Forest Elephant Group Dynamics, Social Interactions, and Population Monitoring

by

Amelia Meier

Environment
Duke University

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Approved:

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John Poulsen, Co-Adviser

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Susan Alberts, Co-Adviser

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Jennifer Swenson

Dissertation submitted in partial fulfillment of
the requirements for the degree of Doctor
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ABSTRACT

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Abstract

Forest elephants (*Loxodonta cyclotis*), the smallest and least studied of the three extant elephant species, predominately inhabit the Guinean and Congolian tropical forests from Guinea to the Democratic Republic of Congo. Known as ecosystem engineers, forest elephants create and maintain forest habitat, shape faunal communities, transport nutrients, and disperse seeds to distant areas. Despite their essential ecological role, very little is known about forest elephant social behavior. Living in social groups provides individuals with many benefits, including information about resources, protection from predators, and access to mates. For highly social species, like elephants, understanding social behavior is crucial to implementing sustainable conservation practices and mitigating the negative impacts of human development. To date, what is known about forest elephant social behavior originates from observations in *baïs* – mineral rich forest clearings. As a result, our understanding is limited by the short periods of time forest elephants spend in baïs, less than 2% of their time, and the small area relative to the rest of their home range and lifespan that we are able to observe.

In this dissertation, I present research from the first project to attempt to understand elephant social interactions from throughout the range of habitats that forest elephants exploit on a daily basis, including dense, closed-canopy forest. I combine

genetic and satellite technologies (GPS tracking and remote sensing) using novel computational methods to address: (1) factors that influence fluctuations in forest elephant group size; (2) forest elephant group age-sex composition and the factors influencing the probability of interactions between two elephants; and (3) improvements to forest elephant monitoring via line transect surveys for dung by creating an adaptive dung decay model. I conclude that: (1) group size is variable with forest elephants displaying a fission-fusion social system – a flexible social system in which individuals or sub-groups intermittently join other groups – across habitats in response to fruit availability and human disturbance; (2) interaction between individuals is influenced by social, but not environmental, factors and forest elephants spend more time in mixed sex groups than Asian or savanna elephants; and (3) estimating dung degradation via remotely sensed imagery is a feasible, cost-efficient alternative or supplement to *in-situ* dung degradation studies for non-invasive population surveys. This dissertation highlights the value of untangling the complex interplay between environmental, social, and anthropogenic drivers of species group composition and social behavior to inform conservation action., the results herein will be informative for monitoring forest elephant populations and promoting human-elephant coexistence through improved management of potential conflict areas.

To A.P.M., who knew staying in school would go so far.

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Acknowledgements

Thank you to the mentors who guided me throughout different portions of my dissertation. Christine Drea, thank you for always pointing me in the right direction for

1. Introduction

The forest elephant (*Loxodonta cyclotis*) faces extinction - its numbers declined by 62% between 2002 and 2011 (Maisels et al., 2013) and after that continued declining at 10-18% per year (Wittemyer et al., 2014). Due to mostly to habitat loss and poaching, forest elephants inhabit just 6-7% of their original habitat in West Africa (Roth & Douglas-Hamilton 1991) and less than 25% of their original habitat in Central Africa (Maisels et al., 2013). A recent study showed that Minkébé National Park (Gabon), which was previously thought to hold the highest density of forest elephants, lost 81% of its elephant population from 2004 to 2014 (Poulsen et al., 2017). Poaching for ivory is the principal cause of mortality, devastating forest elephant populations to a fraction of their former abundance. Compared to the other elephant species - the African savanna elephant (*Loxodonta africana*) and Asian elephant (*Elephas maximus*) - the African forest elephant is understudied and receives the least conservation support (Breuer et al., 2015; Poulsen et al., 2018). Here I review what is known about forest elephants, where knowledge gaps lie, and how filling these gaps can deepen our understanding of environmental influence on social systems and group demographics and forest elephant conservation best practices.

Forest elephant taxonomy, life history, and behavior

Recent mitochondrial and nuclear phylogenetic studies (Figure 1.1) show that African forest elephants are a unique species, more closely related to the extinct

European straight-tusked elephant (*Palaeoloxodon antiuus*) than to African savanna elephants (Meyer et al., 2017; Palkopoulou et al., 2018). Forest elephants are the smallest of the extant elephant species with females and males reaching 2m and 2.5m, respectively, at the shoulder (Figure 1.1). Despite being the smallest of the three species, forest elephants, surprisingly, have a slower life history than savanna elephants (Turkalo, 2013). Notably, females reach reproductive age later than savanna elephants, with a median primiparous age of 23 years as opposed to 14 years (Moss, 2001; Turkalo et al., 2016). Forest elephants range from Guinea in West Africa to the Democratic Republic of Congo in Central Africa (Ishida et al., 2011). Living predominately in humid tropical forests with occasional areas of forest savanna matrices, forest elephants are highly frugivorous, consuming as many as 73 species of fruit (Blake et al., 2009). Variation in fruit availability influences both forest elephant dietary composition and movement behavior, such as how much time they spend exploring and where they walk (Beirne et al., 2020; Blake & Inkamba-nkulu, 2004). In-depth knowledge of forest elephant social behavior is strikingly absent.
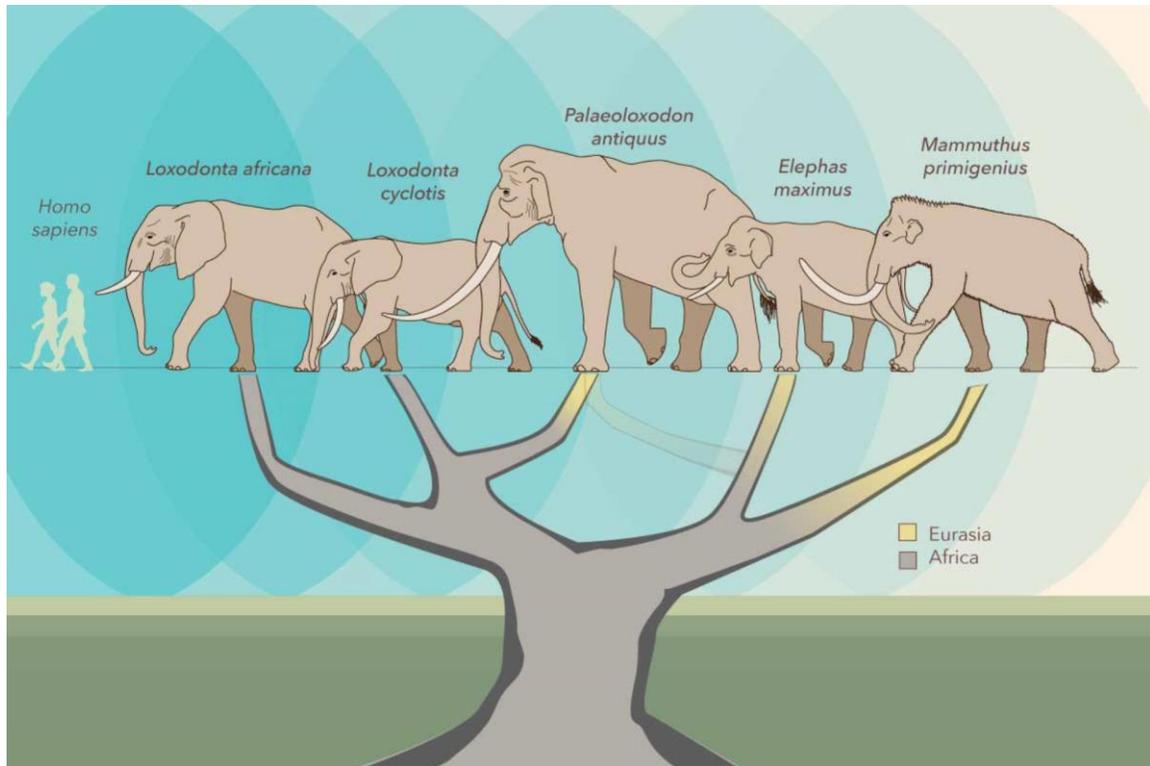
Figure 1.1 Phylogenetic genetic tree of three extant and two extinct elephantids. Image by Asier Larramendi Eskorza and Julie McMahon and adapted from Meyer et al. 2017.

The dearth of knowledge regarding forest elephant social behavior is largely due to their occupation of dense tropical forests and limited infrastructure in range states preventing consistent observations. The difficulty observing forest elephants has limited behavioral studies to habitats within forest ecosystems where the animals can be observed: baïs (mineral rich forest clearings with a water body), savannas in forest clearings (Fishlock & Lee, 2013; Turkalo et al., 2013). These few behavioral studies have been supplemented by genetic analyses using opportunistic sampling of dung piles (Munshi-South et al., 2008; Schuttler, Whittaker, et al., 2014). Based on these observations and genetic analyses, researchers have concluded that forest elephants, like all extant elephants, display a fission-fusion social structure (Schuttler, Whittaker, et al.,

2014). They are reported to have a mean group size ranging from 3.1 to 4.5 individuals depending on study location (Morgan & Lee, 2007; Theuerkauf et al., 2000; Turkalo & Fay, 1995; L. J. T. White et al., 1993), with a maximum cohesive group of 36 individuals (Fishlock & Lee, 2013). And, individuals within these groups are more closely related than by chance (Schuttler, Philbrick, et al., 2014), though there appear to be seasonal fluctuations in genetic relatedness of closely associating group members (Munshi-South, 2011).

Benefits of studying forest elephant behavior

As a large, wide ranging species inhabiting a heterogeneous landscape (Adamescu et al., 2018; Mills et al., 2018; Oliveras & Malhi, 2016) forest elephants are an ideal study system to expand our understanding of ecological constraints on social structure, demography, and how anthropogenic disturbance disrupts those interactions. As one of the largest land mammals, they provide an interesting comparison to other, better studied species that display similar fission-fusion societies, such as savannah elephants, chimpanzees, or hyenas (de Silva & Wittemyer, 2012; Lehmann et al., 2007; Smith et al., 2008). Comparing closely related species, such as chimpanzees and bonobos or various hyena species, provided insights into the factors that influence the evolution of distinct social structures. Comparing all three elephant species living in different habitats presents an opportunity to expand on our understanding of social systems in highly mobile species not limited to territories.

Forest elephants are of conservation concern and understanding social group dynamics is important for ensuring healthy population management. Studies have shown that sub-optimal group sizes results in acute stress in some mammal species, with individuals displaying higher levels of glucocorticoids (Markham et al., 2015; Pride, 2005). In savanna elephants, increased glucocorticoids have been associated with decreased reproductive success (Gobush et al., 2008). Better information on forest elephant social dynamics is necessary to inform management best practices by providing information on healthy groups to enable monitoring of situations where forest elephants come into frequent contact with humans or might be taken into captivity. Determining potential areas of human conflict with large elephant groups could inform antipoaching strategy of areas where elephants are at risk or reduce negative interactions with farmers.

Technological advances enabling further study of wildlife

Recent technological advances in GPS satellite tracking, remote sensing, and genetic analyses have greatly expanded what can be learned about forest elephants and other difficult to observe species. Satellite GPS tags and detailed habitat mapping are increasingly used to study aspects of animal behavior without having to directly observe the focal species, including resource selection (e.g., movement based on water needs: Hooten et al., 2019), animal migrations (e.g., human disturbance disrupting migratory paths: Schaffer-Smith et al., 2017), and social proximity to other tagged individuals (e.g.

individual interactions over time and space: Loretto et al., 2017). Development of genotyping technologies such as real-time PCR and single nucleotide polymorphism (SNP) genotyping has dramatically reduced the cost for detailed genomic analysis. This decrease has made genome wide and/or non-invasive studies of individual identity and relatedness more feasible (Bourgeois et al., 2018; Foroughirad et al., 2019).

Aims of dissertation

To build upon our understanding of ecological factors incluencing social strategies, this dissertation tests several hypotheses associated with forest elephant fission-fusion dynamics and group demographics. In the first chapter, I assess forest elephant social group dynamics by testing the influence of putative environmental factors on elephant social behavior to provide insights regarding ecological constraints on group size. To do so, I reconstruct forest elephant social groups using non-invasive genetic samples extracted from elephant dung collected while tracking GPS collared forest elephants on foot. Using a novel application of group-specific mark recapture models, I assess forest elephant fission-fusion dynamics and the environmental, social, and anthropogenic factors associated with increased or decreased group size.

The second chapter builds upon the first, expands upon our new understanding of group size to determine forest elephant group demographics and the environmental factors related to increased interactions between unrelated individuals. I treat the reconstructed forest elephant social groups as ego networks, extrapolate a global

network from the ego network parameters, and extract average association parameters detailing forest elephant group age and sex structure. This process is done for all individuals whose dung was observed together and for preferred associates - individuals whose dung was observed together at least twice. Then, using the locations emitted from the GPS collars, I determine any time the elephants were in close proximity and run logistic regressions to determine whether environmental or anthropogenic factors are associated with increased likelihoods of interactions. I compare this new understanding of forest elephants to the better studied social structure of savanna and Asian elephants.

In chapter three, I address a major assumption in the most common method employed to estimate forest mammal abundance - line transects for animal sign with distance analysis. Specifically, for sign surveys (e.g., nests, dung), a single number representing total time for decay is used as a multiplier to convert estimated sign density into animal density. Unless it is derived from a study reflecting the spatiotemporal variation in decay times, this multiplier is likely to be inaccurate, potentially creating substantial error in population size estimates. To mediate this, I use Weibull survival models to develop adaptive models based on field collected and remotely sensed variables known to influence dung decay reducing the need for costly (time, effort, and financial) *in-situ* decay studies.

In aggregate, the research presented here examines ecological constraints on fission-fusion social systems, expands our understanding of forest elephant group composition, and promotes informed conservation management. By studying a large species under heavy poaching pressure, we explore the interplay between human disturbance and resource driven behaviors in which the consumptive needs of forest elephants are larger than most more commonly studied species displaying fission-fusion societies (e.g., chimpanzees, dolphins, hyenas). Lastly, the research here includes novel combinations of data collection and computational techniques that expand the possibility of future studies on forest elephant and other cryptic species social behavior.

2. Spatiotemporal ecological factors influencing forest elephant group size

Introduction

Group living provides benefits to individual animals including protection from predators, information regarding resources, and higher fitness than solitary living (Hamilton, 1971; Ward & Zahavi, 1973). But, these benefits come with costs (Alexander, 1974). Thus, the degree to which individuals can live in social groups is limited by ecological constraints such as food availability and quality (Chapman et al., 1995). Fission-fusion societies are those in which the community regularly divides into smaller units (Conradt & Roper, 2000) in response to food availability, mating opportunities, and/or inter- or intra- group competition (Smith et al., 2008). Individuals or subgroups join and leave other subgroups to balance the benefits of social living with the disadvantages of intragroup competition for food and the energetic costs of foraging time, which generally increase with group size (Krause & Ruxton, 2002; Markham et al., 2015). In addition to environmental variability, human disturbance shapes wildlife behavior including group size dynamics (Lacy & Martins, 2003; Sih, 2013). Wildlife responses to anthropogenic disturbance often mirror responses to risks from natural predators (Bejder et al., 2009). Because anthropogenic disturbance triggers natural response, fission-fusion groups may be larger or smaller than expected from the ecological context alone (Chiyo et al., 2011).

The three extant elephant species all display fission-fusion behavior (Kerth et al., 2006). However, they each live in distinctly different habitats that provide different advantages and disadvantages to social living and different environmental limitations to group size. African savanna elephants (*Loxodonta africana*) range in arid regions typically with savanna, wooded savanna or desert habitat. They aggregate more in the wet season than the dry season, with the largest groups reaching up to 400 individuals (Eltringham, 1977; Western & Lindsay, 1984) and the smallest groups being composed of highly related individuals (Wittemyer et al., 2009). Asian elephants (*Elephas maximus*) span a vast variety of habitats from savannas to plantations and Dipterocarp monodominant forests. In Sri Lanka, Asian elephant groups average 3 individuals with a maximum of 17 individuals (De Silva et al., 2011). African forest elephants (*Loxodonta cyclotis*), on the other hand, live predominately in humid tropical forests with occasional areas of forest savanna matrices. They have been reported to have a mean group size ranging from 3.1 to 4.5 individuals depending on study location (Morgan & Lee, 2007; Theuerkauf et al., 2000; Turkalo & Fay, 1995; L. J. T. White et al., 1993), with a maximum cohesive group of 36 individuals (Fishlock & Lee, 2013).

