Molecular sexing**

Sex was determined using the method of Munshi-South et al. (2008) which amplifies a 141 bp portion of the X- and Y-linked zinc finger protein (ZFX/ZFY) genes or following Ahlering et al. (2011) which amplifies two Y-
specific fragments (SRY1 and AMELY2) and one X-specific fragment (PLP1) in one PCR reaction. For the former method, we digested 5 μL of the amplification products with BamHI (New England Biolabs) for 2 hours and products were visualized in a 3% agarose gel. For the latter, products were visualized on a 2% agarose gel. A subset of samples was tested for consistency between the two methods, and because bands may experience dropout in samples belonging to males, three independent runs confirmed females, while males were confirmed twice.

**Mitochondrial DNA**

We amplified a 627 bp fragment of the mitochondrial control region for all individuals identified through unique genotypes. We used the primers MDL3 and MDL5 (Fernando et al. 2000) or the combination of AFDL1, AFDL2, AFDL3, and AFDL4, following the methods described in Eggert et al. (2002). Products were sequenced in both directions on an ABI 3730 DNA Analyzer (Applied Biosystems) using the Big Dye Terminator cycle sequencing chemistry. Sequences were aligned and edited in SEQUENCER version 4.5 (Gene Codes Corporation). Haplotypes were identified by at least one base pair difference.

**Estimating the age of individuals**

We used the averages of three dung boli to establish age classes of juvenile (pre-reproductive) and adult (reproductive) individuals. Eggert et al. (2003) calibrated forest elephant samples based on the age distribution of dung samples from savanna elephants and considered individuals with average bolus sizes greater than 32 cm in circumference to be adults. We compared these estimates
to the samples of known reproductive and pre-reproductive individuals from an accompanying observational study in LNP (Schuttler pers. obs.) and adjusted our criteria for this population; 30 cm and above were considered adults, while below 30 cm were juveniles. For individuals that were captured repeatedly and had sample averages above and below 30 cm, we averaged all measured boli to determine the age class. We also looked for evidence of damage to the sample (e.g. rain, insects) in field notes, in which case, we relied on measurements of undamaged samples to determine age class.

**Data Analysis**

We used MICROCHECKER (van Oosterhout et al. 2004) to test for null alleles, stuttering, and large allelic dropout. We used GENEPOP version 4.0 (Raymond & Rousset 1995) to calculate the observed and expected heterozygosities for each locus, allelic diversity, deviations from expected heterozygosity values under Hardy-Weinberg equilibrium, and linkage disequilibrium.

**Spatial genetic structure**

To examine the relationship between genetic distance and spatial proximity, we conducted spatial autocorrelation analyses for adult individuals using GENALEX version 6.41 (Peakall & Smouse 2006). For adult females, we tested samples collected together on the same day (“single day”), each sampling session (“week”), and combined samples from each year (“year”) for correlations between genetic and geographic distance. We were only able to conduct one single day analysis due to sample size. For the year analyses, samples collected
during the spatial genetics sampling were combined with samples collected
during the observational study. For adult males, we could only conduct analyses
for the year 2008 because sample sizes were too small in other sessions.

Spatial autocorrelation analyses are based on a single location per
individual. For repeat captures of individuals within a designated period (single
day, week, or year), we calculated a midpoint between two locations, or created
centroids using minimum convex polygons with Hawth’s tools v3.2
(www.spatalecology.com/htools/) in ArcGIS 9.2 (ESRI, Redlands, CA) when
more than two locations were observed. Each spatial autocorrelation was run
with 9,999 permutations and bootstraps. Pairwise genetic distances were
calculated from genotypes and changed to $r$, an autocorrelation coefficient
similar to, but not directly comparable to (Smouse & Peakall 1999) Queller &
Goodnight’s $R$ (Queller & Goodnight 1989).

Spatial autocorrelation analyses are influenced by the distance class used
(Peakall et al. 2003). We searched for biologically-meaningful distance classes
that would not be overly influenced by short-term movements of elephants
during the sampling sessions, or by distances between the locations of recaptured
individuals. We explored raw telemetry data reported in Momont (2007) from
four adult female elephants in LNP. These elephants moved 2.8 – 4.4 km every
12 hours (Momont 2007), but did not displace this distance (e.g. one individual’s
entire home range was 8.4 km$^2$). Therefore, we examined displacement distances
of individuals by selecting one six-day period (the average number of days in
week sampling sessions) from each month per individual, and recorded the
longest distance between two of the location points. Average displacement was 4.8 ± 2.3 km with a range of 2.8 – 7.2 km. Therefore, we chose distance classes of 5.0 km.

Significance in spatial autocorrelation can be detected if (1) the spatial autocorrelation coefficient, $r$, exceeds the upper and lower bounds of the 95% confidence interval generated from random permutations, or (2) the 95% error about $r$ generated from bootstrap tests does not intercept the x-axis at $r = 0$. The latter is more conservative and will favor the null hypothesis more frequently (Peakall et al. 2003). When positive significant genetic structure is found, the estimated spatial autocorrelation coefficient will decrease as distance size classes increase. The first distance class size where $r$ is no longer significant is thought to designate the spatial extent at which genetic structure ends in the population (Peakall et al. 2003). However, this can depend on the size of the distance class, which is chosen by the user. To overcome this, we conducted separate analyses that plotted pairwise genetic distances against increasing inclusive distance classes (999 bootstraps) of 1.0 km intervals to determine the distance class at which $r$ was no longer significant (Peakall et al. 2003).

To test for a more general relationship between relatedness and distance, we conducted Mantel tests using genalex 6.4.1 and 9,999 permutations. There is no relatedness estimator that outperforms others, and an estimator is data dependent (Van De Casteele et al. 2001). We used COANCESTRY version 1.0 (Wang 2011) to perform Monte Carlo simulations that calculated correlation coefficients between seven relatedness estimators and the values of known relatedness.
categories generated through simulations using the observed allele frequencies and missing genotype rates. We simulated eight relationship categories of 100 dyads, with 100 reference individuals, and 1,000 bootstraps. We chose the Queller-Goodnight moment estimator (Queller & Goodnight 1989) because it resulted in a strong correlation between true and estimated values ($r = 0.911$).

We calculated pairwise relatedness ($R$) in RELATEDNESS version 5.0.8 (Queller & Goodnight 1989) using the bias correction. To test the effectiveness of this estimator on our dataset, we used eight known mother-calf pairs whose samples were collected during the observational study. The average pairwise relatedness of mother-calf pairs was $0.490 \pm 0.083$, consistent with expectations.

To assess the consequences of using centroids for recaptured locations from the same individual, we conducted permutation tests between matrices of dyads that compared spatial proximity with relatedness, but allowed for the nonindependence of data points. We used Hemelrijk’s Tau $K_r$ test (Hemelrijk 1990) in MATRIXTESTER (www.rug.nl/fmns-research/beso/_people/hemelrijk) with 10,000 permutations. MATRIXTESTER allows for matrices containing dyads of 100 individuals or less, and therefore analyses for adult females year 2008 and 2010 were excluded, as recaptures increased matrix size.

We looked at average distances between related adult female in the week and single day sessions. If dyads had a relatedness value of at least 0.2, the Euclidean distances between the dyads were measured and averaged in ArcGIS 9.2. We chose 0.2 to ensure the following relatedness categories would be captured; mother-daughter ($R=0.5$), full siblings ($R=0.5$), half siblings ($R=0.25$),
and grandmother-daughter ($R=0.25$), as the mean expected relatedness value on average is 0.25, but can be lower or higher. Mitochondrial DNA haplotypes were mapped into ArcGIS 9.2 to examine the distribution of matrilines.

**Group analyses**

For savanna elephants, individuals are considered to be in the same group in ranges of 100-500 m of each other (Archie *et al.* 2006, Wittemyer *et al.* 2005). Samples were considered to be from the same group if they were collected on the same day, within 250 m of each other, and were of the same freshness. For most samples, this was apparent, as it was rare to find numerous dung piles that were less than 24 hours old in the same area. There were only 6 groups from which there was some uncertainty.

We tested if individuals within a group were more related to each other than to individuals from other groups using permutation tests in PERM with 10,000 permutations and 10 iterations (Duchesne *et al.* 2006). We tested adult females found in groups, and all individuals found together. We also investigated group composition based on mitochondrial haplotypes.

To infer longitudinal social patterns, we created genetic networks based on samples collected together, excluding data from samples that were found solitarily. Networks were created in UCINET (Borgatti *et al.* 2002) and visualized in NETDRAW (Borgatti 2002). Networks included all relationships between all individuals across the temporal scale of the study. We reported the number of nodes (individuals), edges (ties between individuals that exist if samples were detected together in groups), and the number of components (a group of nodes
connected only to each other, and not connected to the rest of the network). Edges were weighted according to relatedness and mitochondrial haplotypes were added as an attribute. We calculated average relatedness for each component using RELATEDNESS.

**Dispersal**

We used COANCESTRY version 1.0 (Wang 2011) to test for differences between same sex dyads. We input data containing adult males and females using 100 reference individuals and 1,000 bootstraps to obtain relatedness values. The groups were organized into male-male and female-female dyads to test if the mean relatedness between those groups were different using 10,000 bootstraps.

**RESULTS**

We collected 501 dung samples and were able to identify 89 unique adult females, 24 juvenile females, 15 females of unknown age, 18 adult males, 22 juvenile males, and 10 males of unknown age from genotypes (Table 1). On average, individuals were recaptured 2.249 times with a range of 1-19 recaptures.

After applying a standard Bonferonni correction for multiple tests, all loci except LaT05 conformed to Hardy-Weinberg equilibrium expectations. This locus also showed evidence of large allelic dropout and null alleles. Because LaT05 did not amplify consistently, we removed it from the analyses, as it did not affect the number of successfully genotyped individuals. The average number of alleles per locus was 12 ± 3.9 and the mean observed heterozygosity was 0.820 ±
0.081 (Table 2). The average expected overall reliability after replication was 0.995.

Mitochondrial haplotype diversity was 0.805 ± 0.017 and nucleotide diversity averaged over all loci was 0.008 ± 0.004. Ten haplotypes were identified and differed from those previously reported of the same length.

**Spatial genetic structure**

Sessions 2, 4, the single day analysis, and both years revealed significant positive genetic structure at 0-5 km and negative structure at 5-10 km for adult females (Fig. 2). No genetic structure was detected for sessions 1 and 3 (Fig. 2) or for adult males in 2008 (Fig. 3).

In the inclusive distance classes, we found significant autocorrelation up to 5.0 km distances in sessions 2, 4, the single day, and in 2008 and 2010 for adult females (Table 3). Preceding distance classes occurring from 0-5 km were not always significant. For example, in session 2, distance classes 0-3 and 0-4 km were not significant, but sessions 0-1, 0-2, and 0-5 km were (Table 3). This may be an artifact of the short-term movements captured during sampling sessions and from taking midpoints between recapture locations. No autocorrelation coefficients were significant in sessions 1 and 3. Adult males had significant spatial autocorrelation coefficients in distance classes from 0-3 and 0-4 km (Table 3).