African forest elephants are limited to the tropical forests of west and central Africa and are known for being highly frugivorous, consuming as many as 73 species of fruit (Blake et al., 2009). Fruits are important for forest elephants as they have more gross energy, sugars, and fat than shoots, stems, or bark and ripe fruit tend to not have

defensive proteins (Calvert, 1985; Elizabeth Rogers et al., 1990). Despite presence of fruit in the Afrotropics throughout the year, ripe fruit are often patchily distributed, and abundance varies seasonally as well as spatially (Adamescu et al., 2018; Ban et al., 2014; Beirne et al., 2020). Spatiotemporal variation in fruit availability influences both the dietary composition and movement behavior of forest elephants (Beirne et al., 2020). With the known caloric importance of fruit, its patchy distribution, and its influence on elephant movement, it represents a putative ecological constraint influencing forest elephant fission-fusion dynamics (Schuttler, Whittaker, et al., 2014).

Here we assess forest elephant social group dynamics by testing the influence of ecological, demographic, and anthropogenic factors on elephant social behavior to provide insight regarding ecological constraints on group size in the tropics. As a wide ranging species in a heterogeneous landscape (Adamescu et al., 2018; Mills et al., 2018; Oliveras & Malhi, 2016) with large resource needs, forest elephants provide a comparison to other, better studied fission-fusion societies such as chimpanzees or hyenas (Lehmann et al., 2007; Smith et al., 2008). We test the hypothesis that forest elephant group size will fluctuate over time because of resource availability and vary spatially because of human disturbance. To achieve this, we launched the first ever project to track forest elephants on foot and via satellite GPS collars. While tracking the elephants, we collected genetic samples from dung piles to reconstruct their social group size.

Methods

Study area

From February 2017 to May 2018, we conducted 100 focal follows tracking 28

GPS-collared elephants for up to three consecutive days at a time, in and around Ivindo

National Park and the Wonga Wongué Presidential Reserve (Beirne et al., 2020; Figure

2.1). Ivindo National Park, at 2990 km^2, is a mixture of Atlantic coastal Lower Guinea

forest and semi-deciduous forest of the Congo Basin (Mikolajczak, 2013). Elevation

ranges from 248 to 781 m (Sassen & Wan, 2006). Wonga Wongué, a 4,282 km^2 coastal

Presidential Reserve, is predominantly a matrix of Atlantic coastal forest and savanna,

with mangrove and *Raphia* wetlands along the coast (Mills et al., 2018). Elevation ranges

from sea level to 287 m (Farr et al., 2007).

Sample Collection

At each park we selected a group of five "priority" elephants, based on

accessibility, which were followed every other month for an average of 5.5 follows per

elephant (range 4 - 7). The remaining elephants (n = 1 Ivindo, n = 9 Wonga Wongué)

were followed in a rotating order during alternative months for a maximum of two

follows per elephant. To track GPS collared forest elephants, we worked with BaAka

forest peoples, who have deep knowledge of the forest and tracking, and helped follow

the forest elephants between the hourly GPS locations. To avoid stressing the animal

and risking the safety of the field teams, follows were conducted a minimum of one hour behind the focal elephant.

While tracking the elephants, we collected dung samples for genetic analysis, measured dung boli, and recorded relevant habitat information (details below). As elephants have been observed to defecate synchronously (Rees, 1983), once a dung pile was sampled, the field team searched a radius of 35m for additional dung piles. All newly located dung piles were sampled, and we repeated the search until no new dung piles were found. Dung piles that were discernably different in size or color or greater than 2m apart from each other (approximate distance between two elephants standing side by side) were sampled separately. Different studies have employed different distances to define group membership for forest elephants, including one body length, 35m, 50m, 100m and 250m (Brand et al., 2020; Fishlock & Lee, 2013; Morgan & Lee, 2007). Because we needed to keep pace with focal elephants, we employed the 35m distance. In addition, once per follow we searched for dung in a radius of 100m to verify we were not missing additional dung. All fresh dung, appearing to be the same age (similar warmth, sheen, state of degradation), was swabbed with a buccal swab (Isohelix, Cell Projects) which was stored in buffer solution (500μl of LS buffer and 25μ proteinase K; Stabilizing Kits, Isohelix, Cell Projects) at ambient temperature. After swabbing, if the dung was intact, the circumference of the three largest boli were measured to estimate broad age categories (infant, juvenile, adult; see Eggert &

Woodruff, 2003). We collected habitat information each time a dung pile was observed

unless it was within 10m of a dung pile already sampled that day (details below). After

each follow, we stored samples at the basecamp, either in a refrigerator or a ventilated

room. Every other month, we transported samples to the Institut de Recherche en

Écologie Tropicale laboratory in Libreville, Gabon to store them in a -20°C freezer.
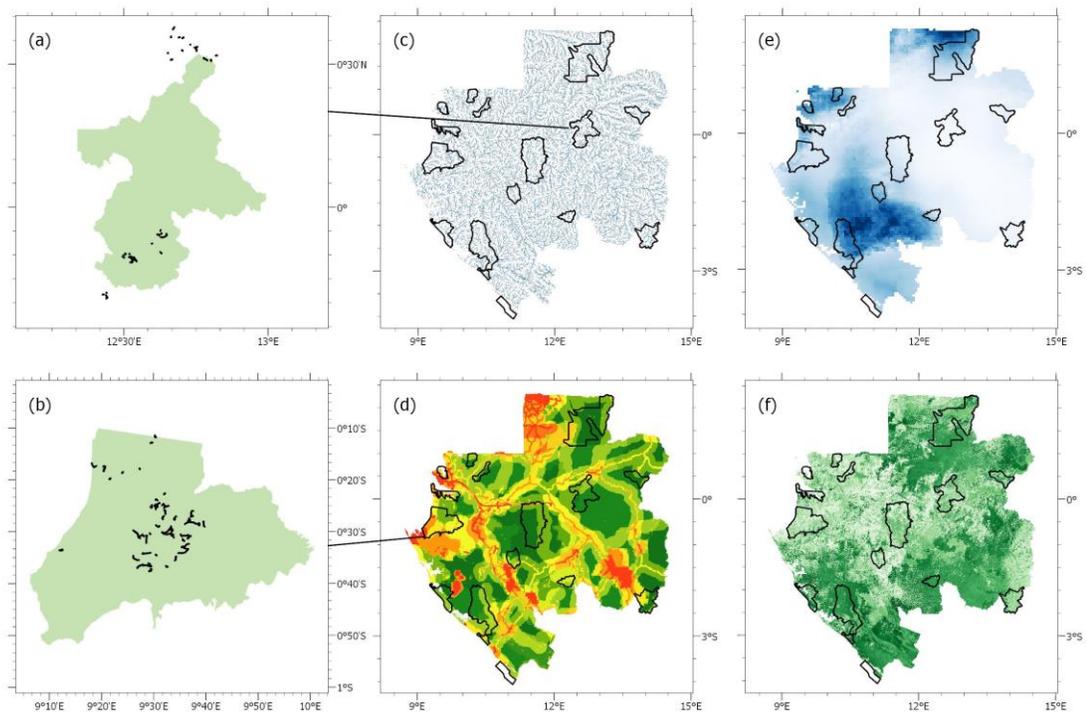
Figure 2.1: Location of study sites and elephant follows in Gabon and example data layers. Panels (a) and (b) indicate the locations of focal elephant follows within Ivindo National Park and Wonga Wongué Presidential Reserve. Panels (c) through (f) each depict different spatial layers with Gabon's protected areas outlined in black: (c) permanent water sources, (d) human disturbance where dark green represents little to no disturbance and red represents high disturbance (WCS 2005), (e) single day precipitation in mm where increasing blue intensity represents more rain, and (f) vegetation density with darker green representing higher EVI.

Individual identification from dung samples

We extracted DNA from the field-collected dung samples using Qiagen QIAamp

DNA Stool Mini Kits. Because of financial limitations, analysis was limited to one day

per focal follow for 89 follows. We quantified the amount of DNA in each sample

through quantitative PCR reactions using QantiNova SYBR Green PCR Kits by Qiagen

on a StepOne Real-time PCR system by Applied Biosystems. We followed the modified

protocols described in Bourgeios *et al.* (2019), except that we did not use OneStep PCR

inhibitor Removal Kits and only diluted fecal samples at a 1:10 ratio for quantification.

Any samples with non-specific amplification or with less than 0.01ng/μl of DNA were

excluded from analysis. Samples were kept at -20°C for long-term storage.

Samples were analyzed for 41 autosomal loci and one sex-linked locus using

Kompetitive Allele Specific PCR (KASP) genotyping for bi-allelic single nucleotide

polymorphisms. The KASP assay contains two allele-specific forward primers that have

a tail sequence associated with one of two fluorescent dyes (FAM and HEX) and a

common reverse primer. Only one of the allele-specific forward primers can bind with

the specific polymorphism for each sample. During thermal cycling, the relevant primer

binds, and the relevant tail sequence is then replicated. The real-time PCR machine then

reads the degree of fluorescence emitted by the replicated primers. Analyses were

conducted on one of three of real-time PCR platforms: StepOne from Applied

Biosystems, RotorGene by Qiagen, or Hydrocycler by LGC. For the StepOne and

RotorGene platforms, methods were adapted from the KASP user guide (LGC, 2014) by

increasing the number of cycles from 35 to 42. For LCG, conditions were run according

to the KASP user guide. Samples with a DNA quantity greater than 0.2 ng/μl were

diluted at 1:10, samples between 0.2 ng/μl and 0.1 ng/μl were diluted at 1:5 and samples

with less than 0.1 but greater than 0.01 were diluted to 1:2. Each plate contained a

minimum of one non-template control (NTC) and two positive controls. Generally, two NTCs and three positive controls were used per plate. At a minimum, we genotyped all samples in duplicate for 38 of the 41 autosomal SNPs. Of the 580 samples extracted and genotyped from the focal follows 342, qualified for the minimum criteria of 20 SNPs and 0.1ng/µl concentration of DNA and were included in the individual identity analysis.

Genotypes were initially assigned by a clustering algorithm, included with the KASP software, that contrasts the normalized reporter dyes (LGC, 2014). The algorithm grouped samples with similar FAM to HEX fluorescent marker ratios. We then visually inspected and manually adjusted genotype assignment based on the agreement of two observers. We employed a multi-tube approach to determine consensus genotypes for all samples (Sethi et al., 2014); this involves amplifying each locus multiple times and comparing across these amplifications to determine the true genotype. We initially created two consensus datasets, one based on the minimum agreement criteria of 2 heterozygous or 3 homozygous genotypes (2|3), the other based on the minimum agreement criteria of 2|2 for each locus. As only 10 of the 8,724 assignments (0.1%) did not agree between the two methods, we used the consensus dataset that employed the 2|2 agreement requirement as this method allowed for the inclusion of more data. Samples ran twice with disagreements or only one successful run were assigned as 0, and samples with only a single run were assigned that value.

We calculated individual identities by using error-tolerant maximum likelihood sample matching (Sethi et al., 2016). This method compares the probability of obtaining a pair of genotypes given the population allelic frequencies (average 0.3, range 0.07-0.50) with the probability of observing the sample genotypes given the genotyping error rates (average 0.018, range 0.002 to 0.128) to determine the likelihood that the two samples are the same individual. We included samples for which we were able to assign genotypes at a minimum of 20 loci, ensuring that our probability of incorrectly identifying siblings as the same individual ($P_{ID(sibs)}$) was less than 0.0005 (Waits et al., 2001). From these samples we identified 178 unique individuals, with an average of 1.78 (range 1- 23 samples) samples originating from a single individual.

During the GPS-collar placement on elephants, Gabon's national park agency (Agence Nationale des Parcs Nationaux; ANPN) collected tissues samples when possible, enabling us to genotype tissue samples for 17 of the 20 focal elephants, using the same SNPs that we analyzed in dung samples. We included these genotypes in the individual identity analysis. This enabled us to determine which dung samples belonged to the focal elephant and to confirm we were following the expected elephant group.

To ensure that we had followed the correct group, focal follows were included if one of the dung samples matched the tissue sample of the focal individual and/or the field team's tracklog closely followed the focal individual's GPS points. Eighteen follows

18

were omitted – 15 follows were omitted because none of the samples were successfully genotyped, one because the tracklog did not match the collared elephant's tracks, and two because we did not have the tracklog data. Seventy-one focal follows (32 in Ivindo National Park and 39 in Wonga Wongué Presidential Reserve) representing 10 males and 10 females had tracklogs that closely matched with locations from the focal elephant's GPS collar, and during 40 of those focal follows we collected dung samples that matched the focal elephant's tissue sample.

Measuring group size

To assess group size, we implemented a hierarchical closed population capture-recapture model for stratified populations (Kery & Royle, 2015). This framework corrects for imperfect detection of forest elephant group members and enables the description of the factors that influence the underlying true population size. To investigate which environmental factors influence group size (N_g), we designated follow days as the unit of sample effort. We assumed N_g follows a Poisson distribution with mean and variance λ_g and modeled the effect of covariates on λ_g using a liner model with a log link (Converse & Royle, 2012; Sollmann et al., 2015). We created encounter histories of the uniquely identified individuals from the dung samples found during each focal follow. For each follow, we divided the field teams' GPS tracklog into 400m segments and included each segment as a potential capture opportunity (total of K capture sites). On average elephants walk 300m an hour and defecate an average of 16 times a day (range

12-20), by using 400m segments we are more likely to observe independent defecation events (Mills et al., 2018; Nchanji et al., 2008).

We employed data augmentation to model patterns of detection probability and account both for observed individuals (N) and individuals present but not detected in a given group (Royle et al., 2007). To do this, we created an arbitrarily large number of potentially unobserved individuals (M) (Kery & Schaub, 2012); in this case, we assigned M = 1000 to be much larger than the largest reported forest elephant group size of 36 (Fishlock & Lee, 2013). Group membership (g_i), of G groups, for each potential member N observed + M is determined by the multinomial distribution with probabilities π, such that $\pi_g = \frac{\lambda_g}{\Sigma_G \lambda_g}$. We estimated whether each potential individual was present and detected, present but undetected, or not present based on a binary indicator z_i from a Bernoulli distribution based on the inclusion probability Ω. Individual encounter frequencies (y_i) were modeled as: $y_i \mid z_i \sim \text{Binomial}(z_i p_i, K)$. Variability in detection probability, represented by p_i, is modeled using a linear model with a logit link. We included identity of the focal elephant and protected area as parameters to account for variance in our ability to find dung across individuals and areas.

Predictors of group size

Data describing elephant demographics and environmental conditions were included as covariates in both the model's detection and group size portions. To investigate the spatiotemporal factors that influence group size, we compiled

demographic, environmental and anthropogenic variables collected either in the field or with remotely sensed data. For the demographic covariate, we included sex of the focal elephant, which was identified during the collaring process. Environmental variables included precipitation, fruit availability, vegetation density, and distance to permanent water sources (Figure 2.1).

Precipitation. Africa wide, 0.05º resolution, daily precipitation data were downloaded from the Climate Hazards Group InfraRed Precipitation with Station data (CHIRPS; Funk et al., 2015) and averaged over the area in which the focal elephant was located (calculated as a 95% minimum convex polygon of the GPS points) over the follow day and the previous four days to create a daily average in millimeters.

Fruit availability. Fruit availability was quantified via 'fruit walks' conducted twice daily, during which field teams recorded all fleshy fruits encountered on a 50m x 2m strip transect perpendicular to the focal elephant's tracks (see Beirne et al., 2020). We log-transformed fruit availability to normalize the observed distribution.

Vegetation density. An Enhanced Vegetation Index (EVI) was used as a proxy to represent vegetation density and gross food available to forest elephants. The EVI was created from 16-day MODIS composites with 250m resolution (Didan, 2015) during the period of each elephant follow.

Permanent water sources. We determined the minimum distance from the elephant's location during the follow to permanent water sources, i.e., rivers and lakes

that do not dry out during the dry season. This layer was calculated with a rivers layer

developed from a 30m Digital Elevation Model (DEM) and large water bodies were

created by Projet Forêt et Environnement (PFE-1999/2000).

Human disturbance. Human disturbance was categorized as degree of disturbance

from the Global Human Footprint (WCS 2005). This index compiles multiple aspects of

human disturbance from population pressure and infrastructure to land use and

accessibility (i.e., logging roads or navigable rivers) and ranges from 0, representing no

disturbance, to 100, representing high disturbance such as a large city surrounded by

exploitive industry.

Implementing the full model.

We fit the model, including both detection probabilities and predictors of group

size, using Markov Chain Monte Carlo (MCMC) with JAGS (Plummer, 2003) interfaced

through the R statistical environment (R Core Team, 2020) via the package jagsUI

(Kellner, 2019). Three chains, 20000 adaptations, 1000 burn-in iterations and 40000

iterations were used to achieve algorithm convergence. We first ensured the MCMC

chains converged with a $\hat{R}$ value < 1.01 and examined traceplots to ensure quality of

chain convergence. To verify model fit, we initially conducted posterior predictive

checks and looked for graphical fit – distribution and shape of observed and simulated

datasets. For the predictive checks, we calculated Tukey-Freeman coefficients for

observed and simulated datasets and chi square coefficients for observed and simulated

group sizes and compared both test sets with Bayesian posterior predictive checks.

Bayesian p-values were used to determine overall model appropriateness (Conn et al., 2018). Similarly, graphical techniques assessing distribution of both original and simulated capture frequencies and predicted group size provided a rapid and intuitive assessment of model fit (Conn et al., 2018). We assessed the consistency of parameters and predictive precision of the model with a 5-fold cross validation. Test distributions from each fold were compared to the training distribution using a paired t-test and comparison of the distributional overlap. Final parameter coefficient estimates are from the full dataset.

Results

Group size

Estimated group size averaged 4.8 ± 2.4 individuals (range 1- 10 individuals). Groups with a male focal elephant averaged 4 ± 2.3 individuals (range 1-10 individuals) and groups with a female focal elephant averaged 5.3 ± 2.4 individuals (range 2-10 individuals). Groups for whom we had multiple measures of group size from multiple follows varied in size by 1 to 5 individuals around their average group size (Figure 2.2).

Factors influencing detection

Both site and identity of the focal individual (representing group identity) influenced detection. The odds of observing elephants in Wonga Wongué Presidential Reserve was 0.90 times the odds of observing elephants in Ivindo National Park. The

odds of observing an individual group ranged from 0.09 to 5.55 times a model selected

random baseline group.
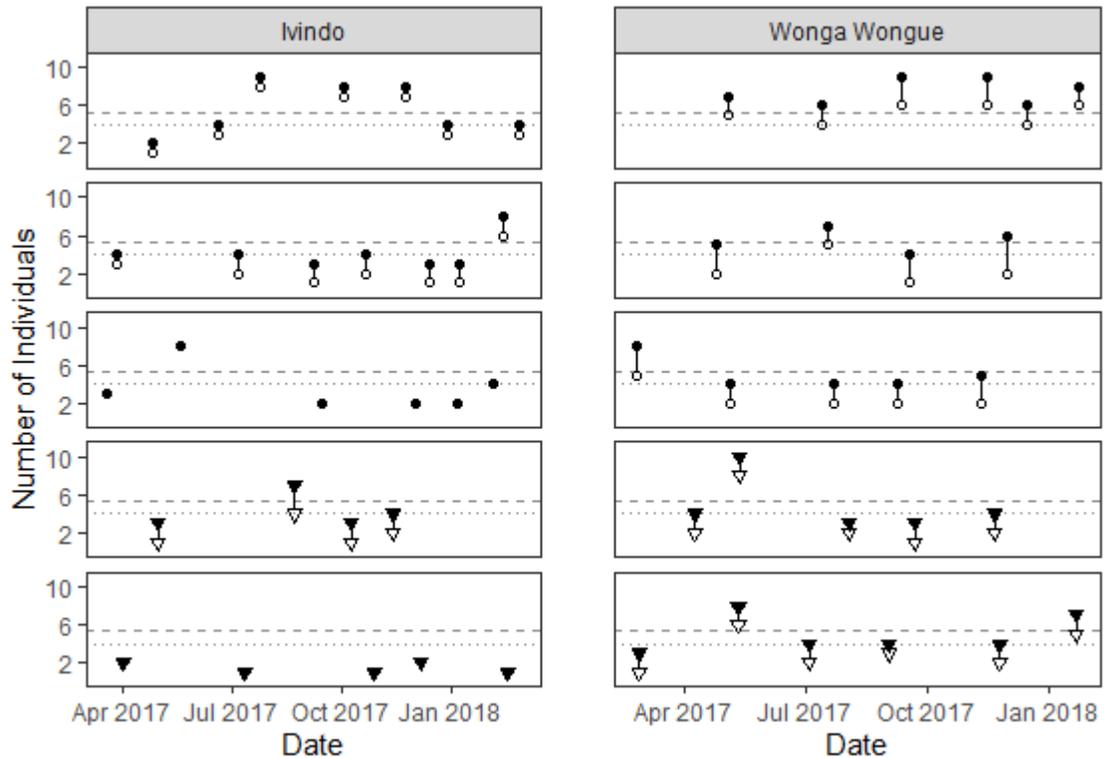
Figure 2.2: Forest elephant group sizes show large individual variability across time.
Circles represent female and triangle represent male focal elephants. Open icons
represent number of unique individuals observed from dung piles. Black icons represent
number of individuals present, but potentially not observed. Dashed lines show the
average group size for focal females, and dotted lines show average group size for focal
males.

Factors influencing group size

Of the six variables tested, fruit availability and human disturbance were

associated with changes in group size (Table 2.1; Figure 2.3). Increases in the log of fruit

availability decreased forest elephant group size -0.08 times (credible interval (CI): -0.15

to -0.01), indicating a 42% decrease in elephant group size across the range of fruit

availability (range: 0-2 fruits/m; Figure 2.3 & 2.4a). Increased human disturbance resulted in a slight increase in group size; for each unit increase in disturbance (range 0-28), forest elephant group size increased 0.03 times (CI: 0.0002 to .059) (Figure 2.4b). Groups in which the focal individual was a female had an average of 0.33 times more individuals than groups with a male focal individual (CI: -0.04 to 0.70; Figure 2.3). Despite the large effect compared to other covariate coefficients, because the credible intervals slightly overlapped zero it is uncertain how important sex of the focal individuals was in determining group size. Increasing EVI also had a relatively large effect of increasing elephant group size by 27%; however, the credible intervals were quite large (-0.82 to 1.35). Both variables representing water availability, distance to water and precipitation, had small effects and credible intervals that overlapped zero (distance to water average 0.03, CI -0.11 to 0.17 and precipitation average -0.01, CI -0.04 to 0.02).

Our model successfully passed all goodness of fit checks. In the two posterior predictive checks, which compared a simulated dataset to the observed dataset for groups size and the distribution of individual encounters, neither had a significant Bayesian p-value indicating good model fit as the parameters were able to predict the underlying data and estimate group size. The distributions of group size from the training and test datasets in the k-fold cross validation largely overlap (59%) and they are not significantly different (t-test, t = 0.786, df = 67, p = 0.43).

Table 2.1: Effects of parameters on group size. Bolded values show credible intervals that do not overlap.

Parameter	Effect	Credible Interval	
Intercept	**0.77**	**0.08**	**1.43**
Distance to Water	0.03	-0.11	0.17
Human Disturbance	**0.03**	**0.0002**	**0.06**
Fruit	**-0.08**	**-0.15**	**-0.01**
Precipitation	-0.01	-0.04	0.02
Vegetation Density	0.27	-0.82	1.35
Sex	0.33	-0.04	0.70
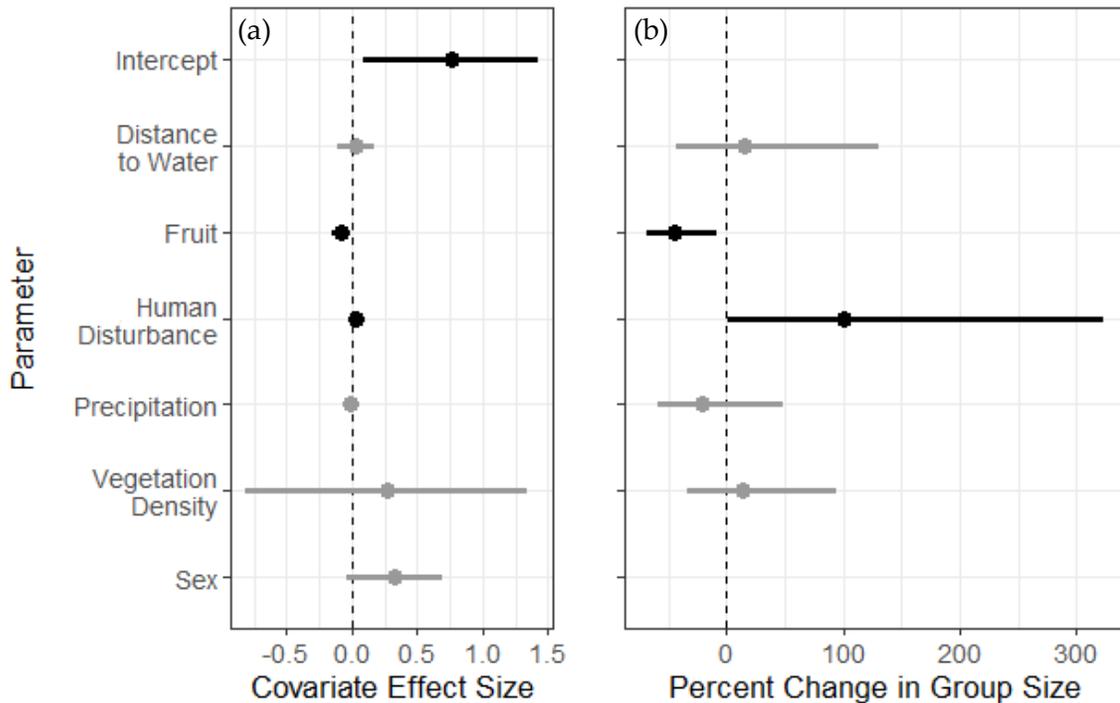
Figure 2.3: Effect plots of parameters in the group size model. (a) Dots represent mean effect sizes of a change in one unit in the predictor and bars represent 95% credible interval for each parameter as reported in Table 2.1. (b) Dots represents percent change in group size as the value of the predictor changes from the lowest to highest value of the observed range. Negative value means an increase in the predictor produces a decrease in group size and positive value means an increase in the predictor produces an increase in group size. In both plots, grey bars represent credible intervals

overlapping zero, whereas black bars do not overlap zero. Distance to water: range 0-5km. Fruit range: 0-2 fruits/m. Human Disturbance Global Human Footprint index range: 3-28. Precipitation range: 0-24mm. Vegetation density EVI range: 0.12-0.62. Sex represents the effect of being a female rather than a male focal elephant.
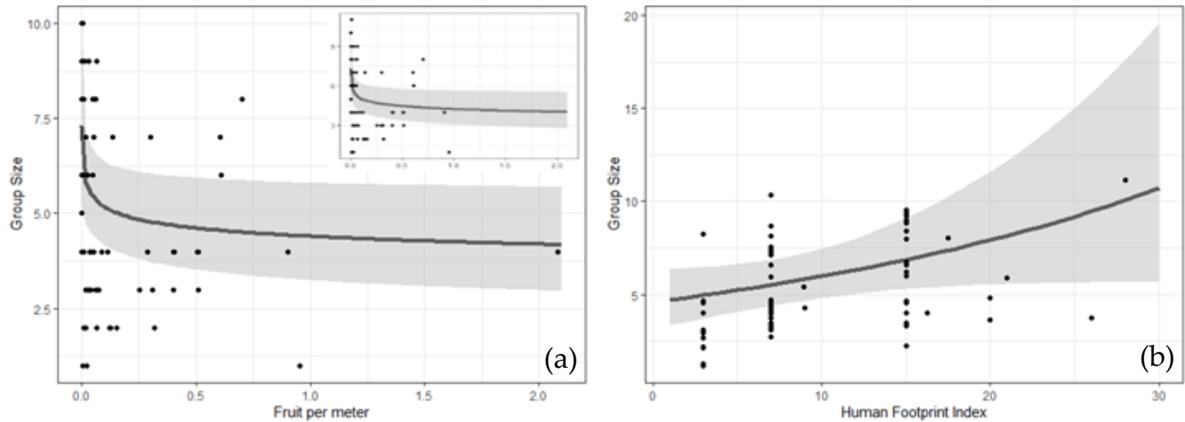
Figure 2.4: Elephant group size decreases with increasing fruit availability (a) and increases with increasing human disturbance (b). The dark center line represents average group size, and the shaded polygon represents the 95% credible intervals. Dots represent model predicted group estimates for each follow. Note the different y-axes units. Inset in panel a shows average relationship without the outlier at fruit/ m > 2.

Discussion

Our study is the first to repeatedly visit forest elephant groups across a focal elephant's home-range and to implement a novel application of hierarchical mark-recapture models to predict group size. We demonstrate that fruit resource availability, and to a lesser degree, human disturbance, influence forest elephant group size. Below, we discuss the implications of our results for understanding the ecological constraints on forest elephant group size, and how this study improves our understanding of ecological constraints on fission-fusion societies.

This study would not have been possible without the combination of GPS tracking and genetic technologies. The GPS collars enabled us to repeatedly follow the same focal individual, previously only possible in open habitats or with habituated primates maintaining small home ranges. Using genetic analysis to identify individuals associated with focal elephant overcame our inability to accurately observe the forest elephants we were following. This novel combination of methods can be applied for many forest dwelling, cryptic species (e.g., Sumatran rhinos, pygmy hippos, forest dwelling ungulates, bovines, or wild pigs), deepening our understanding of social group structure.

The recent development of group-specific, spatial recapture hierarchical models has opened mark-recapture methods to uses beyond simple population size assessment (Converse & Royle, 2012; Sollmann et al., 2015). Because hierarchical models account for imperfect detection, they can also be used to estimate group size, as with this study, or species occupancy and potential distribution. However, as with any computational method, the limitations and assumptions of hierarchical models need to be considered when interpreting results. One assumption of the model, which our focal-follow sampling procedure was designed to adhere to, is the assumption that sampling events (collection of dung samples) are equally likely to sample any individual. Within any focal follow we had an equal probability of finding the dung from any individual in that

group, strengthening our inferences about group size (although estimating the entire population from our focal follows would have violated this assumption).

A limitation of the model relevant to our study is that we cannot know the characteristics of unobserved group members, limiting our ability to describe group level demographics. For example, even if all elephants sampled during a follow were female, we could not assume the undetected individuals were also female. As a result, we address questions about the focal individual and external variables that may influence group size but are unable to elucidate the effects of age, sex and kin relationships (see Chapter 3).

Fission fusion dynamics

By following focal elephants across their home-range, we showed that forest elephants consistently displayed fission-fusion behavior regardless of habitat or presence in social arenas and quantified the degree of fission-fusion in African forest elephants. Previous work from opportunistic observations in savanna openings within forests showed that forest elephant groups are more related than by chance and are not always comprised of the same individuals (Schuttler, Whittaker, et al., 2014). We expanded on this, showing that an individual's group size can fluctuate from two to ten individuals. Group dynamics of forest elephants have previously been reported in studies of rare, open "social arenas" such as baïs (mineral rich forest clearings with a water source; Fishlock & Lee, 2013; Turkalo, Wrege, & Wittemyer, 2013) or savanna

openings in forest clearings (Morgan & Lee, 2007; Schuttler, Whittaker, et al., 2014).

Important as these observation are, forest elephants spend most of their time in forest, with baïs and savannas clearings representing only 2% and 33% of their habitat use (Mills et al., 2018; Turkalo et al., 2013). Additionally, clearings and baïs are rare, and sometimes absent, across the forest elephant range. Our results revealed notable variation in group size and no distinct seasonal trends in fluctuations of group size for forest elephants. This high degree of variation is consistent with other elephant behaviors such as movement patterns or seasonal dietary preference (Beirne et al., 2020; Vogel et al., 2020).

Ecological drivers of group size

Contrary to our expectations, we found that fruit availability had a negative influence on forest elephant group size. An increase in fruit availability from zero to two fruits per meter was associated with a 42% decrease in forest elephant group size. In particular, our finding that elephant group size was smaller when the availability of this preferred resource was higher runs counter to expectations of optimal group size and ecological constraints theory (Chapman et al., 1995; Krause & Ruxton, 2002). Specifically, optimal foraging theory suggests that species will shift their consumption to preferential resources when they become abundant (Lacher et al., 1982) as forest elephants have been observed to do with fruit (Beirne et al., 2020), leading to an expectation that group sizes will increase as a result. These predictions have been supported in studies of other

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tropical frugivorous mammals (ex. chimpanzees; Chapman et al., 1995). Why might forest elephants be different from chimpanzees and other tropical frugivores in their response to increased fruit abundance? The answer may lie in the very large caloric requirements of elephants as a megaherbivore. While a large fruiting tree might be able to accommodate several chimpanzees, that can forage both on fallen fruit and fruit on branches, it is unlikely to satiate several elephants, that can only access fallen fruit. Further, because fruiting trees are patchily distributed (Blake & Inkamba-nkulu, 2004; Takenoshita et al., 2008b) and often have annual fruiting cycles (Adamescu et al., 2018), forest elephants may pursue a scramble competition strategy during fruiting periods by spreading out in the forest to identify individual fruiting trees. This hypothesis would predict a reduction in group size to avoid competition when many trees are fruiting (Dubois & Giraldeau, 2005). The idea that elephants switch to scramble foraging is supported by an increase in forest elephant movement in association to fruit availability (Beirne et al., 2020). It is further supported by our model results which showed and that increasing general browse availability, represented by EVI, had no effect on group size.