For week sessions, as geographic distance increased, overall relatedness decreased in Mantel tests, but session 1 was the only session to have a significant negative relationship (Table 4). This pattern was also significant for adult
females in 2008 and the single day analysis, but not for 2010. In contrast, the Mantel test revealed a positive relationship with distance and relatedness for males, although it was not statistically significant (Table 4).

The Tau $K_r$ tests revealed significance of non-independent data between special proximity and relatedness in session 1, 4, and the single day analysis for adult females (Table 4). No significant pattern was found for adult males (Table 4).

The mean distance between individuals with a relatedness value of 0.2 or greater was 2.984 ± 2.105 km for session 1, 2.208 ± 1.709 km for session 2, 2.599 ± 0.747 km for session 3, and 1.688 ± 1.775 km for session 4. The single day analysis had a smaller mean distance of 0.823 ± 0.548 km. In all sessions, we found dyads that were closer to each other in distance, but less closely related.

We detected a total of ten mitochondrial DNA haplotypes, one of which (Lope10) was found only in a solitary male. While Lope7 was the most common haplotype detected, individuals with different haplotypes were found in close proximity (less than 1.0 km) to samples with this haplotype in each session and overall no spatial segregation was observed. The distribution of haplotypes within the single day session yielded the same pattern, with samples collected less than 100 m from each other having different haplotypes.

**Analysis of groups**

We detected 69 groups, of which 26 involved more than one adult female (Table 5). Individuals within groups were typically related (Fig. 4), and significantly more related to each other than to individuals from distant groups.
for adult females only ($R = 0.219 \pm 0.209, P = 0.000$) and all individuals ($R = 0.256 \pm 0.189, P = 0.000$). In 80.8% of groups (21 of 26), adult females had the same mitochondrial haplotype, and in 81.2% of groups (56 of 69), all individuals shared the same mitochondrial haplotype (Table 5).

One hundred and twelve individuals were included in the network with 29 components and 300 edges (Fig. 5). The largest component had 24 individuals. Eighteen out of 149 dyads were detected two or more times together (12.1%), with six being the largest number of times two individuals were detected together. The average relatedness of network components was $0.182 \pm 0.234$ for all individuals, and $0.182 \pm 0.178$ when including only adult females in components. Twenty-one components consisted of individuals that shared the same haplotype (72.4%), and in four cases, the haplotype differences were from associations with males. Out of the remaining components with mismatching haplotypes, three groups included samples where there was uncertainty if samples belonged to the same group. The other three samples in which there was uncertainty if samples belonged to the same group did match in haplotypes.

**Dispersal**

The mean difference in relatedness between male-male and female-female dyads was significant. Mean relatedness of female dyads was $-0.007 \pm 0.023$, while males was $-0.045 \pm 0.021$. One haplotype (Lope10) was unique to males.

**DISCUSSION**

We found evidence of fine-scale genetic structure in African forest elephants despite high daily movements. Spatial autocorrelation analyses
revealed adult females to be more closely related to each other than expected by chance from 0-5 km in two of the four week sampling sessions, samples collected over four-month periods for years 2008 and 2010, and in the analysis for samples collected on one day. Although no genetic structure through spatial autocorrelation was found in one of the week sampling sessions (session 1), there were significant correlations between distance and relatedness with Mantel and Tau $K_r$ tests. Only one week session, session 3, revealed no genetic structure.

Significant spatial autocorrelation coefficients were 0.014 or lower, and for inclusive distance classes, 0.083 or less within the first distance class. Other species had values up to 0.08 in tree-roosting bats (Rossiter et al. 2012), 0.12 in Australian bushrats, *Rattus fuscipes* (Peakall et al. 2003), 0.04 in black rhinoceros, *Diceros bicornis bicornis* (Van Coeverden de Groot et al. 2011), and 0.07 in Eurasian badgers, *Meles meles* (Pope et al. 2006). Our results are lower, even compared to mobile species. We chose larger distance classes due to the mobility of elephants and the use of midpoints for recaptures, which resulted in pooling dyads into larger, more inclusive distance classes, and may have biased our spatial autocorrelation correlation coefficients downward. The only session with continuously significant distance classes up to five kilometers was the single day analysis, which included recaptures, but likely reduced the effects of movements because of the short time scale. Even though distance classes were large, compared to the range of forest elephants, they were still small. For example, in black rhinoceroses, distance classes ranged from 21 to 224 km (Van Coeverden de Groot et al. 2011). If samples were collected beyond the spatial
extent of the SEGC study zone, it is possible we would have had larger spatial autocorrelation coefficients, and finer resolution between distance classes.

When looking at the spatial patterns of related adult female dyads (those with a relatedness value of at least 0.2), it was not uncommon to find more geographically distant dyads more related to each other than to individuals closer together, even for samples collected on the same day. There was no spatial structure associated with mitochondrial haplotypes, and based on dung locations and dates, individuals appeared to tolerate others with different haplotypes in close proximity. These patterns might be interpreted as evidence that females disperse from their natal group; however, other results suggest individuals in groups are significantly more related to each other than to individuals in other groups. These conflicting results could be due to the mobility of elephants travelling in groups. For example, even though dyads appear to be a distance apart based on dung sampling, they may have actually traveled together, but defecated in different areas. We detected many solitary dung samples, but it is difficult to assess if this reflects solitary individuals, as not all group members may have defecated. Also, individuals may use different strategies. Depending on the fitness benefits and costs of group living, some individuals may disperse and remain solitary, while others form small groups.

We did not find any relationship between rainfall and the results of the spatial genetic analyses. Session 2 occurred during the month with the most rainfall, and we found significant spatial autocorrelation, and almost significant negative relationships between relatedness and spatial proximity in the Mantel
and Tau K tests. In contrast, session 3 had the second highest amount of rainfall, yet no spatial genetic structure was detected. These results suggest that fruiting events or other factors are more influential on the spatial patterns of forest elephants. Forest elephants in LNP consume 230 different plant species (White et al. 1993), and densities have been correlated with the ripening of a preferred fruits (White 1994b).

The patterns in this study reflect family group relationships between adult females (second-tier relationships), as individuals within groups were significantly more related to each other than they were to individuals from other groups, which is consistent with other populations in Gabon (Munshi-South 2011). The average pairwise relatedness of 0.219 among adult female elephants was similar to second-tier relationships in savanna elephants (0.150, Archie et al. 2006; 0.234, Wittemyer et al. 2009), where family groups range from 1-20 adult females (Archie et al. 2006). We detected at most five adult females, which meets the expectations of family groups, but is higher than most forest elephant group sizes based on observational data (Momont 2007; White et al. 1993). The largest component contained 24 individuals, which could be evidence of bond groups (third-tier), as group sizes are likely underestimated because not all members may defecate, and not all samples collected were successfully genotyped. Most individuals detected together shared a mitochondrial DNA haplotype, suggesting associations are based on matrilines. If groups detected in this study were based on resources, we would expect most components to be
made up of individuals of different mitochondrial haplotypes given the high diversity over a small area.

The results of adult males were consistent with male dispersal. No genetic structure was found, the Tau K_r test was not significant, the Mantel test revealed a non-significant positive relationship between distance and relatedness, and the mean difference between relatedness in male-male and female-female dyads was significant. However, for spatial autocorrelation analyses with inclusive distance classes, significant positive genetic structure was found in distance classes 0-3 and 0-4 km. This could be a spurious result from low sample size, or possibly limited dispersal in males. All but one male shared a mitochondrial haplotype with females in the population. This suggests social dispersal, in which males remain in or near their natal range and disperse only to search for females (Isbell & Van Vuren 1996; Vidya & Sukumar 2005). However, our sample size and spatial extent for adult males was small, and it is difficult to ascertain if this is the pattern.

Aureli et al. (2008) developed a framework for fission-fusion dynamics which captures three dimensions of variation among species; spatial cohesion, group (party) size, and group composition. Savanna elephants had high variation in group size and spatial cohesion, and medium variation in group composition. Our study on forest elephants revealed variation in group composition and some variation in spatial cohesion. In the genetic network, only 18 dyads were detected together two or more times and several components reflect larger associations than observed from group sizes alone (Momont 2007; White et al. 1993). We
found groups to be composed of related individuals, yet related dyads could be several kilometers apart. Elephants communicate through infrasound and vibration (Langbauer 2000; O’Connell-Rodwell 2007), and savanna elephants can detect individuals at 2 km distances (Langbauer et al. 1991). Although the extent of infrasound is currently unknown in forest elephants, it is probable that individuals a kilometer or potentially more apart can communicate.

Our study cannot directly address variation in group size because groups detected from dung sampling are unlikely to include all members. However, by tracking associations from dung found together, the genetic network revealed larger components than group sizes from observational studies. Using acoustic sampling, Wrege et al. (2012) found 79% of all forest elephant visitations occur at night, and that diurnal observations are likely to be biased. Genetic methods capture day and night associations, and therefore may reflect a more accurate picture of forest elephant sociality, despite the biased-downward nature of group associations from dung sampling.

It is not clear what benefits forest elephants may gain from group-living. It may be disadvantageous for individuals to forage in larger groups, as patchily distributed fruits will quickly be depleted, resulting in increased travel for forage. Large cooperatively hunting predators are absent in most locations throughout forest elephant range, including LNP, making it unnecessary for large groups to form for defense. This could be a recent occurrence as the historical distribution of lions included all of Africa, excepting only central Sahara and the most dense rainforests (Henschel et al. 2010). There is some evidence that leopards predate
on forest elephant calves (Blake 2004), but they are typically avoided as prey (Hayward et al. 2006). Also, humans are highly effective predators for elephants, as poaching of forest elephants for bushmeat and ivory has reached epidemic proportions (Blake et al. 2007).

Forest elephants may benefit from living in groups with, or associating with older individuals. As forest elephants navigate through the forest for resources, it may be beneficial to associate with more knowledgeable individuals to gain access to the spatial locations of fruiting trees or mineral deposits. In savanna elephants, groups with older matriarchs have higher fitness (Gobush et al. 2008) and form defensive behaviors to predators more quickly (McComb et al. 2011). Matriarchs have a repository of knowledge about their environment, making it beneficial for group members to forage with matriarchs for increased access to resources (McComb et al. 2001).

The results of our study show that sociality in forest elephants does not violate the assumptions of the fission-fusion framework, and that there is evidence that individuals have a higher number of associates than previously determined from observational data. However, our study suggests that forest elephants are the least social of the extant elephant species, and we did not find strong evidence for the multi-tiered hierarchies found in African savanna elephants nor the more socially complex networks found in Asian elephants. We find that forest elephants group according to matriline, and are not always found in groups with the same individuals. As groups inferred from dung sampling are likely underestimated, more research is needed to determine the full extent of
sociality in forest elephants, and to discern any fitness benefits for individuals having a different number of associates.

ACKNOWLEDGEMENTS

We thank the Gabonese government, CENAREST, and ANPN for permission to work in Lopé National Park, SEGC and CIRMF for providing institutional and logistical support for fieldwork, and USFWS African Elephant Conservation Fund (agreement #98210-8-G753 to LSE) and MU Life Sciences fellowship for financial support. J. Dibakou, J.T. Dikangadissi, E. Dimoto, and C. Nzotekoumie provided invaluable logistical support and guidance in the field.
LITERATURE CITED


Table 1. Summary of sample collection, rainfall, genotyped samples, age categories, and sexes of unique individuals. For the year analyses, samples were combined with those from a separate observational study (n=88 from 2008, n=142 from 2010). UK indicates samples of unknown age.