In contrast to fruit availability, anthropogenic disturbance was associated with increased group size in forest elephants in our study, as expected. Given the high levels of mortality from poaching and their large degree of behavioral flexibility, it is unsurprising that forest elephants change their grouping behavior in response to human disturbance (Poulsen et al., 2017; Sih et al., 2011). Both forest and savanna elephants

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respond to natural threats by bunching (savanna: Douglas-Hamilton, 1973; McComb et al., 2011; forest elephants: personal observation). Therefore, an increase in forest elephant group size in response to anthropogenic disturbance aligns with the hypothesis that animals have short term responses to human disturbance as they would to natural predators (Bejder et al., 2006). Savanna elephants also form larger groups when greater risk from humans is perceived (Chiyo et al., 2014). We were surprised by the small effect size (3% increase) of anthropogenic disturbance; however, most of our study groups were well within protected area boundaries (>20km) and two males that regularly went outside of park boundaries were killed by poachers before we could include them in our study. Future studies should tease apart which types of human disturbance have different effects on group size and other behavioral responses.

Neither distance to water nor precipitation was significantly associated with forest elephant group size in our models. This result is contrary to studies in sister species showing that greater water availability is associated with larger group sizes (Wittemyer, Douglas-Hamilton, & Getz, 2005), and that increased water availability is associated with increased forest elephant movement (Beirne et al., 2020; Mills et al., 2018). This difference may reflect the consistent abundance of water in our study areas (precipitation averages of 1553mm per year Ivindo and 1849mm per year Wonga Wongué): it is unlikely that any water sources in Gabon are small enough or distant enough to limit forest elephant group size. In more arid regions of forest elephant range,

water might be a more limiting resource on forest elephant group size, as for savanna

elephants (e.g., 350mm per year in Samburu, Kenya; Wittemyer et al., 2009).

Our models also revealed no statistically significant difference in group size for

male versus female focal elephants. This result contradicts expectations from savanna

elephants, which show strikingly different social grouping behaviors in males versus

females (Chiyo et al., 2011). This potential lack of observed sex differences in group size

in our study could be explained by the fact that female forest elephants have much

smaller groups than African savanna and Asian elephants. Alternatively, this result

could be confounded by our inability to determine entire group demographics. There

might be more distinct differences between all female, mixed sex, and all male group

sizes. Lastly, our study was conducted with twenty focal individuals, which might be

too small a sample size to determine sex specific differences.

Conclusions and future directions

Our study advances understanding of the drivers of forest elephant social

dynamics, but we have only scratched the surface of forest elephant social structure.

Many aspects of forest elephant fission-fusion society dynamics remain a mystery. For

example, what are the demographics of forest elephant social groups and how do they

change as group size increases? Social groups exists when members synchronize their

activities and individual needs often vary between sex and age classes (Conradt &

Roper, 2000). Understanding forest elephant group demographics would provide insight

into individual or group resource needs and tradeoffs between social benefits and intragroup competition. Also, how frequently do forest elephants change social sub-units? The duration of associations varies from species to species, with groups in some species forming and diffusing within a few hours (i.e. dolphins; Lewis, Wartzok, & Heithaus, 2011) and groups in other species remaining stable throughout an entire season (i.e giraffes; Prehn et al., 2019). The number of interactions with unique individuals and duration of time spent together has implications for the transfer of knowledge or disease between groups.

While conservation management often focuses on overall population status, understanding social group dynamics is also important for ensuring healthy population management. Studies have shown that species in sub-optimal groups are stressed, with individuals displaying higher levels of glucocorticoids (Markham et al., 2015; Pride, 2005). In savanna elephants, increased glucocorticoids has been associated with decreased reproductive success (Gobush et al., 2008). Additionally, human elephant conflict and poaching of forest elephants is on the rise (Breuer et al., 2015). Determining potential areas of human contact with large elephant groups could inform antipoaching strategies of areas where elephants are at risk or reduce negative interactions with farmers. In this regard, insight into forest elephant fission-fusion dynamics can be highly informative for forest elephant management. And, our novel fusion of genetic analysis,

satellite remote sensing and computational methods can inform the study of forest

elephants and other cryptic species into the future.

3. The secret life of forest elephants: multi-scale assessment of social interactions and group composition

Introduction

Group living provides benefits to individual animals beyond solitary living, but group living also comes with costs (Alexander, 1974; Hamilton, 1971). Benefits include information regarding resources and protection from predators, whereas costs come from intra-group competition and increased time foraging (Krause & Ruxton, 2002; Silk, 2007). A key aspect of social groups is temporal stability which is determined by repeated interactions between individuals (Prox & Farine, 2020; Wey et al., 2007). The likelihood of repeated interactions is influenced by the synchrony of each individual's needs, including foraging, rest, and reproduction (Conradt & Roper, 2000). To mitigate costs of group living, individuals interact most frequently with individuals that have similar needs or their kin. This often results in social segregation based on relatedness, sex, or age (Ruckstuhl & Neuhaus, 2000). For example, females with offspring might prioritize rest and finding areas safe from predators, whereas males might prioritize foraging or searching for mating opportunities (Alves et al., 2013).

The physical environment and resource availability can moderate the costs or benefits of social interactions and social living (Furuichi, 2009; Markham et al., 2015; Pirotta et al., 2020). Comparing related species exposed to different environmental pressures can elucidate factors that influence the evolution of different group

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compositions. For example, group size varies greatly among the four species of Hyaenidae, ranging from the aardwolf (*Proteles cristata*) whose groups are composed of two individuals to the spotted hyena (*Crocuta crocuta*) whose groups include 10-90 individuals. Comparisons between the hyaenid species suggest that variation in gregariousness is influenced by the degree to which hyenas need to defend territories and carcasses (Watts & Holekamp, 2007). Beyond group size, comparisons between the two closely related chimpanzee species – bonobos (*Pan paniscus*) and common chimpanzees (*Pan troglodytes*) – suggest that more consistent resource availability within the bonobo range compared to the chimpanzee range facilitated the evolution of constant female sociality in bonobos, but not in chimpanzees (F. J. White, 1998). Similarly, comparisons of ungulates suggest that the evolution of mating systems may be affected by terrain, such that group size is smaller in more rugged terrains. Ungulate species that occupy more rugged terrain have more equal sex ratios due to physical limitations on group size and cohesiveness (Bowyer et al., 2020).

Elephants, as highly intelligent, social species with large resource needs, provide a unique comparison of environmental influence on social evolution and, in particular, social structure – patterns of interactions between related individuals, sexes, and age classes. There are currently three extant species of elephant: Asian elephants (*Elephas maximus*), savanna elephant (*Loxodonta africana*), and the lesser-studied forest elephant (*Loxodonta cyclotis*). All three species display a fission-fusion social system, in which

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individuals or sub-groups join other groups when their needs align (Conradt & Roper, 2000). However, each species displays different group sizes and social structures (de Silva & Wittemyer, 2012; Chapter 2). Savanna elephants generally inhabit arid environments with high seasonal variation in resource availability. They maintain a nested, multi-tiered social structure with smaller social units nested within larger units based on relatedness and usually segregated into same sex groups (Archie et al., 2006; Shannon et al., 2006; Wittemyer et al., 2009). Asian elephants generally inhabit tropical forests dominated by Dipterocarp trees and green savannas where there is high primary productivity and low variation in seasonal resource availability. Asian elephants form fewer, weaker bonds than savanna elephants and have a multilevel social structure in which individuals show preferences for specific individuals, but associations are not nested (de Silva et al., 2017; de Silva & Wittemyer, 2012). Female Asian elephants form small groups, averaging three adults, usually with relatives and their offspring; whereas males are often solitary in undisturbed landscapes and form stable male groups of 2-9 individuals in human disturbed landscapes (de Silva & Wittemyer, 2012; Srinivasaiah et al., 2019). It is hypothesized that differences in savanna and Asian elephant average group size and social structure are due to differences in resource availability; although non-human predators also moderate the costs and benefits of social interactions of savanna elephants, but not Asian elephants (de Silva & Wittemyer, 2012; Silk, 2007).

In contrast to the well-studied savannah and Asian elephants, little is known about the structure of forest elephant social groups. Forest elephants live in dense tropical forests, making repeated observation of groups exceedingly difficult. In Central African tropical forests, seasonal variation in bulk resource availability is relatively low, although preferred resources such as fruits are patchily distributed (Adamescu et al., 2018). Studies of forest elephants based on sightings in forest clearings have observed an average group size of three individuals (Morgan & Lee, 2007). However, a more extensive assessment of forest elephants in a range of habitats (including closed-canopy forest as well as open clearings) estimated a larger average group size of 4-5 individuals (Chapter 2). Further, in forest elephant groups at savanna clearings or baïs – mineral rich forest clearings with a water source – individuals are more related than by chance, though opportunistic dung sampling indicated within-group relatedness can vary by season (Fishlock & Lee, 2013; Munshi-South, 2011; Schuttler, Philbrick, et al., 2014). However, we lack comprehensive information about genetic relatedness within forest elephant social groups, especially outside the context of baïs and savanna clearings (Turkalo et al., 2013). The environmental factors that influence interactions between forest elephants and social group structure outside of the 'social arenas' represented by forest clearings and baïs remain unknown (Goldenberg et al., 2021).

Here, we make the first attempt to understand forest elephant social interactions throughout the habitats in which they range on a daily basis, including dense, closed-

canopy forest. Specifically, we seek to answer three distinct, but related questions: (1) What social, environmental, or anthropogenic factors are associated with the probability that two forest elephants will interact, if they are not frequent associates? (2) What is the age-sex composition of typical forest elephant social groups? (3) How do the patterns revealed in asking the first two questions combine to create the spatial distribution of genetic relatedness among forest elephants? To test question one, we employ locations from 56 GPS-collared forest elephants. For questions two and three, we use data collected during focal follows of the GPS-collared elephants. By comparing our results to already known savanna and Asian elephant social behavior, we illuminate the environment influences on social behavior and structure in highly intelligent, wide ranging species.

Methods

Study areas

We tracked 56 elephants fitted with GPS collars in four protected areas in Gabon: Ivindo, Loango, and Moukalaba Doudou National Parks and the Wonga Wongué Presidential Reserve (Figure 3.1). Ivindo National Park, at 2990 km[2], is a mixture of Atlantic coastal Lower Guinea forest and semi-deciduous forest of the Congo Basin (Mikolajczak, 2013). Elevation ranges from 248 to 781 m (Sassen & Wan, 2006). Loango National Park is 1,550 km[2] and composed of closed and open *Sacoglottis gabonensis* dominated forest, swamps, savannas, and coastal scrub, with an elevation range from

sea level to 137 m (Morgan, 2009). Moukalaba-Doudou National Park is 5,028 km² and is

a mosaic of savanna and forest, with a small mountain range reaching 900 m

(Takenoshita et al., 2008a). Wonga Wongué, a 4,282 km² coastal Presidential Reserve, is

predominantly a matrix of Atlantic coastal forest and savanna, with mangrove and

Raphia wetlands, and its elevation ranges from sea level to 204 m.
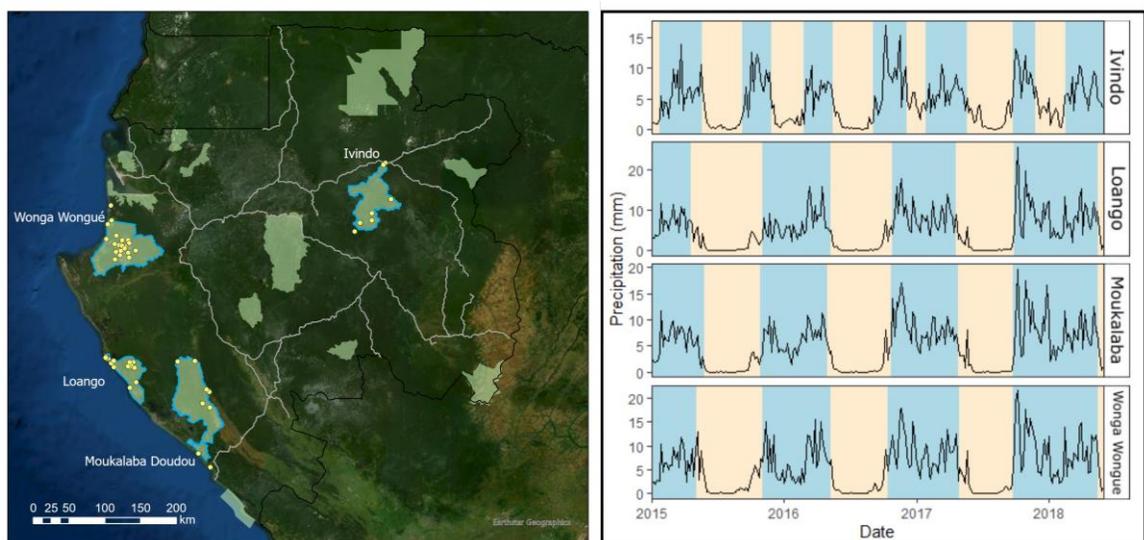
Figure 3.1: Map of Gabon with protected areas and collaring locations of 56 GPS-collared elephants and seasons within each site. The number of focal elephants in each protected area: Ivindo (n =7), Loango (n = 17), and Moukalaba Doudou National Parks (n =10) and the Wonga Wongué Presidential Reserve (n =22). Green areas = protected areas, blue outlines = protected areas with GPS collared elephants, gray lines = roads, black lines = country boarders. Line graph shows pentad mean daily rainfall trends for Ivindo, Loango, Moukalaba Doudou and Wonga Wongué. Blue sections are dates assigned as wet season and tan section are dates assigned as dry season.

GPS collars and proximity events

In October 2015, Gabon's National Park Agency (Agence Nationale des Parcs

Nationaux; ANPN) initiated a forest elephant collaring program. The collaring team

avoided tagging forest elephants found together, aiming to collar elephants belonging to unique groups. The GPS collars were set to emit hourly locations for the first two years, and then daily thereafter until the battery died. For full collaring procedures and summary statistics of GPS location emission, see Mills *et al.* (2018) and Beirne *et al.* (2020). The GPS-collared individuals were not frequent associates and remained largely unaffiliated – two-thirds did not interact with each other and pairs that did come near each other averaged 2.9 (range 0-23) interactions over the duration of the study. We define an "interaction" between collared elephants as proximity events, when two GPS-collared elephants approached within 35 m of each other within a 30-minute timeframe. This 35 m distance is a conservative estimate of the distance within which a pair of elephants likely had visual, auditory, or olfactory awareness of each other. If two elephants occurred within 35 m of each other more than once during a day, we considered this a single proximity event.

Focal Follows

From February 2017 to May 2018, we conducted 100 focal follows, tracking 28 GPS-collared elephants for up to three consecutive days at a time in and around Ivindo National Park and the Wonga Wongué Presidential Reserve (Beirne et al., 2020). In each park, we selected a group of five focal elephants, based on accessibility, which were followed every other month for an average of 5.5 follows per elephant (range 4 - 7). The remaining elephants (n = 1 Ivindo, n = 9 Wonga Wongué) were followed in a rotating

order during alternative months for a maximum of two follows per elephant. We tracked the elephants using the hourly GPS locations and with the aid of local Ba'Aka forest people. To avoid stressing the animals and putting field teams at risk, we followed a minimum of one hour behind the focal elephant.

While tracking the elephants, we collected dung samples for genetic analysis, measured dung boli, and recorded relevant habitat information (details below). As elephants have been observed to defecate synchronously (Rees, 1983), once a dung pile was sampled, the field team searched a radius of 35 m for additional dung piles. While different studies have employed different distances between individual elephants to define group membership for forest elephants, including one body length, 35 m, 50 m, 100 m and 250 m (Brand et al., 2020; Fishlock & Lee, 2013; Morgan & Lee, 2007), we chose 35 m as a conservative estimate of the distance within which individuals are able to monitor each other's activities. This relatively small radius also allowed us to keep pace with focal elephants. Once per follow we also searched a radius of 100 m to verify we were not missing additional dung. All fresh dung, appearing to have been deposited at approximately the same time based on similar warmth, sheen, and state of degradation was swabbed with a buccal swab (Isohelix, Cell Projects) and stored in buffer solution (500 µl of LS buffer and 25 µ proteinase K; Stabilizing Kits, Isohelix, Cell Projects) at ambient temperature. All newly located dung piles were swabbed, and we repeated the search until no new dung piles were found. Dung piles that were

discernably different in size or color or greater than 2 m apart from each other

(approximate distance between two elephants standing side by side) were considered

unique samples. After swabbing, if the dung was intact, the circumferences of the three

largest boli were measured to estimate broad age categories. We categorized the

provenance of dung as from infants (average circumference of 25 cm or less), juvenile

(average circumference from 25 cm to 32 cm), or adult (average circumference greater

than 32 cm; Eggert & Woodruff, 2003). After each follow, we stored samples at the

basecamp, either in a refrigerator or a room with ventilation. Every other month, we

transported samples to the Institut de Recherche en Écologie Tropicale laboratory in

Libreville, Gabon to store them in a -20° C freezer.

Genetic analysis of dung samples

We extracted DNA from the field-collected dung samples using Qiagen QIAamp

DNA Stool Mini Kits. Because of financial limitations, genetic analyses of dung from the

focal follows were limited to all the dung samples collected on one day of each focal

follow, for 89 follows. We quantified the amount of DNA in each sample through

quantitative PCR reactions using QantiNova SYBR Green PCR Kits by Qiagen on a

StepOne Real-time PCR system by Applied Biosystems. We followed the modified

protocols described in Bourgeios *et al.* (2019), except that we did not use OneStep PCR

inhibitor Removal Kits and only diluted fecal samples at a 1:10 ratio for quantification.

Any samples with non-specific amplification or with less than 0.01 ng/µl of DNA were excluded from analysis. Samples were kept at -20°C for long-term storage.

We analyzed samples for 41 autosomal loci and one sex-linked locus using Kompetitive Allele Specific PCR (KASP) genotyping for bi-allelic single nucleotide polymorphisms. The KASP assay contains two allele-specific forward primers that have a tail sequence associated with one of two fluorescent dyes (FAM and HEX) and a common reverse primer. Only one of the allele-specific forward primers can bind with the specific polymorphism for each sample. During thermal cycling, the relevant primer binds, and the relevant tail sequence is then replicated. The real-time PCR machine then reads the degree of fluorescence emitted by the replicated primers. Analyses were conducted on one of three of real-time PCR platforms: StepOne from Applied Biosystems, RotorGene by Qiagen, or Hydrocycler by LGC. For the StepOne and RotorGene platforms, methods were adapted from the KASP user guide (LGC, 2014) by increasing the number of cycles from 35 to 42. For LCG, conditions were run according to the KASP user guide. Samples with a DNA quantity greater than 0.2 ng/µl were diluted at 1:10, samples between 0.2 ng/µl and 0.1 ng/µl were diluted at 1:5 and samples with less than 0.1 but greater than 0.01 were diluted to 1:2. Each plate contained a minimum of one non-template control (NTC) and two positive controls. Generally, two NTCs and three positive controls were used per plate. At a minimum, we genotyped all samples in duplicate for 38 of the 41 autosomal SNPs. Of the 580 samples extracted and

genotyped from the focal follows, 342 qualified for the minimum criteria of 20 SNPs and

0.1ng/µl concentration of DNA and were included in the individual identity analysis.

Genotypes were initially assigned by a clustering algorithm, included with the

KASP software, that contrasts the normalized reporter dyes (LGC, 2014). The algorithm

grouped samples with similar FAM to HEX fluorescent marker ratios. We then visually

inspected and manually adjusted genotype assignment based on the agreement of two

observers. We employed a multi-tube approach to determine consensus genotypes for

all samples (Sethi et al., 2014); this involves amplifying each locus multiple times and

comparing across these amplifications to determine the true genotype. We initially

created two consensus datasets, one based on the minimum agreement criteria of 2

heterozygous or 3 homozygous genotypes (2|3), the other based on the minimum

agreement criteria of 2|2 for each locus. As only 10 of the 8,724 assignments (0.1%) did

not agree between the two methods, we used the consensus dataset that employed the

2|2 agreement requirement as this method allowed for the inclusion of more data.

Samples run twice with disagreements or only one successful run were assigned as a no

call (0), and samples with only a single successful run were assigned that genotype.

Individual Identity

We calculated individual identities associated with each dung sample by using

error-tolerant maximum likelihood sample matching (Sethi et al., 2016). This method

compares the probability of obtaining a pair of genotypes given the allele frequencies of

the study population (calculated with GenAlEx: average 0.3, range 0.07- 0.50) with the

probability of observing the sample genotypes given the genotyping error rates (average

0.018, range 0.002 to 0.128) to determine the likelihood that the two samples are the same

individual. We included samples for which we were able to assign genotypes at a

minimum of 20 loci, ensuring that our probability of incorrectly identifying siblings as

the same individual ($P_{ID(sibs)}$) was less than 0.0005 (Waits et al., 2001). From these

samples, we identified 178 unique individuals, with an average 1.78 (range 1- 23

samples) samples originating from a single individual.

During the GPS-collar placement, the National Park Agency collected tissue

samples when possible, enabling us to genotype tissue samples for 17 of the 20 focal

elephants, using the same SNPs analyzed in dung samples. We included these

genotypes in the individual identity analysis to determine which dung samples

belonged to a focal elephant and to confirm that we followed the expected elephant

group. Focal follows were included in the analyses for questions two and three if the

genotype of one of the dung samples matched the genotype of the tissue sample of the

focal individual and/or the field team's tracklog closely (i.e., same trajectory and general

location) followed the focal individual's GPS points. Eighteen follows were omitted – 15

because none of the samples were successfully genotyped, one because the tracklog did

not match the collared elephant's track, and two because we did not have the tracklog

data. The tracklogs of seventy-one focal follows (32 in Ivindo National Park and 39 in

Wonga Wongué Presidential Reserve), representing 10 males and 10 females, closely

matched with locations from the focal elephant's GPS collar. During 40 of these follows,

we collected dung samples that matched the genotype of the focal elephant's tissue

sample. In our assessments of group composition below, we treated each focal follow as

an observation.

Pairwise relatedness

We first tested six commonly used pairwise relatedness estimators to see which

would best fit our data: Queller & Goodnight (1989), Li (1993), Ritland (1996), Lynch &

Ritland (1999), dyadic likelihood estimator (Milligan, 2003), and the triadic likelihood

estimator (Wang, 2007). From the allele frequencies calculated for individual

identification, we simulated known relationship categories (parent-offspring, full-

sibling, half-sibling, and unrelated individuals) to test each estimator's ability to predict

each pair's association (Pew et al., 2015). Estimators proposed by Queller & Goodnight

(1989), Li (1993), Ritland (1996), Lynch & Ritland (1999) performed equally well, whereas

the dyadic and triadic likelihood estimators overpredicted the coefficient of relatedness

for each relationship category. We subsequently chose to employ the Queller-Goodnight

estimator because of its intuitive calculations and prevalence in the literature (Queller &

Goodnight, 1989). We calculated pairwise relatedness for all pairs of elephants that had

at least 22 successfully genotyped autosomal loci.

Question 1: What social, environmental, or anthropogenic factors are associated with the probability that two forest elephants will interact, if they are not frequent associates?

To assess the social, environmental, and anthropogenic factors that influence interactions between forest elephants, we constructed logistic regressions with a "success" represented by a proximity event within a given season-year. We aggregated the data by season and by year (e.g., the dry season of 2016), because, as mentioned above, the proximity events were relatively rare. To avoid including pairs that did not have the opportunity to interact, we excluded elephant pairs whose home ranges (estimated with an autocorrelated kernel density estimator; Fleming et al., 2015) did not overlap or whose GPS collars were not active at the same time. We tested the following variables, which have been previously shown to influence elephant behavior, as predictors of the probability of a proximity event: season, human disturbance, fruit availability, sex composition, proportion of mutual associations, site, and weighted home range overlap (Archie & Chiyo, 2012; Beirne et al., 2020; Chiyo et al., 2014; de Silva & Wittemyer, 2012).

Season included wet or dry season based on increasing or decreasing cumulative precipitation in each protected area (see Beirne et al., 2020 and Liebmann et al., 2007 for methods). Season start and end dates and the presence of a short dry and short rainy seasons varied by protected area (Figure 3.1). Most commonly, the dry season occurred from mid-May to mid-October and the wet season occurred over the remainder of the

year. Ivindo exhibited a distinct, annual, short wet season after the long dry season from mid-September to the end of November, followed by a short dry season until mid-February.

Human disturbance was calculated by averaging Global Human Footprint Index scores (GHFI; WCS 2005) over the combined home ranges of each elephant pair. The GHFI compiles diverse aspects of human disturbance, from population pressure and infrastructure to land use and accessibility (i.e., logging roads or navigable rivers), and classifies 1 km^2 pixels with scores from 0 (no disturbance; e.g., no human development or access) to 100 (high disturbance; e.g., a large city surrounded by exploitive industry). Our dataset had a bimodal distribution of low values from 0-20, so we created two categories: "next to no disturbance" for average index values less than 11 and "low disturbance" for average index values between 11 and 20.

Fruit availability was quantified with twice daily 'fruit walks.' Field teams recorded all fleshy fruits found on a 50 m x 2 m strip transect perpendicular to the focal elephant's tracks (see Beirne et al., 2020). We calculated the average number of fruits per transect in a given season/year for each protected area in which we conducted focal follows. Fruit walks were conducted only in Ivindo National Park and the Wonga Wongué Presidential Reserve during focal follows.

Sex composition represents whether the individuals in each pair were both female (female-female), both male (male-male), or mixed sex (female-male).

Proportion of mutual associates. For each pair, we created a score for the number of

elephants with which both members of a pair interact. The proxy is equal to the number

of mutual associates divided by the total number of associates in the pair combined.

Associates are pairs of elephants that had a proximity event at least once over the total

time they were collared.

Site. We included site as a fixed effect because we were interested in site specific

differences in elephant interactions. We expected site to account for unmeasured

variation between the protected areas caused by habitat differences and differences in

collaring effort (number and density of collars).

Weighted home range overlap. We expected both degree of home range overlap and

home range size to affect the probability that two individuals might interact. We

calculated a weighted overlap as $\frac{PA_i \times PA_j}{AO}$ where AO is the total area of home-range

overlap (km^2) and PA is the percent of total home range represented by AO for

individuals *i* and *j*. We log-transformed weighted overlap values so that they were

approximately normally distributed.

Not all the above variables were available for each pair or season-year

combination within each pair. For example, fruit availability data were only available for

Ivindo National Park and the Wonga Wongué Presidential Reserve. Because of these

limitations, we conducted three logistic regressions on subsets of data to maximize

inference. First, we created an "overall model" that allowed us to broadly compare the

influence of seasonality, human disturbance, sex composition, site, and weighted home range overlap. Second, to test how preferred resource availability influenced the probability of interaction, we created a "fruit availability model." In this model, we considered only pairs of elephants for which we had data on fruit availability, including the predictors in the overall model plus fruit availability. Third, to test the influence of having mutual associates, we created an "associates model", including only pairs of elephants for which the home ranges of both individuals overlapped with at least one other collared elephant. In the associates model, we included the same predictors as the overall model plus the proportion of mutual associations. Including only pairs of elephants with the potential of mutual associates was necessary because of uneven spatial distribution of GPS-collared elephants within and across protected areas, where not all elephant pairs had the possibility of mutual associations. All three models included pair identity as a random factor to account for unequal temporal coverage across pairs. We conducted all analyses in RStudio (RStudio Team, 2020), using the lme4 package for logistic regressions (Bates et al., 2015).

Question 2: What is the age-sex composition of typical forest elephant social groups?

To characterize forest elephant social groups, we used the characteristics of individuals identified via genetic analysis of dung during each focal follow (Figure 3.2). We used this information to describe average group composition in terms of sex and age. We explored three aspects of forest elephant social group structure: (1) sex

composition of adults in a group; (2) average coefficient of relatedness between adults; and (3) composition of groups with juveniles. Because there were limited repeat follows, as well as imperfect detection of dung piles and variable genotyping success (see Chapter 2), we report descriptive results as comparisons, ratios, or percentages. Our sampling procedure was blind with respect to the sex and age of the individual who deposited the dung bolus, i.e., we expect our sampling to be unbiased with respect to these characteristics.
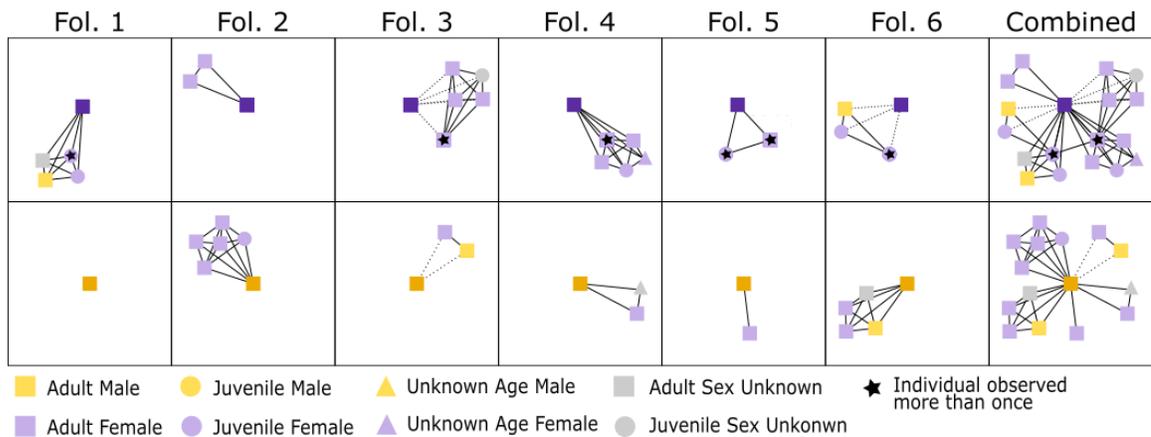
Figure 3.2: Ego network visualization of focal follows tracking female and male GPS-collared elephants. Each follow (Fol.) represents an observation of group sex and age composition. The top row represents the focal follows of an adult female, Malaika, (dark purple square) and the bottom row represents the focal follows of an adult male, Kigali (dark orange square). Solid lines represent dung found during the same focal follow; dashed lines represent assumed connection to the focal individual though dung from the focal individual was not observed during the follow.

Sex composition of adults in a group

By treating each focal follow as a unique group observation, we first describe the percentage of groups in which the adults were all female, all male, or both sexes occurred (i.e., at least one male and one female elephant were present). We excluded

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groups in which all genotyped individuals were the same sex but at least one individual was of unknown sex. We then compared group size across group sex compositions. For mixed sex groups, we looked at the average ratio and skew of males to females in a group. Lastly, for focal individuals followed at least 5 times, we explored whether elephants spend the same proportion of follows in same sex or mixed sexed groups.

Average genetic relatedness of pairs based on sex composition

For each focal follow, we calculated the average pairwise relatedness for all adults based on the sex composition of each pair. We then compared the distributions of relatedness for each sex composition with an analysis of variance and used the Games-Howell test to account for unequal sample sizes and variance (S. Lee & Lee, 2018).

Composition of groups with juveniles

While we sampled dung piles from infant elephants occasionally, the small dung piles were difficult to find and likely often missed. Therefore, we only compared ratios of adults to juveniles in which biased sampling is unlikely. We first calculated the percentage of groups with juveniles. Then, we assessed the sex composition of adults in groups with juveniles. Lastly, we explored the average ratio and skew of adults to juveniles in a group.

Question 3: How do the patterns revealed in asking the first two questions combine to create the spatial distribution of genetic relatedness among forest elephants?

To explore how interactions and group composition influence the spatial distribution of pairwise relatedness, we employed an analysis of variance and Games-Howell test to assess the average pairwise relatedness across three categories of association: elephants observed together, elephants in the same site, and elephants belonging to unique sites.

Results

What social, environmental, or anthropogenic factors are associated with the probability that two forest elephants will interact, if they are not frequent associates?