<table>
<thead>
<tr>
<th>sampling session</th>
<th>dates</th>
<th>total monthly rainfall (mm)</th>
<th>samples collected</th>
<th>samples genotyped</th>
<th>unique females</th>
<th>unique males</th>
</tr>
</thead>
<tbody>
<tr>
<td>single day</td>
<td>10/24/08</td>
<td>-</td>
<td>40</td>
<td>34</td>
<td>16</td>
<td>2</td>
</tr>
<tr>
<td>session 1</td>
<td>9/23/08 - 9/26/08</td>
<td>134.8</td>
<td>48</td>
<td>39</td>
<td>18</td>
<td>3</td>
</tr>
<tr>
<td>session 2</td>
<td>10/20/08 - 10/24/08</td>
<td>418.5</td>
<td>102</td>
<td>85</td>
<td>25</td>
<td>11</td>
</tr>
<tr>
<td>session 3</td>
<td>3/21/10 - 3/27/10</td>
<td>157.9</td>
<td>63</td>
<td>37</td>
<td>14</td>
<td>3</td>
</tr>
<tr>
<td>session 4</td>
<td>5/10/10 - 5/15/10</td>
<td>115.5</td>
<td>56</td>
<td>51</td>
<td>15</td>
<td>6</td>
</tr>
<tr>
<td>year 2008</td>
<td>8/12/08 - 11/7/08</td>
<td>728.2</td>
<td>239</td>
<td>196</td>
<td>55</td>
<td>16</td>
</tr>
<tr>
<td>year 2010</td>
<td>2/17/10 - 5/10/10</td>
<td>423.5</td>
<td>262</td>
<td>202</td>
<td>56</td>
<td>13</td>
</tr>
</tbody>
</table>
Table 2. Genetic diversity values for elephants at Lopé National Park, Gabon

(N_a=allelic diversity, H_e=expected and H_o=observed heterozygosity). Multiplexes 1 and 4 had an annealing temperature of 60°C, while 2 and 3 were at 58°C.

<table>
<thead>
<tr>
<th>locus</th>
<th>N_a</th>
<th>H_e</th>
<th>H_o</th>
<th>multiplex number</th>
</tr>
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<tbody>
<tr>
<td>FH94R</td>
<td>9</td>
<td>0.653</td>
<td>0.676</td>
<td>2</td>
</tr>
<tr>
<td>FH126</td>
<td>16</td>
<td>0.884</td>
<td>0.879</td>
<td>2, 3, 4</td>
</tr>
<tr>
<td>FH103R</td>
<td>8</td>
<td>0.794</td>
<td>0.785</td>
<td>2</td>
</tr>
<tr>
<td>LaT13R</td>
<td>20</td>
<td>0.917</td>
<td>0.905</td>
<td>1, 2, 3, 4</td>
</tr>
<tr>
<td>FH67</td>
<td>8</td>
<td>0.728</td>
<td>0.729</td>
<td>3</td>
</tr>
<tr>
<td>FH48R</td>
<td>13</td>
<td>0.832</td>
<td>0.829</td>
<td>1</td>
</tr>
<tr>
<td>LA6R</td>
<td>10</td>
<td>0.723</td>
<td>0.750</td>
<td>3</td>
</tr>
<tr>
<td>FH60R</td>
<td>12</td>
<td>0.850</td>
<td>0.867</td>
<td>1</td>
</tr>
<tr>
<td>FH19R</td>
<td>15</td>
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<td>0.910</td>
<td>1, 4</td>
</tr>
<tr>
<td>FH129</td>
<td>12</td>
<td>0.861</td>
<td>0.870</td>
<td>4</td>
</tr>
<tr>
<td>Mean</td>
<td>12</td>
<td>0.841</td>
<td>0.820</td>
<td></td>
</tr>
<tr>
<td>SD</td>
<td>3.9</td>
<td>0.087</td>
<td>0.081</td>
<td></td>
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</table>
Table 3. Summary of $r$ coefficients from autocorrelation analyses with inclusive distance classes for adult female (AF) and male (AM) forest elephants in Lopé National Park, Gabon. Significant $r$ coefficients from one-tailed $P$ values are in bold type.

<table>
<thead>
<tr>
<th>sampling session</th>
<th>0 to 1</th>
<th>0 to 2</th>
<th>0 to 3</th>
<th>0 to 4</th>
<th>0 to 5</th>
<th>0 to 6</th>
<th>0 to 7</th>
<th>0 to 8</th>
<th>0 to 9</th>
<th>0 to 10</th>
</tr>
</thead>
<tbody>
<tr>
<td>session 1 AF</td>
<td>0.083</td>
<td>0.044</td>
<td>0.013</td>
<td>0.022</td>
<td>0.011</td>
<td>0.015</td>
<td>0.006</td>
<td>0.002</td>
<td>0.001</td>
<td>-0.001</td>
</tr>
<tr>
<td>session 2 AF</td>
<td><strong>0.059</strong></td>
<td><strong>0.016</strong></td>
<td>0.008</td>
<td>0.004</td>
<td><strong>0.006</strong></td>
<td>-0.001</td>
<td>0.001</td>
<td>0.000</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>session 3 AF</td>
<td>-0.011</td>
<td>-0.004</td>
<td>-0.016</td>
<td>0.000</td>
<td>-0.002</td>
<td>0.002</td>
<td>0.003</td>
<td>-0.002</td>
<td>-0.001</td>
<td>-0.001</td>
</tr>
<tr>
<td>session 4 AF</td>
<td>0.033</td>
<td>0.029</td>
<td>0.015</td>
<td>0.002</td>
<td><strong>0.008</strong></td>
<td>0.003</td>
<td>0.003</td>
<td>0.000</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>single day</td>
<td><strong>0.075</strong></td>
<td><strong>0.025</strong></td>
<td><strong>0.013</strong></td>
<td><strong>0.014</strong></td>
<td><strong>0.014</strong></td>
<td>0.007</td>
<td>0.002</td>
<td>-0.001</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>year 2008 AF</td>
<td><strong>0.026</strong></td>
<td>0.005</td>
<td>0.003</td>
<td>0.004</td>
<td><strong>0.006</strong></td>
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Table 4. Results of spatial genetic tests for adult female (AF) and male (AM) forest elephants at Lopé National Park, Gabon.

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Table 5. Group composition, mitochondrial haplotypes, average pairwise relatedness (R) and 95% confidence intervals (CI) within groups detected at Lopé National Park, Gabon. A–adult, J–juvenile, U–unknown age category, F–female, and M – male.

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Figure 1. Map showing the SEGC study zone within Lopé National Park, Gabon.
Figure 2. Correlograms from spatial autocorrelation for week analyses on adult females; (a) session 1, (b) 2, (c) 3, and (d) 4. Significant distance classes are designated with an asterisk (*). Dotted lines represent the upper and lower bounds of the 95% confidence interval generated from random permutations, while bars represent 95% error generated from bootstrap tests.
Figure 3. Correlograms from spatial autocorrelation analyses on adult females in (a) year 2008, (b) 2010, (c) a single day, (d) and for males in 2008. Significant distance classes are designated with an asterisk (*). Dotted lines represent the upper and lower bounds of the 95% confidence interval generated from random permutations, while bars represent 95% error generated from bootstrap tests.
Figure 4. Histogram of average pairwise relatedness within groups including all group members detected.
Figure 5. Network constructed from dung sample group data using all individuals. Dung samples that were collected outside of groups were not included. Nodes represent individuals and edges indicate individuals whose dung was collected as part of the group. Squares represent males, while circles represent females. The size of the node reflects the age category; adults are the largest, unknown ages are of medium size, and juveniles are the smallest. Colors represent mitochondrial DNA haplotype; pink, Lope1; orange, Lope3; yellow, Lope4; light green, Lope5; aqua, Lope6; blue, Lope7; purple, Lope9; white, Lope11. Edges are weighted according to relatedness; those with thicker lines representing more closely related dyads.
CHAPTER 4
SOCIAL NETWORK ANALYSES REVEAL LIMITED
FISSION-FUSION SOCIALITY IN AFRICAN FOREST
ELEPHANTS

ABSTRACT

Social network models are a powerful tool for unraveling social structure patterns in animal species. They can elucidate social patterns because they capture interactions among individuals over time, and can be especially important for species where interactions are dynamic or cryptic. We tested the hypothesis that African forest elephants (*Loxodonta cyclotis*) have a fission-fusion social structure based on kinship consistent with the other extant elephant species. Observational studies suggest small group sizes in forest elephants, but it is unknown if group composition changes over time allowing individuals to have a large number of associates. We tested if group sizes change over time and space, and if accumulative associations are larger than those observed from group sizes alone. We observed groups and individuals of forest elephants in savanna habitats of Lopé National Park, Gabon in 2006, 2008, and 2010 and recorded associations between identified individuals. Where possible, dung was collected from individuals for genetic analyses using ten nuclear microsatellite loci and the mitochondrial DNA control region. We created network models using adult females based on simple ratio association indices for each year, for wet and dry seasons, for individuals detected two times, and for all adult females.
identified throughout the study. We identified 118 unique adult females and were able to collect dung samples from 40 individuals. All networks were characterized by low densities, many disconnected components, short average path lengths, and high clustering coefficients. The average relatedness of adult females within a component was 0.093 ± 0.071 and components appeared to share the same mitochondrial haplotype. One very large component consisting of 22 adult females was discovered, although there were very few preferred associations (8 out of 65 associations, 12.3%). There was no indication of differences between dry and wet season networks, or between years. Although our results offer some support for fission-fusion sociality in African forest elephants, they suggest that it is different than the other extant elephant species.

INTRODUCTION

Within a species, individuals interact non-randomly. They may compete over resources and mates, or cooperate to defend and obtain resources and protect against predators. Social structure is a such synthesis of interactions between individuals, and captures the individual differences while summarizing the overall actions and relationships with conspecifics (Whitehead 2008). Social structure affects how individuals exploit their habitat (Hoelzel 1993), transfer knowledge within a population (Weimerskirch et al. 2010), transmit diseases (Hamede et al. 2009), and search for mates (Ortega et al. 2003; Rossiter et al. 2012).
Hinde (1976) a three-level framework for conceptualizing sociality: (1) interactions between individuals, (2) the quality, type, and patterns of interactions, which form relationships between individuals, and (3) structure, as described by quality, type and patterns of relationships. For some species, documenting and understanding interactions between individuals is difficult because group composition rapidly changes over time and space. For example, chimpanzees (*Pan troglodytes*, Lehmann and Boesch 2004), bats (Kerth & Konig 1999; Willis & Brigham 2005), African buffalo (*Synerus caffer*, Prins 1989), dolphins (Parra *et al.* 2011), and African savanna elephants (*Loxondonta africana*, Archie *et al.* 2006) have fission-fusion societies, in which group composition and structure can change monthly, daily, or even hourly in response to resources or group dynamics. Understanding the social structure of these species therefore requires longitudinal studies in which individuals and their relationships are tracked.