The overall model showed that sex composition, site, and weighted home range overlap were significantly associated with variation in the odds of a proximity event between two GPS-collared individuals (Table 3.1). The odds of a male-male proximity event, controlling for site differences and the effect of home range overlap, were 4.01 times higher than the odds of a female-female proximity event (SE $\pm$ 1.64; $p = 0.004$), and there was no statistically significant difference in the odds of a proximity event between female-female and female-male pairs. Variation between sites had the largest influence on the odds of a proximity event. Compared to Ivindo, the odds of a proximity event in Moukalaba-Doudou were 12.94 times greater (SE $\pm$ 2.74; $p = 0.01$). The odds of a proximity event in Loango or Wonga Wongué were not statistically significantly

different than those in Ivindo. As the weighted home range overlap between two

individuals increased, the odds of a proximity event increased 10.70 times (SE ± 3.24; *p*

<0.001). Neither human disturbance nor seasonality had a significant effect on the odds

of a proximity event occurring.

Table 3.1: Logistic regression coefficients for predictor variables in the three mixed models predicting the probability of a proximity event between collared elephants. Std. Error = Standard error; Env. = Environmental Parameters; Soc. = Social Parameters; Spat. = Spatial Parameters; No Disturbance = Human disturbance level "Next to no disturbance;" Sex Comp. M-F = pair sex composition level male-female; Sex Comp. M-M = pair sex composition level male-male; Fruit Avail. = Fruit availability; Prop. Mutual Assoc. = Proportion of mutual associations; Pair = random effect of pair. Bolded values are statistically significant. Baseline for sites = Ivindo National Park.

		Parameter	Estimate	Std. Error	Z	p	Interpretation
Overall Model		Intercept	**-6.64**	**-1.09**	**-6.10**	**< 0.001**	DF = 1018
		Pair (Variance)	0.96	0.98 sd			
	Env.	Wet Season	0.02	0.23	0.11	0.92	
		No Disturbance	0.53	0.36	1.46	0.14	
	Soc.	Sex Comp. M-F	0.67	0.44	1.53	0.13	
		Sex Comp. M-M	**1.39**	**0.49**	**2.82**	**0.004**	↑ odds of M-M events than other events
	Spatial	Weighted Overlap	**0.86**	**0.16**	**5.35**	**< 0.001**	↑ odds of event with increased overlap
		Loango	0.10	0.91	0.11	0.91	
		Moukalaba Doudou	**2.56**	**1.01**	**2.54**	**0.01**	↑ odds of event at this site
		Wonga Wongué	1.37	0.87	1.56	0.12	
Fruit Model		Intercept	**-9.79**	**2.63**	**-3.73**	**< 0.001**	DF = 293
		Pair (Variance)	1.93	1.39 sd			
	Env.	Wet Season	0.48	0.74	0.65	0.52	
		No Disturbance	0.46	0.59	0.78	0.44	
		Fruit	-0.001	0.06	-0.02	0.98	

		Availability					
	Soc.	Sex Comp. M-F	1.86	1.07	1.74	0.08	
		Sex Comp. M-M	**2.88**	**1.2**	**2.41**	**0.02**	↑ odds of M-M events than other events
	Spat.	Weighted Overlap	**1.51**	**0.46**	**3.32**	**< 0.001**	↑ odds of event with increased overlap
		Wonga Wongué	1.25	1.42	0.89	0.38	
Associates Model		Intercept	**-6.35**	**1.1**	**-5.76**	**< 0.001**	DF = 1005
		Pair (Variance)	0.91	0.95 sd			
	Env.	Wet Season	0.06	0.24	0.24	0.81	
		No Disturbance	0.39	0.37	1.05	0.29	
	Social	Sex Comp. M-F	0.68	0.46	1.48	0.14	
		Sex Comp. M-M	**1.42**	**0.51**	**2.80**	**0.005**	↑ odds of M-M events than other events
		Proportion Mutual Associates	**1.90**	**0.62**	**3.09**	**0.002**	↑ odds of event with increased mutual associates
	Spatial	Weighted Overlap	**0.86**	**0.17**	**5.08**	**< 0.001**	↑ odds of event with increased overlap
		Loango	-0.52	0.95	-0.55	0.59	
		Moukalaba Doudou	1.66	1.07	1.54	0.12	
		Wonga Wongué	0.68	0.91	0.74	0.46	

When including fruit availability as a predictor variable (and limiting the analysis Ivindo and Wonga Wongué), the odds of a proximity event was again significantly predicted by sex composition and weighted overlap, but not fruit availability, human disturbance, season, or site (Table 3.1). Specifically, in the fruit availability model, male-male pairs were 17.78 times more likely to have a proximity event than female-female pairs (SE ± 3.31; *p* = 0.02). In this model, we found only modest

evidence that the odds of a proximity event between female-male pairs were higher than between female-female pairs 6.44 times (SE ± 2.92; *p* = 0.08), but note the smaller sample size and limited number of study sites in the model. As the weighted overlap between two individuals increased, the odds of a proximity event increased 93.9 times (SE ± 3.84; *p* < 0.001). Like the overall model, elephants from Ivindo and Wonga Wongué did not differ significantly in the odds of a proximity event.

In the associates model, the proportion of associates was significantly associated with the odds of a proximity event, as were sex composition and weighted home range overlap (Table 3.1). As the number of mutual associations increased, the odds of a proximity event increased 6.72 times (SE ± 1.85; *p* = 0.002). Like the other models, male-male pairs experienced an increased odds of a proximity event: male-male proximity event were 4.14 (SE ± 1.66; *p* = 0.005) times greater than the odds of a female-female proximity event. As weighted home range overlap increased, the odds of a proximity event increased 10.52 times (SE ± 3.27; *p* < 0.001). Season, human disturbance, and site did not significantly affect the odds of a proximity event between two elephants.

What is the age-sex composition of typical forest elephant groups?

Sex composition of adults in a group

We were able to assign a sex composition to social groups in 56 of 71 focal follows. We observed 32.2% mixed sex groups, 46.4% female-only groups, and 21.4% male-only groups (for example follows see Figure 3.2). Females were observed in 44

social groups, of which 41% were mixed sex. Males were observed in 30 social groups, of which 60% were mixed sex groups. On average, the mixed sex groups were larger (3.4 individuals) than all-female (2.2 individuals) or all-male (1.5 individuals) groups, though the largest group of identified individuals was all female (7 individuals). For the 18 mixed sex groups for which we successfully genotyped the sex-based locus for all members in the group, the most common ratio of males to females was 1:1 (Figure 3.2). The highest observed sex ratio was 4:1 male:female and the lowest observed sex ratio was 1:4 male:female. We conducted more than five focal follows on three males and five females. Among the five female focal elephants, two focal elephants were never observed in mixed sex groups, and the other three were observed in all-female groups during at least three of five follows (Figure 3.3). Among the male focal elephants, all individuals were observed in a mixed sex group during at least one focal follow. However, we observed two males more often in mixed sex groups (three of five follows) than all-male groups, and one male more often in all-male groups than mixed sex groups (one of six

follows).
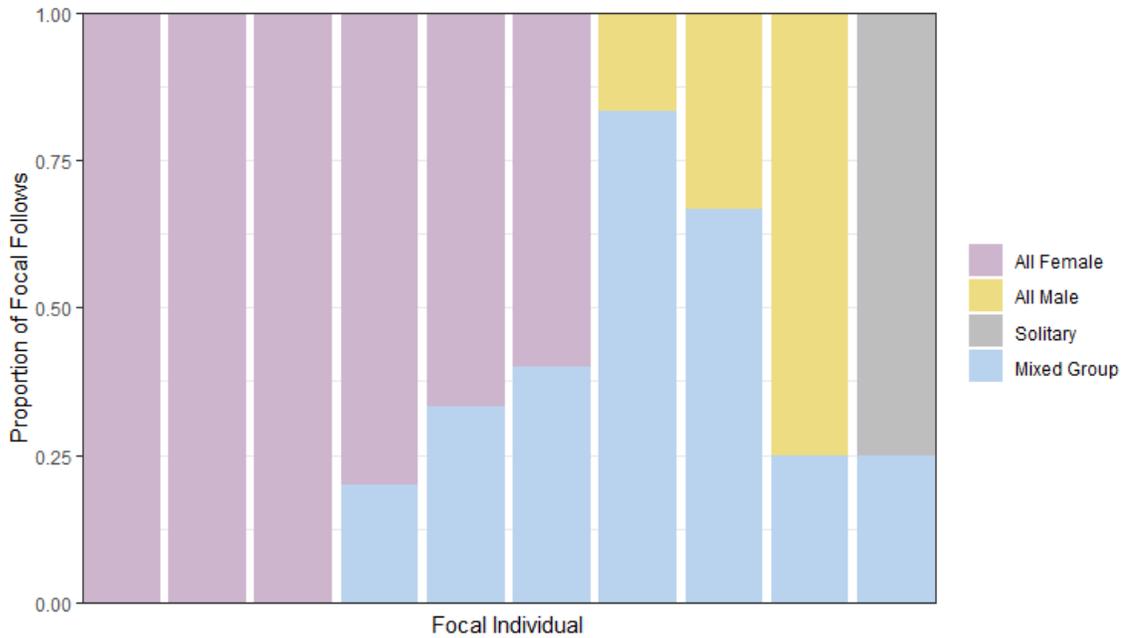
Figure 3.3: Proportion of follows focal elephant was observed in different group compositions. Each bar represents a unique focal elephant, the first six are female elephants and the last four are male elephants. Color represents the group composition.
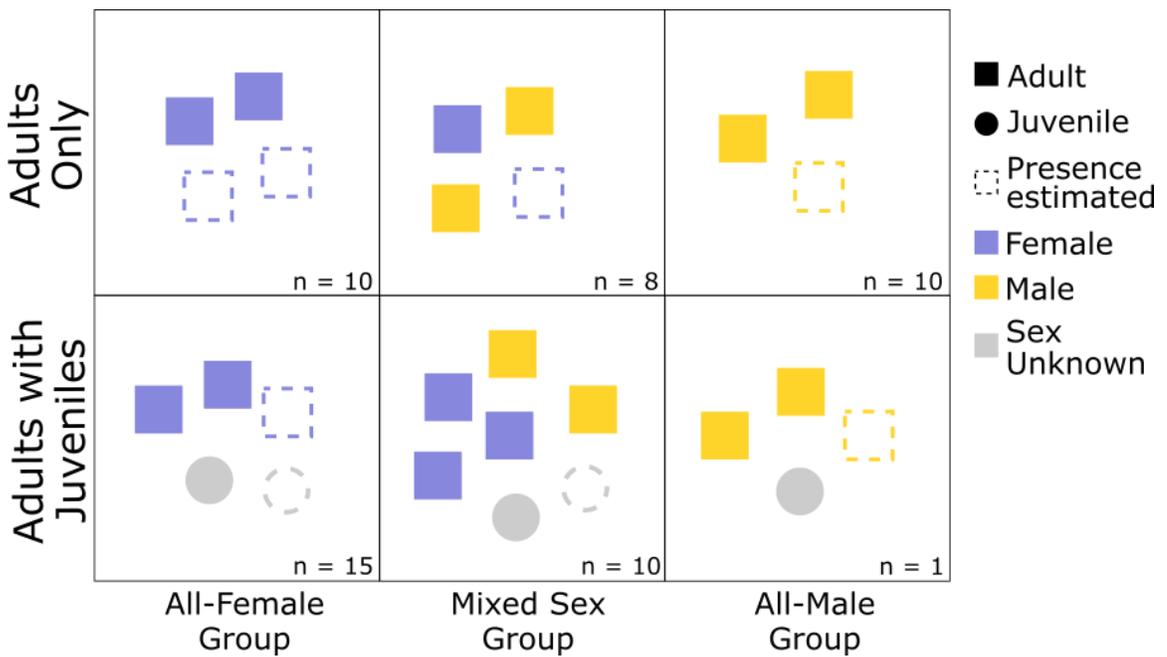
Figure 3.4: Estimated age-sex composition for typical forest elephant groups.
Numbers, ages, and sexes of identified individuals in typical groups (solid symbols)
based on genotypes from dung samples collected during focal follows. Estimated
individuals (dashed symbols) were added based on group size information from
Chapter 2 to provide a more complete picture of typical social groups. For estimated
individuals, age and sex were assigned by using age and sex ratios of identified
individuals.

Average coefficient of relatedness between adults

In the forest elephant groups identified during focal follows, we found

statistically significant differences in pairwise genetic relatedness between different

types of adult pairs ($F_{(2, 71)}$ = 4.34, p = 0.017; Figure 3.5). Female-female pairs had the

highest average pairwise relatedness coefficient of 0.25 ± 0.29 (SD), indicating that

female-female pairs were, on average, half siblings. In contrast, the average pairwise

relatedness of female-male pairs was statistically significantly lower (0.06 ± 0.20 SD; p =

0.002), indicating an average relatedness at the level of half-first cousins on average, and

probably including many unrelated pairs. Male-male pairs identified together in groups

were more closely related on average than male-female pairs, at 0.15 ± 0.24 (SD), but less

closely related on average than female-female pairs, although these differences were not

statistically significant (female-female: p = 0.96; female-male: p = 0.18). The small sample

sizes may influence the lack of statistical significance (Figure 3.5).
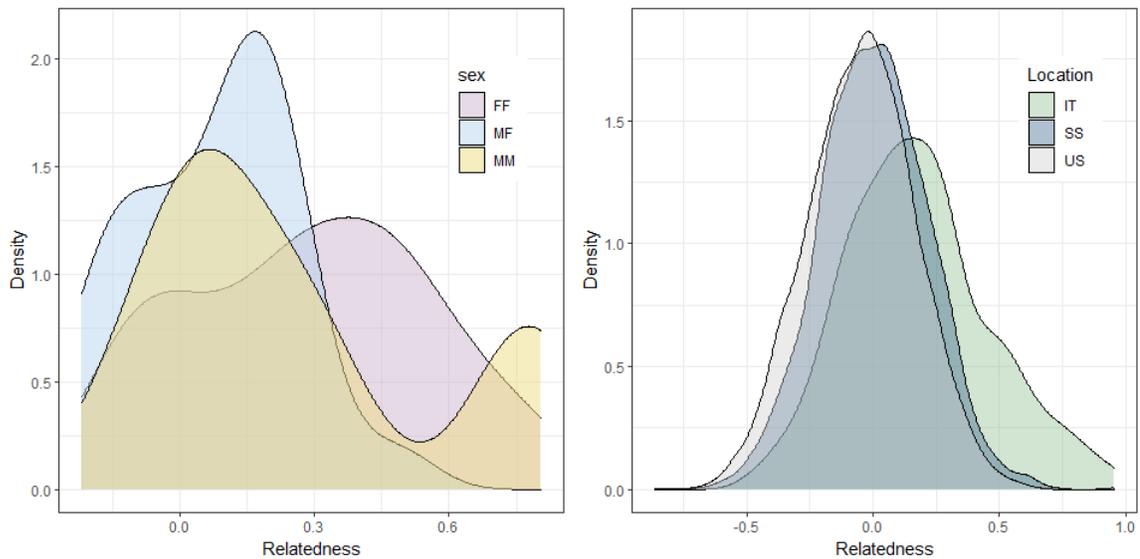
Figure 3.5: Distribution of average pairwise relatedness coefficients for (a) sex composition of female-female (FF) pairs, n = 35; male-female (MF) pairs, n = 27; and male-male (MM) pairs, n = 13, observed together during the same focal follow; and (b) individuals identified together in groups (IT), n = 186; pairs of elephants found in the same site (SS), n = 3291; and pairs of elephants from different sites (US), n = 6071.

Composition of groups with juveniles

We determined the proportion of groups that contained juveniles, based on 67 of the 71 focal follows, as some boli were too broken up to accurately measure to estimate age. Forty-three percent of the groups identified during focal follows had juveniles. Of the 26 mixed age groups for which we determined the age classes of all members, the most common ratio of adults to juveniles was 2:1 (n = 7), followed closely by 1:1 (n = 6; Figure 3.4). The highest ratio of adults to juveniles was 7:1 and the lowest ratio of adults to juveniles was 1:2.

How do the patterns revealed in asking the first two questions combine to create the spatial distribution of genetic relatedness among forest elephants?

Average pairwise relatedness among individuals identified together in groups was 0.18 ± 0.28, indicating groups tended to include a substantial number of related pairs. In contrast, pairwise relatedness of all animals that lived in the same site was 0.007 ± 0.21, slightly higher than zero. Elephants in groups were significantly more closely related than pairs living in the same site ($p < 0.001$), which in turn was significantly higher than average pairwise relatedness for individuals in different sites (-0.05 ± 0.21, *p* < 0.001; Figure 3.5).

Discussion

By coupling spatial data from GPS-collared elephants with non-invasive genetic sampling of dung collected during focal follows, we gained multilevel inference on interactions between unaffiliated elephants and group composition of elephants. We demonstrated that mutual associations and sex composition influenced interactions between random individuals, that there was remarkable heterogeneity in forest elephant group sex composition, and that, within groups, females were more closely related to each other than males were to each other. We discuss the implications of our results for understanding interactions between forest elephants, forest elephant social group composition, and how these aspects of social behavior vary across elephant species. Because our definitions of 'interaction' and 'group' are based on physical proximity and

not affiliative behavior (e.g., grooming), we cannot know the true social relationship between two individuals (Franks et al., 2010). As we are primarily focused on description of individuals present together, we are not making assumptions on individual gains or reasons for being near other individuals.

Social factors, interactions, and group composition

Social factors (sex composition and number of mutual associations), but not environmental factors (preferred resource availability, and human disturbance), were associated with increased odds of an interaction (a proximity event) between two forest elephants that were not frequent associates. Among the collared elephants, male-male pairs had greater odds of proximity events than male-female or female-female pairs. This may be due to males having larger home ranges, which increases their probability of interacting with more elephants (Mills et al., 2018; Beirne et al., In Review). Of note, the more mutual associates two GPS-collared elephants had, the more likely they were to interact. This finding of mutual associates influencing proximity events might be an example of triadic closure, in which individuals are more likely to form bonds with 'friends of friends,' which is hypothesized to facilitate the evolution of cohesive subgroups and cooperation within a social group (Borgeaud et al., 2016; Lusseau, 2003; Righi & Takács, 2014). Triadic closure in forest elephants, even at the level of generally unaffiliated individuals, suggests an underlying pattern of preferential associations that would influence the spread of information or disease (Lusseau et al., 2006).

During our focal follows, repeat sampling of the adult pairs together in a group was rare (n = 4 of 122 adult pairs; 2-6 times each). The lack of repeated interactions is preliminarily congruent with observations from forest elephants in baïs, where some individuals repeatedly entered the bai together, but there was not cohesion across all individuals in the bai (Goldenberg et al., 2021). Thus, forest elephants likely have some community structure, which is more akin to the multilevel social structure in Asian elephants than the nested social structure of savanna elephants (de Silva & Wittemyer, 2012), though further study is necessary. If, however, having mutual associates predicts multiple interactions between individual forest elephants that are not frequent associates, this would lead to relatively tightly knit, stable communities (Ilany et al., 2013, 2015), similar to savanna elephants in which members within each nested social level (i.e., mother-calf, core groups, bond groups, and clan groups) are more likely to interact with each other than individuals from the next level (Wittemyer et al., 2009). However, we were unable to test whether triadic closure also increased the probability of two forest elephants being observed together multiple times.

Male focal elephants were observed in mixed sex groups more often than female focal elephants. The percent of focal follows males spent in mixed sex groups (60%, n = 30) was much more than the amount of time male Asian and savanna elephants were observed in mixed-sex groups (29.6%, Keerthipriya et al., 2018; and 18.4%, Chiyo et al., 2011). One potential explanation for the relative lack of sexual segregation in forest

elephants is an absence or muted importance of environmental drivers (such as resource availability) on social segregation. Sexual segregation in many taxa is attributed to differences in foraging strategy and diet (e.g., seabirds, Phillips et al., 2011; ungulates, Ruckstuhl & Neuhaus, 2000; savanna elephants, Shannon et al., 2006), but preferred food resources like fruit are equally available to male and female forest elephants. Future studies of dietary assessments could determine if forest elephants display sex-specific forage selection.

In addition to environmental drivers of sexual segregation, sexual segregation might be influenced by social motivations such as affinity for same-sex groups and/or aversion between the two sexes (Wearmouth & Sims, 2008). For example, segregation in bottlenose dolphins is driven by females avoiding males (Galezo et al., 2018). In forest elephants, bai observations suggested that mixed sex groups were formed by males joining female groups (Fishlock & Lee, 2013). This hypothesis implies that males initiate mixed groupings and has preliminary support from our observation that all repeatedly followed focal males were observed in a mixed sex group at least once, whereas only 50% of female focal elephants were observed in a mixed group. Interestingly, there was also individual variation in the amount of time (represented by proportion of focal follows) an elephant was sampled in a mixed sexed group for both males and females. While we do not identify the mechanism, previous studies on Asian and savanna elephants showed that degree of human disturbance (and primary productivity for

savanna elephants) influenced the amount of time males spent in mixed sex groups (Chiyo et al., 2014; Srinivasaiah et al., 2019). Future research should assess the ecological and social factors associated with the amount of time individuals spend in mixed sex groups.

Mixed sex groups were, on average, larger than all-female groups, which were in turn larger than all-male groups. Mixed sex groups, however, were not large enough to suggest simple fusing of male and female groups. More likely, forest elephant groups are highly fluid with one or two individuals separating from one group to join another group, or female groups splitting after male(s) join. We observed that male forest elephants were not overtly solitary; this result contradicts observations from baïs, where less than 1% of males entered in all-male groups (Turkalo et al., 2013). In our study, when males were not in mixed sex groups, 42% of the follows included two or more adult males. This is likely an underestimation of male associations because the percentage is based only on dung found and does not account for imperfect detection or incomplete genotyping (see Chapter 2). While many species display sexual segregation, patterns of male association within segregated groups has rarely been studied (Chiyo et al., 2011; Fischhoff et al., 2009; Lettevall et al., 2002).

Spatial influence of the odds of interaction

Several GPS-collared elephant pairs with overlapping home range did not interact; even so, increasing weighted overlap of a pair's home ranges was associated

with increased odds of forest elephant proximity events. Although we had expected either intrinsic habitat differences between sites or the distribution of GPS-collared elephants within sites to influence the odds of two elephants interacting, once we added the term for mutual associates, site was not statistically significant. As discussed for environmental variability above, we suspect that habitat differences among sites were strong enough to create observable differences in the probability of interactions. Forest elephant social behavior is likely maintained across habitats just like savanna elephant social behavior and structure is maintained across a diversity of habitats (Archie et al., 2006; Wall et al., 2013; Wittemyer et al., 2005).

Environmental influence on the odds of interaction

The lack of association between proximity events and environmental variables (fruit availability and human disturbance) is likely due to relatively low environmental variation and the importance of social interactions for forest elephants. The association between low fruit availability or high human disturbance and increased group size (Chapter 2) might only influence individuals that already know each other, rather than individuals that are not frequent associates – interact about once a year. Similarly, savanna elephants will interact with more elephants as resources increase, but they preferentially interact with their relatives and not random individuals (Wittemyer et al., 2009). Additionally, it is unlikely that when forest elephant groups fission because of

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scramble competition for fruit (Chapter 2), individual group members would affiliate with random individuals.

We had expected higher numbers of interactions in more disturbed areas because all three elephant species have been previously shown to form larger groups in areas of increased anthropogenic disturbance (Chiyo et al., 2011; Srinivasaiah et al., 2019; Chapter 2). However, the elephants in our study primarily inhabited protected areas with relatively little disturbance and did not display increased probability of interacting in low compared to undisturbed areas. Further study of forest elephants outside of national parks with a larger human footprint could elucidate whether human disturbance increases interactions between random individuals as observed with savanna elephants (Chiyo et al., 2014).

We must be wary that 35 m might not be the most relevant threshold distance to define a proximity event. At times, forest density makes it difficult to observe forest elephants at 5-10 m let alone 35 m (personal observations) and, depending on the wind direction, elephants might not be able to see or smell each other at 35 m. On the other hand, elephants are known to communicate via infrasound that can travel up to 800 m in a forested environment (Hedwig et al., 2018). If forest elephants communicate similarly to savanna elephants, which have been shown to precipitate group fusion with rumble calls (Leighty et al., 2008), a much greater distance would be necessary to account for potential contact between individuals. Eight hundred meters, however, risks many false

positive proximity events which is why we maintained a conservative distance based on elephant sight and smell.

Age composition

Juveniles were present in only 46% of all groups, and 60% of all-female groups - less than we had expected from literature on savanna elephants stating mothers were regularly with offspring (P. C. Lee, 1987; Moss et al., 2011). Groups observed with juveniles most often had one juvenile for every two adults. Forest elephants have a later primiparous date and longer interbirth interval than savanna elephants (Turkalo et al., 2016). The longer interbirth interval combined with juvenile male and female dispersal with protracted reliance on their mother (Turkalo et al., 2018) are the likely causes for the lower proportion of juveniles to adults in forest elephants compared to savanna elephants (P. C. Lee, 1987; Moss et al., 2011). We did not observe any all-juvenile groups; but because we conducted focal follows on adults, we were unlikely to observe them.

Pairwise relatedness

Forest elephant identified in groups together during focal follows had higher coefficients of pairwise relatedness than individuals in the same site, similar to Asian and savanna elephants (Archie et al., 2006; Chiyo et al., 2011; Vidya & Sukumar, 2005). This trend was driven by female and not male groups - females in the same group had an average pairwise relatedness of 0.25. Female forest elephants likely benefit from staying in groups of related individuals by engaging in allomothering, like savanna

elephants and many other mammals (Briga et al., 2012; P. C. Lee, 1987). Male forest

elephants observed in the same focal follow had an average pairwise relatedness of 0.15;

but relatedness coefficients for male pairs were indistinguishable from zero, regardless

of whether they were in single or mixed sex groups. Our finding is contrary to finding

for male groups of Asian and savanna elephants that were more genetically similar than

predicted by chance (Chiyo et al., 2011; Vidya & Sukumar, 2005). For forest elephant

males, the regular occurrence of mixed sex groups and low average relatedness between

males in a group suggest that they likely benefit from group living, perhaps gaining

sparring partners or access to foraging information. A larger sample size of repeated

male focal follows could elucidate when males are present in different group

compositions. Coupling this data with an endocrine study would elucidate if time spent

in the different group compositions is associated with reproductive state in male forest

elephants.

Conclusions

Our study provides novel insights by using the most comprehensive datasets to

date on forest elephants outside of baïs and forest clearings. While we observed trends

in group composition like those of Asian and savanna elephants, we also found marked

differences - such as a higher proportion of mixed sex groups and infrequent repeat

observations of associates during focal follows. We lay the groundwork for future

studies to assess how foraging strategies of male and female elephants drive the sex

composition of groups and to test what environmental or social factors influence

repeated interactions between individual forest elephants.

4. Improving population estimates of difficult-to-observe species: a dung decay model for forest elephants with remotely sensed imagery

Introduction

As animal populations continue to decline globally (Dirzo et al., 2014), accurate estimates of wildlife abundance are essential for conservation planning and management (Ahrestani et al., 2018). Counting animal sign along line transects is one of the most commonly used methods for many elusive tropical forest species that leave distinctive sign (Nuñez et al., 2019). Surveys of animal sign typically count dung (e.g., elephants, deer, great apes; Plumptre, 2000; Todd, Kuehl, Cipoletta, & Walsh, 2008; Poulsen et al., 2017) or nests (e.g., great apes; Stokes et al., 2010). Distance sampling can be used to apply a detection function – the probability that dung or nests at some distance from the transect will be observed – to derive the point estimate and error in sign density (Buckland et al., 2001). To convert sign density to animal density, the sign

density is divided by its estimated production rate and time to decay (Laing et al., 2003). These multipliers, however, introduce additional sources of error into density estimates when decay rates from non-representative sites or seasons are used.

Though previous studies proposed alternatives to dung production and decay estimates, such as the clearance plot method (Marques et al., 2001), sigmoidal curves in iterative modeling (Plumptre & Harris, 1995), and rainfall models (Barnes & Dunn,

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2002), most studies still employ these conversion multipliers. Several attempts have been made to minimize errors or increase transparency in estimates of animal density or the multipliers. For example, addressing spatial heterogeneity in decay rate of nests or dung can improve precision 10-20 fold (Kuehl et al., 2007). Similarly, employing more accurate representations of defecation events per number of dung piles improve gorilla population estimate accuracy by 30% (Todd et al., 2008). Reporting sign density along with population estimates (Stokes et al., 2010) and coefficients of variation (Plumptre, 2000) improves transparency. Since 1970, seven studies measured forest elephant (*Loxodonta cyclotis*) dung production, reporting 12.2-19.8 defecations/elephant/day (Ruggiero, 1992; Tchamba, 1992). Many more studies have measured dung decay, reporting rates of 30-166 days with variation attributable to location, season, and other environmental conditions (Barnes et al., 1995; Vanleeuwe & Probert, 2014).

There is, unfortunately, little agreement about the factors that influence dung decay rate (e.g., sunlight, rainfall, canopy cover; White, 1995; Breuer & Hockemba, 2007). Large variation across sites has prevented adoption of a single model, necessitating that practitioners derive costly and time-consuming, site-specific estimates of dung decay rate (Laing et al., 2003) or employ decay rates from other sites at the risk of introducing substantial error into abundance conversions. For example, Poulsen et al. (2017) found that varying defecation rate between 18.1 and 19 dung/day and decay rate between 45

and 90 days yielded a difference in population estimates of 9,000 elephants – 11% of the global population – in a single area (Maisels et al., 2013).

With such high variability in dung decay rates, and because forest elephant surveys often occur at the landscape or national scale, consistent tools for measuring the factors that influence decay are necessary. Remote sensing can provide spatially and temporally consistent measures of these factors across forest elephant range by enabling access to information at large spatial scales where field data collection is otherwise impractical (Bonter et al., 2009), difficult (Luo et al., 2016), or not previously available (Ho et al., 2017). Improved sensor accuracy (e.g., evolution of the Landsat band accuracy and precision), coverage frequency, access to imagery (i.e., Google Earth Engine), and advancements in environmental and climatological modeling (Roy et al., 2016) have resulted in a plethora of publicly available, cohesive data. As a result, daily or near daily information at fine spatial scales is available for many environmental variables that purportedly affect dung decay (e.g., forest cover, drought risk, climate).

We present alternative methods to improve the accuracy of sign decay measurements without the need for costly, labor intensive *in situ* decay studies. Using dung decay data from three different, highly variable sites in Gabon, we build Weibull survival models to estimate dung decay rates to: (1) investigate the climate and environmental variables that most strongly affect dung decay rate; (2) test whether field data, remotely sensed data, or a combination of data best predict dung decay; and, (3)

estimate bias in population estimates caused by failing to account for spatial and temporal variation in dung decay.