Social network analyses have the capability to reveal cryptic relationships or social structure because they can capture interactions among individuals within a population over time. For example, Mourier *et al.* (2012) found nonrandom and stable associations in blacktip reef sharks (*Carcharhinus melanopterus*), a species typically considered a solitary marine predator. In Asian elephants (*Elephas maximus*), de Silva *et al.* (2011) found group sizes to be small in field observations, but longitudinal studies of individually identified elephants using social network models revealed larger social units with stable relationships. Using network analyses and genetic information, we used a similar
approach on a population of African forest elephants (*Loxondonta cyclotis*) to attempt to elucidate their social structure.

There are two extant species of elephant; African savanna and African forest. Several populations of African savanna elephants have been studied in detail, revealing a fission-fusion social structure where related females make up core groups that repeatedly join and separate from other groups (Archie *et al.* 2006; Moss 1988; Wittemyer *et al.* 2005). Female savanna elephants cooperatively rear young, who benefit from exposure to more individuals and a larger repertoire of behaviors and situations (Sukumar 2003). Groups are also more capable of defending young calves against cooperatively-hunting savanna predators (McComb *et al.* 2011).

Less is known about the social structure of forest elephants, as their dense and remote habitats make it more difficult to conduct behavioral studies. Observational studies at forest clearings or in patches of savanna within forested regions show that forest elephant groups are typically composed of an adult female and her dependent calves (Turkalo & Fay 1996; White *et al.* 1993). These results suggest that it may be disadvantageous for individuals to navigate the forest with other individuals, possibly making it harder to forage and exploit resources (Sukumar 2003). The diet of forest elephants is heavily composed of fruits (Campos-Arceiz & Blake 2011) and trees may become more easily depleted when foraged on by large groups.

However, there is evidence to suggest that forest elephants may have more associates than indicated by observed group sizes alone, and possibly a
fission-fusion form of social structure may occur. A study at Dzangha Bai, a large, natural forest clearing in the Central African Republic, found that some females arrive in groups, but associate with other groups (Turkalo & Fay 1996). At Mbeli Bai, Republic of Congo, individuals had preferred associates, but were not always observed in the same group, or found consistently in groups of the same size (Fishlock et al. 2008). Using genetic networks from dung samples found in groups, Schuttler et al. (see Chapter 3) found some elephants had more associations than typically observed, and associations were largely based on matrilineal kinship. However, because not all group members would be expected to defecate in the same place at the same time, these networks likely bias group sizes downwards. Nonetheless, collectively this data suggests that individuals have more associates than what is observed through group sizes alone, and that individuals are not always found with the same associates over time.

Forest elephants may maintain associations with other individuals to receive benefits in the form of information about forest resources. In savanna elephants, the eldest individual, or matriarch of the group retains knowledge about important resources and guides groups (McComb et al. 2001; Sukumar 2003). Forest elephants aggregate at bais to acquire minerals, which are found in high concentrations in the soils of these clearings (Turkalo & Fay 1996). Bais are patchy throughout the forest zone and females may remain with mothers and other kin because they have greater knowledge of the locations of these important resources. Fruiting trees may have a similar influence on elephants. White et al. (1993) speculated that forest elephants may coordinate movements with
infrasound (low frequency vocalizations, Langbauer et al. 1991) in response to availability of fruit. Although trees appear to be evenly distributed throughout the forest, their fruits ripen at different times and in different intensities, making them ephemeral and patchy.

Using behavioral observations, genetic data and network analyses, we tracked individual forest elephants to quantify the number of associates that they have, and the quality of relationships based on how often individuals are seen together. We tested the hypothesis that African forest elephants have a fission-fusion social structure based on kinship where group sizes change over time and space, and associations are more extensive than observed group sizes.

METHODS

Study Area and Sample Collection

Field research was conducted in northeastern Lopé National Park (LNP), Gabon at the Station d’Etudes des Gorilles et Chimpanzees (SEGC, Figure 1). LNP consists largely of mature forest, but the northeastern section contains a mosaic of secondary forest and savanna habitat, facilitating observations of forest elephants (White et al. 1993). The SEGC study zone (approximately 200 km²) makes up about 3% of the park (4,910 km²), but has higher elephant densities at approximately 3.0 elephants/km² (White 1994a), and higher encounter rates (Maisels et al. 2006) than other areas of LNP. There are two dry seasons, one from June until August, and a less defined one from December to February. Wet seasons occur in October/November, and again in March/April, although variation occurs between years.
Forest elephant groups and individuals were searched for by vehicle in 2006 (3/1/06 – 9/17/06), 2008 (8/12/08–11/7/08) and 2010 (2/17/10–5/12/10). Circuits on ~30 km of LNP roads (Figure 1) were typically conducted after sunrise and before sunset, and opportunistically after rainfall. All roads in LNP were used in circuits, but not all roads were searched each day. Roads form a loop in the northeastern section of the park covering mostly savanna, but some forest habitat. We changed the routes and directions of each circuit during each session to provide equal sampling effort to different areas of the park and different times of the day. A previous study on forest elephants considered individuals to be in the same group if individuals were 50 m or less apart (Morgan & Lee 2007), while other studies on African savanna elephants consider individuals to be of the same group when individuals were 500 m or less from the center of the aggregation (Archie et al. 2006; Wittemyer et al. 2005). In our study, we found 50 m to be too small a distance as adults and their calves could be separated by distances greater than that while clearly being in the same group. Therefore, we considered all individuals within visual range of the observer to be in the same group if they were observed within 250 m of one another, and arrived and left an area together (if this was possible to observe), as well as moved together, rested, and shared resources as a group. It was not difficult to differentiate between groups, as they were typically found at least several kilometers apart, and there were only a few groups (2.91%, 8 of 275), where group membership was uncertain.
When an individual or group of forest elephants was found, we photographed individuals, focusing on the morphological characteristics important in identification: both ears to capture tears and vein patterns, tusks, and tail brush. Individuals were typically observed for 15-30 minutes, depending on the number and visibility of individuals present. We recorded the date, time, number of individuals present, sex, and age class (juvenile, pre-reproductive; adult, reproductive). Observational studies identifying individuals have been conducted in LNP since 1999, and based on these data, individuals estimated at ≥15 years were considered to be adults. Age estimates were based on the size of individuals and/or the presence of calves.

In 2008 and 2010, we collected fresh dung samples for genetic analysis. Approximately 10 grams were collected in polypropylene tubes, GPS coordinates were recorded, and if samples were not disturbed by rain or trampling, circumferences of up to three boli were recorded. Samples were boiled for 15 minutes to destroy pathogens and preserved with Queen’s College buffer (20% DMSO, 100 mM Tris pH7.5, 0.25 EDTA, saturated with NaCl; (Amos et al. 1992). Samples were stored in the dark in the field and were imported into the US under USDA permit #48529. In the lab, they were stored at 4°C.

Defecation was directly observed for some individuals, however, for most groups defecation was not directly observed, and dung searches were conducted only after elephants had left the area. Since elephant groups were frequently spotted in savannas at dusk and remained until nightfall, searches for fresh dung were sometimes delayed until the following morning. Although elephant dung
can remain visible for months after defecation (White 1995), the appearance and odor changes, making it possible to discern fresh dung. Samples older than 24 hours often lose the circular shape of the bolus due to insects, animals, or rain, which flatten the sample, and lose their odor and sheen. Elephants often act as seed dispersers for forest plants, and therefore old dung piles have plants or fungus growing from the boli.

It is possible that individuals not belonging to the observed group could defecate in the same vicinity at or near the same time. Therefore, we categorized dung samples from individuals as: (1) Definite – individual is seen defecating or sample is collected immediately after elephant group has left, (2) Probable – dung samples were collected multiple times from a group observed with the individual, (3) Tentative – dung was collected the following morning or hours after observations from a group or individual, but the individual was only seen once, or only collected from once, and therefore there is some uncertainty if the sample belongs to the assigned individual or group. We were confident that most samples belonged to the groups observed for several reasons; when searching for dung samples, we rarely found more dung samples present than there were individuals observed, we used fresh tracks and trails to follow group movements based on the elephants’ locations from the observations, and elephant groups were often separated by several kilometers or more. When conducting observations, we would rarely see large groups of individuals or areas used by multiple groups.
**DNA extraction and microsatellite genotyping**

DNA was extracted using the QIAamp Mini Stool Kit (QIAGEN) with modifications outlined in Archie *et al.* (2003) or following the Guanadine Thiocyanate method in Eggert *et al.* (2005). Extractions took place in a separate laboratory with equipment designated exclusively for the extraction of DNA from non-invasive samples to reduce the possibility of contamination.

We selected 12 polymorphic microsatellite loci: FH60R, FH94R, FH48R, FH19R, LA6R, LafMS02R (Eggert *et al.* 2008), FH67, FH126, FH103R (Comstock *et al.* 2000) FH129 (5'-3' F-TGGCTAAAATGCCTATCACTCA, R-CCAGCTAAACTAAGTCTGCTCTTTT, Gobush *et al.* 2009), LaT05, (Archie *et al.* 2003), and LaT13R (Ahlering *et al.* 2012). We redesigned primers for FH103R (5'-3' F-GCTGCCACTTCCTACACCTT, R-CCTTTGCTTTTCTAATGAGTCC) and LafMS02R (5'-3' F-GTCTATCTCCACCCCTGCT, R-TGTCTGTTGGTAAAANTCGCTTG) to shorten the fragments. All amplifications using the polymerase chain reaction (PCRs) were performed in a PCR Workstation (Fisher Scientific), in which ultraviolet light was used between PCRs to decontaminate surfaces.

Samples were amplified in single locus or multiplex reactions (Table 1). Single locus reactions contained 0.5 U AmpliTaq Gold Polymerase (Applied Biosystems), 1X PCR Gold Buffer (Applied Biosystems), 0.4 µM fluorescently labeled forward primer, 0.4 µM unlabeled reverse primer, 2 mM MgCl2, 0.2 mM each dNTP, 1.5 µl 20X BSA, and 3 µl of the DNA extract in 25 µl reactions. The profile consisted of 95°C for 10 minutes, 45 cycles of denaturation at 95°C for 1
minute, primer annealing at locus specific temperatures for 1 minute, and primer extension at 72°C for 1 minute, followed by a final extension of 72°C for 10 minutes. Loci amplified well at either 58°C or 60°C and were arranged into four multiplex reactions based on allele sizes and annealing temperatures. Loci LaT05 and LaT13R were included in all multiplexes as they have larger fragment sizes and yielded the same genotypes at 58°C or 60°C. Locus LA6R differed in annealing temperature from the single to the multiplex reactions (from 54°C to 58°C) and was tested on two positive controls and 16 samples to confirm that the different temperatures resulted in the same genotypes. Multiplex reactions were performed in 8.0 μL volumes containing 4.0 μL Master multiplex mix (QIAGEN), 0.2 μM diluted primer mix, 0.8x BSA, and 1.0-2.5 μL fecal DNA extract. Amplifications were performed with an initial cycle of 95°C for 15 minutes, followed by 40-45 cycles (depending on the quality of the sample) of denaturation at 94°C for 0.5 minutes, primer annealing at 58°C or 60°C for 1.5 minutes, primer extension at 72°C for 1 minute, and a final extension cycle at 60°C for 30 minutes. Each reaction included a positive control to standardize allele scoring and a negative control to detect reagent contamination. PCR products were visualized in 2% agarose gels containing Gel Star (Lonza) to verify successful amplification.

Fragment analysis was performed using an ABI 3730 DNA Analyzer with Liz 600 size standard (Applied Biosystems) and genotypes were scored in GENEMARKER v1.6 (Soft Genetics LLC). Matching heterozygotes were scored at least twice and matching homozygotes were scored at least three times (Frantz et
al. 2003; Hansen et al. 2008), and the same researcher scored all genotypes to reduce the potential for scoring errors. We calculated PID$_{\text{Sib}}$, the power to differentiate between siblings (Waits et al. 2001), using a subset of 20 genotyped individuals in GENALEX version 6.41 (Peakall & Smouse 2006). We chose the PID$_{\text{Sib}}$ test over the PID$_{\text{Random}}$ test because it is more conservative and elephants may be found in groups of related individuals (Archie et al. 2006). Based on the results, only genotypes that included at least six loci (PID$_{\text{Sib}}$=0.002, (Waits et al. 2001) were included in the analyses. PID$_{\text{Sib}}$ was calculated again once all samples were genotyped, and the results did not change. Locus LafMS02R did not amplify reliably and was removed from the study.

Our genotyping error rate was calculated using 25 randomly selected samples in RELIOTYPE (Miller et al. 2002). We used default settings and 10,000 bootstrap replicates. We used the program DROPOUT (McKelvey & Schwartz 2005) to compare all individuals that differed at two or less loci, and those genotypes were checked manually. We considered samples to represent the same individual if they met the following criteria: (1) at least six matching loci (2) mismatches could be explained by allelic dropout, and (3) one mismatch was allowed if the alleles were difficult to score. Bolus circumferences, behavioral observations, mitochondrial DNA haplotypes, and sex were used as supporting evidence for assigning matches.

**Molecular sexing**

Sex was assessed genetically using the method of Munshi-South et al. (2008) which amplifies a 141 bp portion of the X- and Y-linked zinc finger protein
(ZFX/ZFY) genes or the method of Ahlering et al. (2011) which amplifies two Y-specific fragments (SRY1 and AMELY2) and one X-specific fragment (PLP1) in one PCR reaction. For the former method, we digested 5 µL of the amplification products with BamHI (New England Biolabs) for 2 hours and visualized products in a 3% agarose gel. For the latter method, products were visualized on a 2% agarose gel. A subset of samples were tested to confirm the consistency of results between the two methods, and for all samples, three independent tests confirmed females, while males were confirmed twice, with the exception of individuals that were directly observed defecating, and for whom the dung sample was collected immediately after defecation.

**Mitochondrial DNA**

We amplified a 627 bp fragment of the mitochondrial control region for all individuals identified through unique genotypes. We used the primers MDL3 and MDL5 (Fernando et al. 2000) or the combination of AFDL1, AFDL2, AFDL3, and AFDL4, following the methods described in Eggert et al. (2002). Products were sequenced in both directions on an ABI 3730 DNA Analyzer (Applied Biosystems) using the Big Dye Terminator cycle sequencing chemistry. Sequences were aligned and edited in SEQUENCHER version 4.5 (Gene Codes Corporation).

**Assigning age to individuals**

We used the averages of three dung boli measured in the field to estimate age classes of juvenile (pre-reproductive) and adult (reproductive) individuals. Eggert et al. (2003) calibrated forest elephant samples based on the age
distribution of dung samples from savanna elephants and considered individuals with average bolus sizes >32 cm in circumference to be adults. We compared these estimates to the samples of known reproductive and pre-reproductive individuals and adjusted our criteria for this population such that ≥30 cm and above were considered adult elephants, while <30 cm were considered juveniles. Few individuals were captured repeatedly and had sample averages that were both above and below 30 cm. Therefore, we averaged all measured boli and used this average to determine the age class.

**Data Analysis**

For microsatellite data, we used MICROCHECKER (van Oosterhout et al. 2004) to test for null alleles, stuttering, and large allelic dropout. We used GENEPOP version 4.0 (Raymond & Rousset 1995) and GENALEX version 6.41 (Peakall & Smouse 2006) to calculate allelic diversity and observed and expected heterozygosity values for each locus, and to test for significant deviations from expected heterozygosity values under Hardy-Weinberg equilibrium, and for linkage disequilibrium.

**Social networks**

We computed simple ratio association indices (AI) between each dyad of adult females observed in the population, where AI = N_{AB}/(N_{A}+N_{B}+N_{AB}). N_{AB} represents the total number of times A and B were seen together, while N_{A} and N_{B} represent each time that individual was seen alone (Ginsberg & Young 1992). We then used linear regression to test whether the number of times an individual
was seen influenced the number of associates an individual had and the maximum AI.

We created network models of adult females based on AI values to visualize associations within the population 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 them (edges), and individuals connected to one another, but not connected to the rest of the network are components. Subadults and calves were removed as they are dependent on mothers, and all networks included only individuals that could be identified. We created several types of social networks to allow us to retain information on all individuals and associations observed, while highlighting important associations including: (1) global, (2) preferred associates, (3) year, and (4) season. For individuals that were sampled for genetic analysis, we estimated relatedness; the resulting values are shown in the edges between dyads, and nodes are colored according to their mtDNA haplotype. There is no single relatedness estimator that outperforms others, and an estimator’s performance is data dependent (Van De Casteele et al. 2001). We used COANCESTRY version 1.0 (Wang 2011) to perform Monte Carlo simulations that calculated correlation coefficients between seven relatedness estimators and the values of known relatedness categories generated through simulations using the observed allele frequencies and missing genotype rates. We simulated eight relationship categories of 100 dyads, with 100 reference individuals, and 1,000 bootstraps. We chose the Queller-Goodnight moment estimator (Queller &
Goodnight 1989) because it resulted in a strong correlation between true and estimated values ($r=0.911$). We calculated pairwise relatedness ($R$) in RELATEDNESS version 5.0.8 (Queller & Goodnight 1989) using the bias correction. We used eight known mother-calf pairs whose samples were collected to test the effectiveness of this estimator. The average pairwise relatedness of mother-calf pairs was $0.490 \pm 0.083$, consistent with expectations of 0.5.

The global network represents all adult females observed in the population based on high quality photographs and all associations observed over all years of the study. As forest elephants are difficult to observe in the dense vegetation, this network is intended to portray all interactions observed and therefore show the extent of social occurrences in this population. However, studies often include in analyses only individuals seen a number of times (de Silva et al. 2011) to remove potentially spurious results, as well as ensure the social interactions observed are typical of the individual’s behavior. The preferred associates network includes individuals that have been observed $\geq 2$ times, and highlights preferred associations. Preferred associations are defined as those for which we calculated an AI value at least two times more than the mean AI (Whitehead 2008).

The three-year networks represent 2006, 2008, and 2010, and include only individuals found during those years. The season social network investigates differences in associations between wet and dry seasons and combines data across years. Months that had higher total rainfall than the three-year monthly average were considered “wet,” while those with less were considered “dry.” More observations were conducted in wet season months,
therefore to reduce bias from extended observation periods and ensure an equal sampling time for both networks, we chose 3.5 months worth of observational data from months that were considered to occur in the wet season to compare to data collected during the 3.5 months of dry season data. The networks were created from these data subsets.

We ran several network measures to further understand social structure and to compare networks in UCINET version 6.415 (Borgatti et al. 2002). We report the number of nodes, edges and components. Density describes the ratio of the edges that exist between nodes out of all that could possibly exist (Croft et al. 2008). The mean degree is the average number of edges a node is connected to, while the mean path length is the on average the shortest path for one node to connect to another node (Croft et al. 2008), and in our analyses only for nodes which were connected to other nodes. The clustering coefficient measures the degree to which associates of an individual are associated within the network (Whitehead 2008), and can be thought of as a measure of “cliquishness” (Croft et al. 2008).

We tested for preferred/avoided associations in SOCPROG version 2.4 (Whitehead 2009) using seven-day sampling periods to test the null hypothesis that there are no preferred or avoided associations for both the global and preferred networks. Seven days were chosen because it was long enough that enough observations could be collected, but limit the amount of immigration/emigration into the sampling area (Whitehead 2008). We permuted groups within samples and used a two-sided significance level of 0.05
with 1,000 trials/permutation and 20,000 permutations to determine the number of dyads preferred or avoided as determined by statistically significant high or low association indices. Analyses were run at different numbers of permutations and 20,000 was determined to be a sufficient number as indicated by stabilizing p-values (Bejder et al. 1998).

RESULTS

We identified 118 unique adult females, each of which was seen an average of 2.99 times (range of 1-34, mode 2). New individuals were identified throughout the study, and increased as the cumulative number of identifications increased (Figure 2). We were able to assign 40 dung samples to individuals as definite (n=20), probable (n=4), or tentative (n=16).

Average group sizes observed were ranged from 2.73-3.69 when including all individuals and 1.29–1.63 adult individuals when excluding dependent calves (Table 2). Similar mean group sizes were observed across years. 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 that were only seen once, this pattern disappeared (Figure 3).

Genetic analyses

After applying a standard Bonferonni correction for multiple tests, all loci except LaT05 conformed to Hardy-Weinberg equilibrium expectations. Locus LaT05 did not amplify consistently and showed evidence of large allelic dropout and null alleles. As it did not affect the number of successfully genotyped individuals, we removed it from subsequent analyses. For the remaining 10 loci,
the average number of alleles per locus was 12 ± 3.9 (SD) and the mean observed heterozygosity was 0.820 ± 0.08 (SD, Table 1). The average expected overall reliability of all loci after replication was 0.995.

Mitochondrial haplotype diversity was 0.805 ± 0.017 (SD) and nucleotide diversity averaged over all loci was 0.008 ± 0.004 (SD). Seven haplotypes were identified and differed from those previously reported of the same length.

**Social Analyses and Networks**

There was a statistically significant, but biologically weak relationship between the number of times an individual was seen and the number of associates it had ($R^2=0.103$, $P<0.000$). There was no influence on the maximum AI value for an individual ($R^2=0.010$, $P=0.290$). Therefore, individuals observed more often were more likely to have more associates, but did not necessarily have stronger associations. When removing individuals only seen once (for the preferred association network), there was no significant relationship between the number of times an individual was seen and the number of associates it had ($R^2=0.030$, $P=0.200$), but there was a significant, although weak biologically relationship between the number of sightings and the maximum AI of an individual ($R^2=0.076$, $P=0.036$).

About a quarter of the global network (25.4%) was made up of solitary individuals (Table 3, Figure 4a). There was one large component consisting of 22 adult females, all but one individual of those that were sampled for genetic analysis shared the same haplotype. The next largest component size was four
individuals, detected five times. The average relatedness of adult females within a component was $0.093 \pm 0.071$ (SD) with a range of 0.031 to 0.180 (SD).

The networks for each year included solitary individuals, and 2006 and 2008 contained components with a maximum of five and four individuals, respectively, while year 2010 contained one large component of 14 individuals (Table 3). This component is largely due to an observation of the largest group observed of eight adult females and their calves (22 individuals total including dependent calves). However, when looking at the preferred associates network, a large component of 17 adult females still exists consisting of many of these individuals, in addition to other adult females not present in the group of 22 individuals (Table 3, Figure 4b).

Fifty-five individuals were seen only once during the study and were removed from the preferred associates network (Table 3, Figure 4). Almost half of these females ($n = 23$) were solitary, accompanied only by dependent calves. The mean AI for dyads in the preferred association network was $0.339 \pm 0.270$ (SD) and few preferred associations (those equal to or greater than 0.679) were identified (8 out of 65 associations, 12.3%) overall (Figure 4b).

Rainfall data from SEGC is show in Figure 5. There were no clear differences between dry and wet season networks (Table 3). The wet season network had more individuals, but did not have larger components. The largest component in both networks consisted of four females. The wet season network had a larger number of solitary individuals (17 versus 4), but also had more individuals observed overall.
All networks were characterized by very low densities (range: 0.014-0.049, Table 3) and were composed of many disconnected components. The networks have short average path lengths from 1.091-2.272 (Table 3), meaning that individuals were typically connected to each other directly or through one other individual. The density, which reflects the number of edges connected to a node, was also low for all of the networks (Table 3). This is likely driven by the large number of components in each network consisting of only a pair of individuals. Finally, the clustering coefficient, in all networks was high (Table 3). The associates of individuals tended to also be associated with one another. Most components consisted of individuals that were all connected to one another.

Global and preferred networks showed mean levels of association that were significantly different from those expected from chance (Table 4). The standard deviation (SD) and coefficient of variation (CV) of the association indices were also significantly higher than expected values, which indicate that individuals preferentially associate across sampling periods, and suggests long-term companionships. However in both networks, only a few dyads were non-randomly associated (global: 23 out of 345 expected, 6.66%; preferred: 19 out of 104 expected, 18.27%) as indicated by the low number of significant dyads that had preferred associations (P>0.975). No dyads were found to be avoided (P<0.025), but the proportion of nonzero association indices was lower in the real data than in the expected data, suggesting that some individuals avoid others (Table 4).
DISCUSSION

Through the use of social network analyses, we revealed evidence of fission-fusion sociality in African forest elephants. We found one large component consisting of twenty-two adult females (excluding dependent group members), which is larger than any group observed throughout the study, and larger for forest elephants than reported in general (Morgan & Lee 2007; Turkalo & Fay 1996; White et al. 1993). For individuals that had genetic information, this component was composed of individuals within the same matriline, with only one exception. The exception involved a sample that was tentatively assigned to the individual, and therefore could have been mischaracterized. This large component suggests that associations of African forest elephants are based on matrilines, and could represent a large bond group (tier three) similar to African savanna elephant (Wittemyer & Getz 2007).

In the preferred network model where females seen only once were removed, one large component consisting of 17 adult females remained, and less solitary females were observed compared to the global network containing all adult females (8 compared to 30). Although we had a low number of repeat observations for individuals, our data do not suggest this led to missed associations. For example, the elephant seen most often (34 times) had five different associates, but was most often seen alone. The number of associates increased with an increased number of observations, which could reflect temporary resource-based groupings or chance associations rather than preferred relationships, but our data do not support this, as we found individuals within
components to belong to the same matriline, suggesting non-random associations. Also, there was no influence of the number of times an individual was seen on its maximum AI value.

Despite the large kin-based component, we observed many solitary females throughout the study (those only with dependent calves), and the next largest components consisted of only four adult females. This is larger than almost all groups observed in the park, but not as large as those in African savanna or Asian elephants (Archie & Chiyo 2012; de Silva et al. 2011). When looking at dyads that have preferred associations, defined as those with an AI value of at least twice the mean, very few individuals had preferred associations, and those that did were only between dyads, and not interconnected as larger components. In other words, although forest elephant females associate with other females in fission-fusion patterns, our data suggest they frequently separate from them, and when preferred associations do form, it is typically with only one other individual.

Ecological factors underlying social structure can be better understood through the comparison of closely related species in different habitats (Krebs & Davies 1993; Rubenstein & Wrangham 1986) because phylogenetic effects are lessened. When contrasting the data from this study to that generalized for a social network of 89 female African savanna elephants in Amboseli National Park, Kenya, several differences are apparent (Archie & Chiyo 2012). The Amboseli population is one only component, and individuals are well connected throughout the population. Excluding associations between Amboseli individuals
that spend <5 percent of their time together, bond groups and family groups become apparent as represented by connected components. When only including associations between individuals that spend >10 percent of their time together, large family groups still exist in components ranging from 5-13 females. In contrast, our social networks have 26 components and 28 solitary individuals without any filtering, and overall the individuals are largely disconnected. We did have one large component involving 22 females, but there were very few preferred associations in the network.

The largest aggregations in savanna elephants occur in the wet seasons when resources are less limited and there is less competition (Western & Lindsay 1984). Individuals break down into smaller groups during dry seasons when competition is higher, and in one population, studies have shown that dominant groups were able to monopolize higher quality habitats (Wittemyer et al. 2007). We found no evidence of seasonal differences, as the networks of the dry and wet seasons were similar in network metrics, with the exception that more individuals were observed in the wet season network. In a previous study in LNP, White et al. (1993) found that there was no tendency for forest elephants to form large groups even in the wet season. Savanna elephants also form groups for defense against predators (McComb et al. 2011), but in most central and west African forest habitats, larger cooperatively-hunting predators such as lions are absent today (Henschel et al. 2010), and small groups may be sufficient for defense against solitary leopards (Blake 2004).
Our results also differ from those of the social networks of Asian elephants. De Silva et al. (2011) observed small group sizes in Asian elephants (2.8-3.0 adult females), but found through network analyses that individuals have a larger number of associates that remained stable across years. Their analyses revealed larger components connecting many individuals throughout the population. Solitary individuals and smaller components containing two to four individuals were detected, but in the population analyses, individuals were much more connected than our network models reveal. Additionally, when looking at networks that focused on individual resident females observed at least 30 times, all components were made up of at least four adult females. Therefore, although African forest elephants appear to more similar to Asian elephants based on group sizes alone, our network model results did not detect the existence of the more extensive associations throughout the population seen in Asian elephants.

Forest elephants have the most “closed” habitats of the three extant elephant species, which may be a factor contributing to the lower levels of associations. Although Asian elephants live in forests, many are less dense and more open than those of central Africa, and are often near grasslands (Sukumar 2003). The study that revealed larger networks in Asian elephants was conducted in grassland/savanna type habitat (de Silva et al. 2011), and it’s possible that Asian elephants living in denser forests may differ, and have more limited sociality. Savanna elephants have the most open habitats, which physically allows for large aggregations of individuals. However, in a study of
forest elephants in LNP, White et al. (1993) found no difference between group sizes observed in the forests and the savannas.

A caveat to our study is that elephants associate at night, and there is a bias involved in diurnal sampling (Wrege et al. 2012). Forest elephants throughout the Congo Basin have been heavily poached (Blake et al. 2007) and individuals may have developed different tolerances to the savanna habitats due to the perceived risks. When conducting observations, it was apparent that some groups did not tolerate the presence of vehicles and rapidly fled. The results of Schuttler et al. (see Chapter 3) use genotypes of forest elephants collected from dung sampling to create network models of associations. Dung sampling overcomes the problem of diurnal sampling bias, and their study found more extensive groupings than from observation studies, and that the associations were based on matrilines. It is possible that more groups have extensive networks such as the haplotype Lope7 large component, but they are not apparent to researchers because associations occur at night. This group may have recognized the more recent reduced risks of savanna habitat in LNP because although poaching has occurred in the past, it is currently not frequent in the tourism/SEGC study zone.

Additionally, the identifications of new individuals did not plateau over the course of the study. It’s possible that individuals in this large component represent more “resident” elephants that do not range as far as others. The results of a telemetry study on three collared elephants in LNP showed in the annual home ranges of individuals between 9–343 km² (Momont 2007). One
elephant appeared to be a “resident” individual, and remained in the northeastern section of the park throughout the study with a small home range. Therefore, potentially the large Lope7 haplotype component may represent a more “complete” resident group of individuals, while other components are small groups at the edges of their range. Forest elephant densities also temporally increase in response to the ripening of preferred fruit species (White 1994b), in which case small groups or solitary females and their calves may range to the savanna areas of LNP temporarily for savanna-specific fruits or after prescribed burns when vegetation is more palatable. Individuals farther from their central ranges may display different behavioral and social patterns. In killer whales (Orcinus orca), Baird & Whitehead (2000) that individuals from resident pods traveled in larger groups and rarely shared prey, which was mostly composed of fish. Feeding in groups did not appear to reduce the chances of catching prey for an individual. In contrast, individuals from transient pods, which fed mostly on marine mammals, dispersed from groups likely from the increased costs from reduced energy associated with foraging in large groups. Further research is needed in LNP to determine if individuals in the SEGC study zone area, which is composed of a mosaic of savannas and secondary forest, differ socially from those in the rest of the park, which is largely composed of mature forest. This may be a contributing factor to the variation observed in the number of associates in different components.

Past poaching events may have also influenced our results. Although poaching has reached crisis levels for forest elephants recently, it has also
occurred in the past (Blake et al. 2007). Poaching may have disrupted social structure in the LNP population by removing individuals from the population and therefore reducing the associations observed in many groups of individuals. Individuals within the large Lope7 haplotype may have been able to evade poaching events and still associate. Gobush et al. (2009) found that when savanna elephant populations are disturbed, that individuals will still group together even if the groups are not kin-based. It is not certain that forest elephants would respond the same way given the ecological pressures from the forest environment favoring smaller group sizes.

When comparing the three extant elephant species, our data suggest that although there is evidence of fission-fusion sociality, African forest elephant vary from the fission-fusion social system of savanna elephants. White et al. (1994) suggested that the fission-fusion social system of forest elephants is more similar to that of chimpanzees (Pan troglodytes) than of African savanna elephants. Chimpanzees live in a community, but spend most of their time in parties or subgroups that vary in size (Pusey et al. 2007). The advantages of fission–fusion sociality in chimpanzees lie in reducing the costs of moving (Lehmann et al. 2007). By splitting into smaller parties during foraging, individuals are able to reduce moving time to more manageable proportions, which also reduces their energy demand, and therefore reduces feeding time. As the diets of forest elephants and chimpanzees overlap extensively and both are frugivorous (White et al. 1994), the spatial patchiness of forest fruits as well as their ephemeral nature may have a similar influence on forest elephants, favoring small groups
compared to savanna elephants that feed largely on browse and grasses. It may be too competitive for groups to sufficiently forage on fruiting trees in the forest environment without a significant increase in travel time, as fruits at each tree would be depleted faster with more individuals feeding on them. We found that individuals have the ability to network in large components, but that this is rare and not found across all components. Although forest elephants meet with other members of the community, this is rare, and they most often are found in small groups, similar to foraging “parties” observed in chimpanzees.

Finally, it is possible that individual forest elephants choose different strategies, even in the same park, according to accrued fitness benefits. Though our data suggest that forest elephant groups consist of solitary females with dependent calves, or small groups of adult females, there is evidence that larger associations do occasionally form, and these associations appear to be based on matrilineal kinship. It is currently unknown what benefits these individuals may gain from associating with kin, but research on savanna elephants suggest that access to information or the sharing of information about important resources could be one, as savanna elephants benefit from the matriarch’s knowledge about the environment (McComb et al. 2001; McComb et al. 2011). Further research is needed to better understand the environmental conditions that favor group formation in the forest environment, and to discern any fitness benefits for individuals living in groups or for individuals that have a larger number of associates.
ACKNOWLEDGEMENTS

We thank the Gabonese government, CENAREST, and ANPN for permission to work in Lopé National Park, SEGC and CIRMF for providing institutional and logistical support for fieldwork, and USFWS African Elephant Conservation Fund (agreement #98210-8-G753 to LSE) and MU Life Sciences fellowship for financial support. J. Dibakou, J.T. Dikangadissi, E. Dimoto, and C. Nzotekoumie provided invaluable logistical support and guidance in the field.
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Table 1. Genetic diversity values for elephants at LNP, Gabon (N\textsubscript{a}=allelic diversity, H\textsubscript{e}=expected and H\textsubscript{o}=observed heterozygosity). Multiplexes 1 and 4 had an annealing temperature of 60°C, while 2 and 3 had an annealing temperature of 58°C.

<table>
<thead>
<tr>
<th>locus</th>
<th>N\textsubscript{a}</th>
<th>H\textsubscript{e}</th>
<th>H\textsubscript{o}</th>
<th>multiplex number</th>
</tr>
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<tbody>
<tr>
<td>FH94R</td>
<td>9</td>
<td>0.653</td>
<td>0.676</td>
<td>2</td>
</tr>
<tr>
<td>FH126</td>
<td>16</td>
<td>0.884</td>
<td>0.879</td>
<td>2, 3, 4</td>
</tr>
<tr>
<td>FH103R</td>
<td>8</td>
<td>0.794</td>
<td>0.785</td>
<td>2</td>
</tr>
<tr>
<td>LaT13R</td>
<td>20</td>
<td>0.917</td>
<td>0.905</td>
<td>1, 2, 3, 4</td>
</tr>
<tr>
<td>FH67</td>
<td>8</td>
<td>0.728</td>
<td>0.729</td>
<td>3</td>
</tr>
<tr>
<td>FH48R</td>
<td>13</td>
<td>0.832</td>
<td>0.829</td>
<td>1</td>
</tr>
<tr>
<td>LA6R</td>
<td>10</td>
<td>0.723</td>
<td>0.750</td>
<td>3</td>
</tr>
<tr>
<td>FH60R</td>
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<td>1</td>
</tr>
<tr>
<td>FH19R</td>
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<td>0.898</td>
<td>0.910</td>
<td>1, 4</td>
</tr>
<tr>
<td>FH129</td>
<td>12</td>
<td>0.861</td>
<td>0.870</td>
<td>4</td>
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<tr>
<td>Mean</td>
<td>12</td>
<td>0.841</td>
<td>0.820</td>
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<tr>
<td>SD</td>
<td>3.9</td>
<td>0.087</td>
<td>0.081</td>
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Table 2. Group size data of forest elephants observed in LNP including all age classes and sexes.

<table>
<thead>
<tr>
<th></th>
<th>number of groups observed</th>
<th>number of solitary individuals observed</th>
<th>mean group size</th>
<th>mean group size excluding solitary individuals</th>
<th>mean group size excluding dependent calves</th>
</tr>
</thead>
<tbody>
<tr>
<td>all years</td>
<td>275</td>
<td>65</td>
<td>3.13 ± 2.00</td>
<td>3.68 ± 1.89</td>
<td>1.48 ± 0.80</td>
</tr>
<tr>
<td>year 2006</td>
<td>142</td>
<td>31</td>
<td>3.19 ± 1.94</td>
<td>3.80 ± 1.77</td>
<td>1.34 ± 0.76</td>
</tr>
<tr>
<td>year 2008</td>
<td>92</td>
<td>40</td>
<td>2.73 ± 1.66</td>
<td>3.44 ± 1.46</td>
<td>1.29 ± 0.60</td>
</tr>
<tr>
<td>year 2010</td>
<td>112</td>
<td>25</td>
<td>3.33 ± 2.38</td>
<td>3.84 ± 2.33</td>
<td>1.63 ± 0.97</td>
</tr>
</tbody>
</table>
Table 3. Network metrics from different observation periods of forest elephants in LNP.

<table>
<thead>
<tr>
<th>social network</th>
<th>nodes</th>
<th>edges</th>
<th>solitary individuals</th>
<th>connected components</th>
<th>largest connected component</th>
<th>density</th>
<th>mean degree</th>
<th>mean path length</th>
<th>clustering coefficient</th>
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<tbody>
<tr>
<td>global preferred associates</td>
<td>118</td>
<td>98</td>
<td>30</td>
<td>27</td>
<td>22</td>
<td>0.014</td>
<td>1.661</td>
<td>2.272</td>
<td>0.785</td>
</tr>
<tr>
<td>year 2006</td>
<td>63</td>
<td>65</td>
<td>8</td>
<td>17</td>
<td>17</td>
<td>0.033</td>
<td>2.063</td>
<td>2.157</td>
<td>0.857</td>
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<tr>
<td>year 2008</td>
<td>43</td>
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<td>6</td>
<td>14</td>
<td>5</td>
<td>0.034</td>
<td>1.442</td>
<td>1.167</td>
<td>0.870</td>
</tr>
<tr>
<td>year 2010</td>
<td>58</td>
<td>29</td>
<td>19</td>
<td>16</td>
<td>4</td>
<td>0.018</td>
<td>1.000</td>
<td>1.094</td>
<td>0.881</td>
</tr>
<tr>
<td>wet season</td>
<td>68</td>
<td>59</td>
<td>20</td>
<td>16</td>
<td>14</td>
<td>0.026</td>
<td>1.735</td>
<td>1.836</td>
<td>0.832</td>
</tr>
<tr>
<td>dry season</td>
<td>52</td>
<td>56</td>
<td>15</td>
<td>15</td>
<td>4</td>
<td>0.021</td>
<td>1.077</td>
<td>1.125</td>
<td>0.897</td>
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<tr>
<td></td>
<td>29</td>
<td>24</td>
<td>8</td>
<td>10</td>
<td>3</td>
<td>0.049</td>
<td>1.379</td>
<td>1.091</td>
<td>0.933</td>
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Table 4. Observed and expected association indices (simple ratio association index) for all adult females sighted (global) and for adult females observed two times or more (preferred).

<table>
<thead>
<tr>
<th></th>
<th>simple ratio</th>
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<tbody>
<tr>
<td></td>
<td>AI</td>
<td>observed</td>
<td>expected</td>
<td>P</td>
</tr>
<tr>
<td>global</td>
<td>mean</td>
<td>0.007</td>
<td>0.005</td>
<td><strong>0.998</strong></td>
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<tr>
<td></td>
<td>SD</td>
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<td>0.049</td>
<td><strong>1.000</strong></td>
</tr>
<tr>
<td></td>
<td>CV</td>
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<td><strong>0.998</strong></td>
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<tr>
<td>nonzero</td>
<td>mean</td>
<td>0.014</td>
<td>0.024</td>
<td><strong>0.001</strong></td>
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<tr>
<td>preferred</td>
<td>mean</td>
<td>0.013</td>
<td>0.010</td>
<td><strong>1.000</strong></td>
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<tr>
<td></td>
<td>SD</td>
<td>0.086</td>
<td>0.048</td>
<td><strong>1.000</strong></td>
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<tr>
<td></td>
<td>CV</td>
<td>6.576</td>
<td>4.843</td>
<td><strong>1.000</strong></td>
</tr>
<tr>
<td>nonzero</td>
<td>mean</td>
<td>0.033</td>
<td>0.067</td>
<td><strong>0.000</strong></td>
</tr>
</tbody>
</table>
Figure 1. Map of the SEGC study zone (left). The green rectangle in Lopé National Park represents the SEGC study zone area (bottom right), while the top right figure shows Gabon.
Figure 2. The number of individuals identified in LNP according to (a) the cumulative number of identifications. The sampling period was set at seven day intervals.
Figure 3. Histogram of AI values in all adult females dyads observed (black bars) and dyads in which the adult females were observed two or more times (grey bars).
Figure 4. (a) Global social network including 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 two 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 two times of the mean. For both networks, the shape of the node designates the certainty of the genetic sample collected for the individual; square, no sample collected; circle, definite; diamond, probable; triangle, 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.
This dissertation focuses on understanding the sociality of African forest elephants (*Loxodonta cyclotis*) using satellite telemetry, non-invasive genetic approaches, and social network models. Specifically the aims are to: (1) analyze space use patterns using satellite telemetry, (2) assess fine-scale genetic structure, and (3) model associations between individuals using direct observations, individual identifications, and relatedness. I tested the hypothesis that African forest elephants have a fission-fusion social structure based on kinship where group sizes change over time and space, and associations are more extensive than observed group sizes. Using a combination of methods enable one to elucidate the social patterns of forest elephants because each contributes to understanding an aspect of sociality, but each also has an innate bias or caveat. The methods were chosen to compliment each other, and therefore describe the bigger picture of forest elephant social structure. The sociality of forest elephants is then compared to the other extant species, African savanna (*Loxodonta africana*) and Asian elephants (*Elephas maximus*), to better understand the ecological factors shaping sociality in the *Proboscidea* species.

The second chapter describes satellite telemetry results from six adult female forest elephants in Loango National Park. These results revealed small,
adjacent home ranges of individuals that had minimal overlap. As home range overlap can provide indirect information about the social interactions between individuals (Clutton-Brock 1989), this study found low volume of intersection indices between individuals, which indicate that the probability of co-occurrence between dyads of individuals in the same area is also low. This suggests spatial avoidance among these adult females, which contrasts with the patterns of family groups overlapping in home ranges within sub-populations in African savanna elephants (Charif et al. 2005, Galanti et al. 2006).

Although the results from the second chapter suggest that forest elephants are not as social as savanna elephants as indicated from the little overlap observed in home ranges, these results must be interpreted with caution as this only represents six adult female elephants. Loango National Park has a high density of elephants (Morgan 2007) and it’s possible that other females not collared in the population may overlap with one another or the individuals in this study. Therefore, the individuals in this portion of the broader dissertation may not be representative of the social interactions of the population at large.

In Chapter 3, I increased the sample size of individuals by using non-invasive genetic approaches and inferred sociality from spatial-genetic patterns of African forest elephants in Lopé National Park (LNP), Gabon. In this chapter, we found evidence of fine-scale genetic structure with individuals being more closely related to each other than expected by chance at distances of five kilometers or less. Through network models created from data generated from dung samples collected together at the same time, location, and of the same
freshness, I found larger group sizes of forest elephants compared to those from observations alone and that the components of the network largely consisted of individuals of the same matriline. These results conflict with the inferences made from Chapter 2. Those results support limited social interactions between adult females as inferred from home range overlap, while the results in Chapter 3 support evidence of higher order social structure including family groups between adult females (representing second tier relationships), and possibly even bond groups (third tier, Wittemyer & Getz 2007).

In Chapter 4, I directly tracked the relationships of known individuals and created social networks of adult females within the population. Social networks revealed evidence of kin-based fission-fusion sociality in African forest elephants with components as large as twenty-two adult females. Although I detected larger components than observed group sizes, we also observed many solitary females throughout the study (those only with dependent calves). The second largest component consisted of four adult females, which is larger than almost all groups observed in the park, but not as large as those in African savanna or Asian elephants (de Silva et al. 2011, Archie & Chiyo 2012). Also, very few individuals had preferred associations, and those that did were only between dyads, and not interconnected as larger components. Although these results reveal that forest elephant females associate with other females in fission-fusion patterns, they frequently separate from them, and when preferred associations do form, it is typically with only one other individual.
Species with fission-fusion dynamics can range along a spectrum of variation within spatial cohesion, group (party) size, and group composition (Aureli et al. 2008). African savanna elephants are described as having variation in group size and spatial cohesion, and medium variation in group composition. My study supports low to medium variation in all three components of the fission-spectrum in forest elephants, and overall forest elephants can be best described as a “lower-fission-fusion” group or taxa.

I detected some variation in the first aspect of fission-fusion sociality, group size, as both the genetic network and social networks revealed several larger components than observed from group sizes alone. However, although these components were larger, the most frequently observed component in the social network was a solitary individual, followed by dyads. The genetic network excluded dung samples found solitarily, but revealed that dyads represented the most frequent component. Therefore, although I did find large components, there were not many of them and the most common component in both types of networks were dyads of adult females or solitary females. It is possible that more groups have extensive networks such as the large haplotype7 component observed in the social network, but they are not detected through diurnal research because most associations occur at night. Using acoustic sampling, Wrege et al. (2012) found 79% of all forest elephant visitations occur at night, and that diurnal observations are likely to be biased. Although the genetic approach used in Chapter 3 overcomes this bias, there is still a downward sampling bias of group sizes using non-invasive genetic sampling because not all
group members will defecate in the same location, and not all samples may be genotyped successfully.

Also, my research found that new individuals were discovered throughout the study, and that identifications of new individuals did not plateau over time. It is possible that individuals in the larger components represent “resident” elephants that may not range far. A telemetry study on three collared elephants in LNP supports this, with variation in annual home ranges between 9–343 km² (Momont 2007). Potentially the large Lope7 haplotype component may represent a more “complete” resident group of individuals, while other components may be smaller groups at the edges of their range. Baird & Whitehead (2000) found similar results in killer whales (*Orcinus orca*). Individuals in resident pods traveled in larger groups and rarely shared prey, mostly composed of fish. In contrast, individuals from transient pods, which fed mostly on marine mammals, dispersed from groups likely from the increased costs from reduced energy associated with foraging in large groups. Further research is needed in LNP to determine if individuals in the SEGC study zone area, which is composed of a mosaic of savannas and secondary forest, differ socially from those in the rest of the park, which is largely composed of mature forest. This may be a contributing factor to the variation observed in the number of associates in different components.

My results suggest medium to high variation in the second aspect, group composition. Both the network created from genetic data and the social networks created from observational data revealed that individuals were not always found
in groups with the same other individuals. In the preferred associates network (Chapter 4), individuals observed two times or more had up to ten other associates, but actual preferred associations between individuals (dyads seen at least more than twice the mean association index) was very low. Only eight dyads were detected, and of those only one individual had more than one preferred associate. These results suggest that forest elephants do not tend to form strong associations with other individuals.

I also found some evidence of variation in the last aspect, spatial cohesion, although it is difficult to discern how much. From observational data, I rarely observed groups spread out over large areas. However in some areas of the park this was difficult to observe because forest habitat was in close proximity to savanna clearings. Using genetic methods, I found groups of dung samples collected together at the same time and location to be composed of related individuals, when looking at non-group related individuals across the landscape during sampling sessions, dyads could be several kilometers apart. This could be due partially to the time lag in sampling. Although I collected fresh dung samples less than 24 hours old, elephants can still travel long distances in that time frame. However, elephants can communicate through infrasound and vibration (Langbauer 2000, O’Connell-Rodwell 2007), and savanna elephants can detect individuals at 2 km distances (Langbauer et al. 1991). Although the extent of vocal communication is currently unknown in forest elephants, it is likely that they can communicate across similar distances and possibly coordinate group
activities of larger spatial extent than what is possible through observations alone.

When comparing my results with knowledge about the sociality of the other extant elephant species, my data suggest that although there is evidence of fission-fusion sociality, African forest elephants do not have the same type of fission fusion sociality as African and Asian elephants. Social networks from both African savanna and Asian elephants have more connected networks, and larger component sizes in networks (Archie & Chiyo 2012). Savanna elephants in Amboseli National Park, Kenya are all connected with one another when including all observations. When including only associations between individuals that spend more than ten percent of their time together, large family groups can still be detected in components ranging from 5-13 females. Asian elephant networks were not as connected as savanna elephants. They had solitary individuals and smaller components containing two to four individuals, but in the population level analyses, individuals were more connected than my network models for forest elephants reveal. Associates in Asian elephants remained stable across years and when looking at ego-networks that focused on individual resident females observed at least 30 times and their relationships, all components were made up of at least four adult females (de Silva et al. 2011). In contrast, forest elephant social networks had many small components and solitary individuals, few large components, and was disconnected without any filtering.
Several ecological factors may contribute to the more limited sociality observed in forest elephants. Forest elephants have the most “closed” habitats of the three extant species, which may physically prevent larger aggregations. Although Asian elephants live in forests, many are less dense and more open than those of central Africa, and are often near grasslands (Sukumar 2003). However, there is no evidence that group sizes of forest elephants are larger in the savanna habitats of LNP. White et al. (1993) found no difference between group sizes observed in the forest compared to savannas, despite the downward bias associated with the forest habitat due to less visibility.

The diet of forest elephants and ecological characteristics of the forest may also limit sociality. There may be costs associated with foraging in larger groups, as patchily distributed fruits will quickly be depleted, resulting in increased travel for forage. Large cooperatively hunting predators are currently absent in most locations throughout forest elephant range, although this could be a recent occurrence as the historical distribution of lions included all of Africa, excepting only central Sahara and the most dense rainforests (Henschel et al. 2010). There is some evidence that leopards predate on forest elephant calves (Blake 2004), but they are typically avoided as prey (Hayward et al. 2006), and small groups would likely be sufficient for defense. Humans however are highly effective predators for elephants and the largest threat, as poaching of forest elephants for bushmeat and ivory has reached epidemic proportions (Blake et al. 2007).

White et al. (1994) suggested that forest elephants shared more similarities with chimpanzees (Pan troglodytes) than African savanna elephants
in terms of fission-fusion sociality. Chimpanzees live in a community in which all members rarely or never get together, and spend most of their time in parties or subgroups that vary in size (Pusey et al. 2007). Smaller foraging parties allow individuals to reduce moving time to more manageable proportions, which reduces their energy demand, and therefore feeding time (Lehmann et al. 2007). The diets of forest elephants and chimpanzees overlap extensively (White et al. 1994), and the spatial patchiness and ephemeral nature of forest fruits may have a similar influence both species, favoring small groups. Although forest elephants can associate with members of the community as seen from the larger components observed in the networks, this occurs more rarely, and they most often are found in small groups, similar to the foraging “parties” observed in chimpanzees.

While forest elephants do not have as extensive associations as the other elephant species, associations still do form, and these associations appear to be based on matrilineal kinship. It is unlikely that the resource dispersion hypothesis explains associations because most individuals associating with one another shared the same haplotype and were related. If individuals were tolerating another individual’s presence at a resource, one would expect a random mixture of haplotypes for individuals within groups, especially given the diversity in this population. There may be two explanations for why I observed variation in the social strategies of individuals within the same population. First, forest elephants may choose different social strategies depending on fitness benefits they receive. Research on savanna elephants shows that individuals benefit from
the matriarch’s knowledge about the environment (McComb et al. 2001, McComb et al. 2011). Forest elephants may receive similar benefits by maintaining relationships with other individuals. As forest elephants navigate through the forest for resources, it may be beneficial to associate with more knowledgeable individuals to gain access to the spatial locations of fruiting trees or mineral deposits. In savanna elephants, groups with older matriarchs have higher fitness (Gobush et al. 2008) and form defensive behaviors to predators more quickly (McComb et al. 2011). However, there appear to be costs associated with large groups for forest elephants, and some individuals may choose to reduce these costs rather than accrue potential fitness benefits.

Although poaching has reached crisis levels for forest elephants recently, it has also occurred in the past (Blake et al. 2007). Poaching may have disrupted social structure in the LNP population by removing individuals from the population and therefore reducing the associations observed in many groups of individuals. Perhaps the reason why I are able to detect the large Lope7 haplotype is because these individuals were able to evade poaching events. Gobush et al. (2009) found that when savanna elephant populations are disturbed, that individuals will still group together even if the groups are not kin-based. It is not certain that forest elephants would respond the same way given the ecological pressures from the forest environment favoring smaller group sizes. Further research is needed to better understand the environmental conditions that favor group formation in the forest, and to discern fitness benefits.
for individuals living in groups or for individuals that have a large number of associates.

This dissertation used satellite telemetry tracking to look at the long-term, fine-scale movements of six individual elephants, spatial genetic methods to understand the relatedness patterns of individuals across a landscape, and social network models to track individual elephants and quantify their associations and genetic relationships with individuals in the population. These methods combined reveal that African forest elephants have fission-fusion patterns primarily based on kinship, but compared to other taxa with fission-fusion sociality, can be best described as a lower fission-fusion species where individuals frequently separate from other individuals. Although I found evidence of individuals having more extensive associations larger than those observed from group sizes alone, I still detected many individuals that had no associations with other individuals. There appears to be a fundamental difference in African forest elephant sociality from both African savanna and Asian elephants and more research is needed to determine the ecological factors driving these differences.
LITERATURE CITED


VITA

Stephanie Grace Schuttler née Stephanie Grace Manka was born in Buffalo, NY on September 27th, 1981 to Peter and Judith Manka. She graduated from Clarence Senior High School in Clarence, NY and attended the State University of New York at Buffalo where she majored in biological sciences and minored in theater. During her undergraduate experience, she participated in The School for Field Studies’ summer study abroad program in Kenya, where she discovered a love for wildlife, ecology, animal behavior, and conservation.

In the years following graduation, she participated in three internship positions. First she worked at the Bureau of Land Management in St. George, Utah locating water catchments and analyzing telemetry data on bats. Next worked at Disney’s Animal Kingdom as a reproductive biology intern. Here she used fecal samples to monitor hormones for research involving the management of captive species. Finally she returned to Kenya for an internship with the School for Field Studies. She collaborated with Dr. Moses Okello on research involving tourists’ perceptions of wildlife in Kenya.

In 2006, she moved to Columbia, Missouri and entered the Ph.D. program at the University of Missouri under the advisement of Dr. Lori Eggert. After 6.5 years, Stephanie earned her doctoral degree. Stephanie is now a postdoctoral researcher at the University of Missouri and works with Dr. Matthew Gompper.