Methods

Field observations

From February 2017 to June 2018, we collected data on dung decay in three Gabonese protected areas: Ivindo and Loango National Parks and the Wonga Wongué Presidential Reserve (Figure 4.1). Ivindo National Park covers 2,990 km^2, most of which is a mixture of Atlantic coastal Lower Guinea forest and semi-deciduous forest typical of central Congo Basin (Mikolajczak, 2013), with some areas of seasonally inundated forest, swamps, and forest clearings. Elevation ranges from 248 to 781 m (Sassen & Wan, 2006). During the study, the park had a mean annual precipitation of 1,787 mm (daily 0-62 mm; calculated from the CHIRPS database) and an average temperature of 28.1°C (range 23.1-34.2°C; calculated from the MODIS satellite imagery). Loango National Park is 1,550 km^2 and composed of closed and open *Sacoglottis gabonensis* dominated forest, swamps, savannas, and coastal scrub, with an elevation range from sea level to 137 m (Morgan, 2009). The park had a mean annual precipitation of 2,036 mm (daily 0-73 mm) and an average temperature of 27.5°C (range 21.4-33.8°C). The Wonga Wongué Presidential Reserve is 4,282 km^2 predominately composed of Atlantic coastal forest and savannah matrix, with mangrove wetlands and beaches along the coast (Mills et al., 2018). Elevation ranges from sea level to 287 m (Farr et al., 2007). During the study, the reserve

had a mean annual precipitation of 2,256 mm (0-72 mm) and an average temperature of

28.9°C (range 23.2-38.2°C).
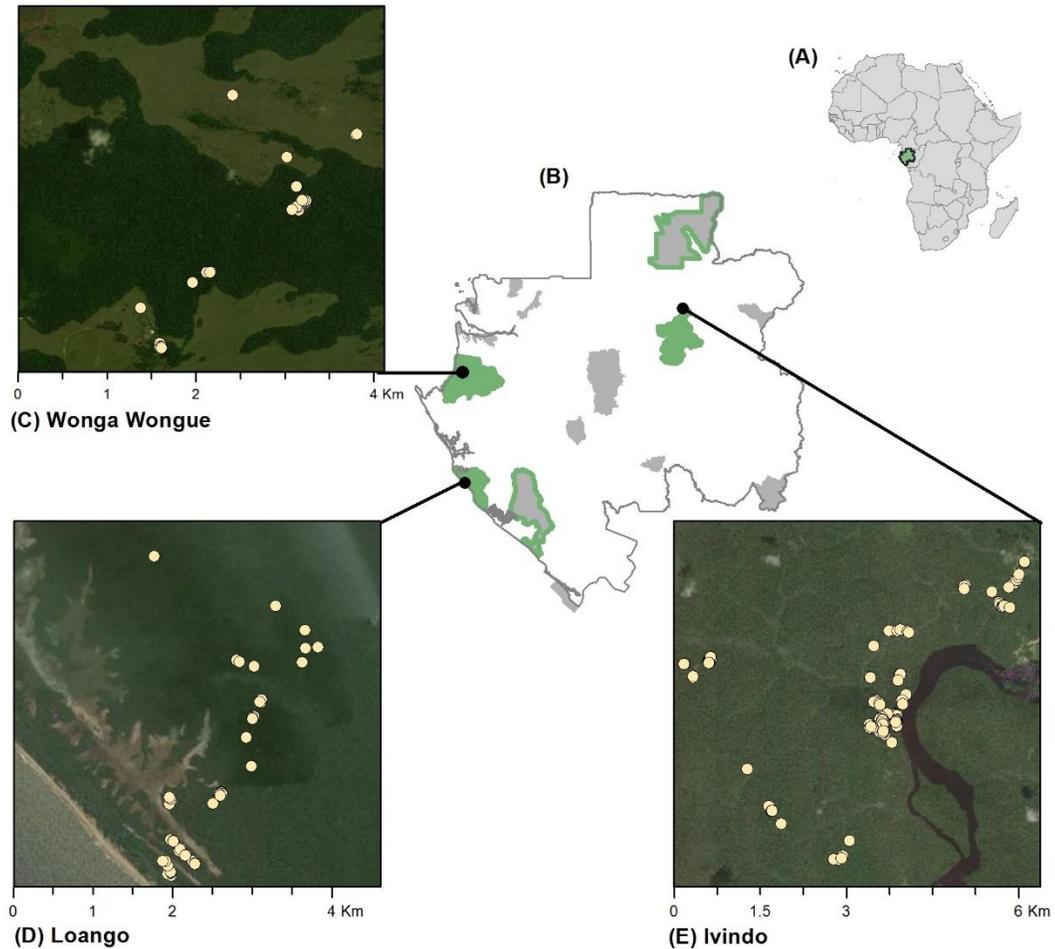
Figure 4.1: Study sites and distribution of observed dung piles in Gabon. (A) Gabon (green) in Africa; (B) Focal protected areas (green) and other protected areas (grey). Green outlines indicate Moukalaba Doudou and Minkébé National Parks used in spatiotemporal variability simulations. Yellow points show dung piles overlaid on a satellite image of each protected areas.

We followed GPS-collared elephants (Beirne et al., 2020) to locate and monitor

fresh dung, less than 24 hours old. We determined the age of dung as the difference

between discovery time and the time that the GPS-collared elephant occurred in the

same location. During the initial observation of dung, we recorded the GPS location and characteristics of the dung pile and its surrounding habitat. Dung characteristics included the decay state (S Group) according to the Monitoring the Illegal Killing of Elephants scale (i.e., S1 = all boli intact; S2 = some boli intact; S3 = no boli intact but fecal material present; S4 = no fecal material, only fibers; S5 = nothing remains; Table 4.1; Hedges et al. 2012), presence of mucous, darkness of the dung pile on a four point scale (1-straw colored to 4-nearly black), number of boli present, circumference of the three largest boli, and evidence of animal disturbance such as trampling or dung beetles (presence and/or removal of dung). We used a densiometer (Forestry Suppliers Spherical Crown Densiometer) to measure percent canopy cover as the proportion of leaf cover over the dung and recorded categories of vegetation type in three categories (forest, inundated areas, and human disturbance zones) and ground substrate (dead leaves, dry soil, live vegetation, or mud). After initially locating dung piles, we revisited them daily for the following two days and approximately weekly thereafter. During each return observation, we recorded any change in S Group, signs of new animal disturbance, and presence of fungi. We revisited dung piles until they completely disappeared – neither fecal material nor fiber remained. We calculated decay time as the number of days from the initial observation until the first observed S4 phase because most transect surveys do not count dung plies at S4 or S5 stages. We quantified animal disturbance as the proportion of all revisits where new animal sign occurred between

visits. As a putative cause of dung decay, we calculated the average number of seeds (> 1

cm) per dung (L. J. T. White et al., 1993) for each month from diet assessments

conducted on every third dung encountered (but not subsequently monitored for decay

rate) during elephant focal follows (see Beirne et al. 2020 for methods).

   We incorporated data collected by Breuer *et al.* (2007) to help build remotely

sensed models (see below) and test whether they could accurately predict dung decay

times. These data contain 160 daily dung decay observations along 2.6 km of the Mbeli

Bai trail in Noubalé-Ndoki National Park (Republic of Congo) from 2002-2006.

Table 4.1: Field data collected during dung decay observations. E = Every Visit; I = Initial Visit; R = Returning visits.

Environmental Variable	Measurement	Frequency
S Group	S1- All boli intact	E
	S2- Some boli intact	E
	S3- No boli intact but fecal material present	E
	S4- No fecal material	E
	S5- Nothing remains	E
Animal disturbance	Yes/No- new sign of disturbance from insects or larger animals	E
Mucous	Presence/ Absence	I
Darkness of dung pile	Straw Color	I
	Caramel	I
	Chocolate brown	I
	Nearly black	I
Number of Boli	Count	I
Circumference of three largest boli	Centimeters	I
Canopy Cover	Proportion of leaf cover over dung	I
Habitat Type	Forest	I
	Inundated areas	I
	Disturbed areas	I
Substrate	Dead leaves	I
	Dry soil	I
	Live Vegetation	I
	Mud	I
Presence of Fungi	Yes/ No	R

Remotely sensed imagery

We accessed satellite imagery that either directly measured or modeled environmental covariates previously reported or hypothesized to be important drivers of rates of dung decay, including canopy cover, humidity, insolation, precipitation, slope, temperature, vegetation complexity (NDVI), and cloud cover (Table 4.1; White 1995; Nchanji & Plumptre 2001; Barnes et al. 2006; Breuer & Hockemba 2007). We

preferentially selected publicly available layers with the highest coverage frequency and smallest pixel size. We recognize that not all the layers are strictly remotely sensed, and some layers, such as precipitation, are modeled. However, for cohesion and simplicity we are calling the layers and models remotely sensed. For data layers with low frequency of coverage for which data were not available during the time of dung pile observation, we first averaged values for the dates of dung observation from the previous five years. If there was still a lack of coverage, we averaged the previous five years of values one week before and after the dates of dung observation, and then two weeks before and after the dates of observation. If none of these time periods resulted in data, we finally used the yearly average for the locations of the observed dung piles. We obtained modeled daily precipitation from the CHIRPS database (Funk et al., 2015) and used it for both the remotely sensed dataset and the field dataset because daily precipitation was not recorded in the field.

Table 4.2: Remotely sensed layers used in dung decay analysis. Res = spatial resolution.

Layer	Data Source	Date Range	Res.	Measurement Used
Canopy Cover	GLCF/GLS_TCC	2000- 2010	30m^2	% of pixel covered by wood vegetation > 5m height
Cloud Cover	Global 1-km Cloud Cover	2000-2014	1km^2	Monthly cloud frequencies
Humidity	NASA/GLDAS/V021/ NOAH/G025/T3H	2000-Present	.25˚	Grams of water vapor/kg of air
Insolation	CSP/ERGo/1_0/Global/ SRTM_CHILI	2006-2011	90m^2	Integer representing warmer or colder based on topographic shading and evapotranspiration in early afternoon
Precipitation	CHIRPS	1981-Present	.05˚	Centimeters of rain (Interpolated)
NDVI	LANDSAT/LC08/C01/T1_SR	1999-	30m^2	(NIR-RED)/(NIR+RED)

	LANDSAT/LE07/C01/T1_SR	Present		
Slope	USGS/SRTMGL1_003	2000	30m^2	Radians
Temperature	MODIS/006/MYD11A1	2002-Present	1km^2	Celsius

Weibull survival model

Following previous studies (e.g., Barnes et al. 2006; Breuer & Hockemba 2007), we used survival analysis to model the time to disappearance of dung and assess the influence of different covariates on dung decay. To improve transparency and replicability (R. A. Fleming, 2001), we employed the fully parametric Weibull model as opposed to the previously used Cox-proportional hazards model. Cox-hazard models are non-parametric, make no assumptions about underlying distributions, and produce instantaneous hazards at different time steps (Cox & Oakes, 1984). However, reproduction and implementation of the model with new data is difficult as the underlying baseline survival function is undefined (Miladinovic et al., 2012). Weibull models describe hazard ratios and assess how covariates affect the relative increase or decrease of survival time (Pinder, Wiener, & Smith, 1978; Zhang, 2016).

We created three different model types of dung decay: 1) *field models*, using ground-truthed covariates and the remotely sensed values for precipitation; 2) *remote models*, using remotely sensed covariates; and, 3) the *combined model*, using ground-truthed and remotely sensed covariates from the best field and remote models. Within both the remote and field models, we separately tested eight different precipitation

variables previously shown to significantly influence dung decay: cumulative precipitation in the month of dung deposition, cumulative precipitation in the month of deposition plus the two months prior, cumulative precipitation in the two months prior to deposition, cumulative precipitation the month of deposition and the month following, cumulative rainfall for the first 30 days after deposition, mean daily rainfall for the first 30 days after deposition, number of consecutive days without rain from deposition, and proportion of dry days over thirty days (Barnes et al., 1997; Nchanji & Plumptre, 2001; L. J. T. White, 1995). For the combined model, we retained cumulative precipitation for the month of deposition and the following month as the measure of precipitation based on results of the field and remote models.

In addition to the above covariates, we also hypothesized that country and season would affect dung decay. We tested models incorporating season (measured as changes in sign of difference between pentad precipitation and mean annual precipitation; see Beirne et al., 2020) as a covariate, but they did not perform as well as creating separate seasonal models. Similarly, the Gabon and Congo studies included different field-collected covariates. We, therefore, partitioned our data by season and country, to examine these factors. For the *field models*, we separately assessed three data subsets: (1) all dung observations from Gabon, "Gabon"; (2) observations during Gabon's wet seasons, "Gabon Wet"; and, (3) observations during Gabon's dry seasons, "Gabon Dry". For the *remote models*, we separately assessed seven data subsets as

separate models: (1) Gabon and Congo datasets combined, "All"; (2-3) the combined dataset split into dry and rainy seasons, "All Wet" and "All Dry"; (4) the full Gabon dataset only, "Gabon"; (5) the full Congo dataset only, "Congo"; and (6-7) Gabon split into the dry and wet seasons, "Gabon Dry", "Gabon Wet". For the *combined model*, we included the covariates retained in the final field and remotely sensed models for the Gabon dataset. Because of the large number of covariates in the *combined model* (n = 14), we did not have a large enough sample size to test the seasonal models.

Survival models can incorporate incomplete data where the fate of the subject is unknown through censoring (Carroll, 2003). In the field, we could not always monitor dung piles to disappearance (S4); for example, not all dung piles disappeared by the termination of the study. In addition, whenever the interval between revisits of dung was more than two weeks, we censored the sample after the last consistent observation. However, Weibull models require complete covariate datasets (Therneau, 2020), so we only included data on dung piles for which we had values for all covariates. We could not extract precipitation data for 16 dung piles in Loango National Park because the raster layer did not cover their locations, and instead used precipitation data from the neighbor pixel less than 500m away.

We built and validated the survival models in two steps. First, we tested all combinations of covariates and retained the most supported combination of variables for each model (covariate selection). Second, we conducted a repeated k-fold cross

validation to (a) fine tune the coefficients and (b) validate the ability of the models to predict a withheld portion of our dataset (coefficient tuning and model validation).

Covariate selection

We implemented all models in the Survival package (Therneau, 2020) in the R statistical environment (R Core Team, 2020). To select the relevant covariates for each model type (field, remote, combined), we built a full model and conducted model selection with the MuMin package (Barton, 2019). Working in an information theoretic framework, we retained the model with the most support and reported the top model set: all models within a $\Delta AICc < 6$ of the most supported model (Richards et al. 2011). Additionally, to avoid over interpretation of covariates, we discounted any models that were more complex than the most supported model.

Coefficient tuning and model validation

To determine the optimal coefficients for variables in each of the most supported models (selected above), we used a repeated k-fold cross validation test with five blocks and 10 repeats. We iteratively withheld 20% of the data, fit a model to the remaining 80%, and then tested the ability of the model to predict the withheld data. During each iteration, we recorded the values of coefficients and calculated model accuracy as the percent root mean square error (pRMSE) between the observed dung decay time and the predicted decay time. Repeating this process 10 times for each model increased the precision of model estimates for dung survival. Finally, we retained the coefficients from

the model with the lowest pRMSE as the best-fitting coefficients (James et al., 2013). To

predict the mean decay time for the withheld data, we used the Weibull survival

equation, $S(t) = e^{-\left(\frac{t}{b}\right)^a}$, where t = time in days, a = shape, and b = scale. The scale

parameter is the linear combination of environmental covariates,

$b = e^{(\beta_0 + \beta_1 X_1 + \beta_2 X_2 \ldots + \beta_i X_i)}$, where β is the coefficient for the ith covariate, X. We also

recorded the median pRMSE (standard reporting; Xu et al. 2018), R^2, and model bias, the

difference between the observed and predicted means, to evaluate the fit of the models

(Table 4.3).

Population estimation from environmental variation

To assess the effect of failing to account for temporal and spatial variation in

dung decay rates, we simulated elephant population estimates under two different

scenarios: only temporal variation and only spatial variation. We chose four protected

areas within Gabon as example sites for the simulations: Ivindo, Minkébé, and

Moukalaba Doudou National Parks, and the Wonga Wongué Presidential Reserve. To

obtain the necessary covariate data, we created a lattice of at least 193 points separated

by 3.9-km for each of the protected areas and accessed the remote sensed variables

associated with these points for the year 2017. In the first scenario, we assessed the effect

of spatial variation by mimicking a survey conducted during a single season in each of

the four parks. We treated each point as a unique location representing no more than

0.1% of the entire park and compared the variance of dung decay and elephant density

estimates to those estimated by the park average. This represents biases highlighted in

Kuehl et al. (2007) that arise from collecting data in small or non-representative study

sites. In the second scenario, we assessed the effect of temporal variation by estimating

elephant densities from the same number of dung piles in the exact same locations at

two different time periods: the height of the dry season and the height of the wet season.

For both scenarios we used the Gabon seasonal remote models to estimate the dung

decay rate. We then estimated elephant density using the formula $\widehat{D}_a = \frac{\widehat{D}_s}{\hat{p} \, x \, \hat{t}}$, with a $\widehat{D}_s$

of 1,000 dung piles/km² and a $\hat{p}$ of 15.9 dung piles produced per day (Nchanji et al.,

2008).

Population reassessment for Minkébé National Park, Gabon

We obtained transect data from two surveys conducted in Minkébé National

Park, Gabon in 2004 and 2014 (Blake, 2005; Poulsen et al., 2017). Both surveys reported

and used dung decay rates from previous studies that suggested 90 days average decay

rate; Poulsen *et al.* (2017) also included results from a site-specific rainfall model. We

separately analyzed the transects based on the season they were walked and estimated

decay times with our relevant seasonal models. We then estimated average and

weighted average (based on number of dung piles per transect) decay times across the

study, and recalculated the population estimates for both surveys and the change in

population over the ten-year period.

Results

Field observations

We found and revisited 365 dung piles (Ivindo = 228, Loango = 77, and Wonga Wongué = 60), but ultimately retained only 222 dung piles for analysis (Ivindo = 149, Loango = 44, Wonga Wongué = 29). For dung that were not censored (n = 153), the average decay was 32 ± 17 days (mean ± SD; median = 30 days, range 1–74 days). Dry season dung decay averaged 30 days (median 33, range 9-74 days) and wet season dung decay averaged 35 days (median 33, range 1-74 days).

Survival models and validation

Model 1: Field models. For the Gabon dataset, we retained four models in the top model set (AICc < 6). The full model (best pRMSE = 38%) was the best supported and included the average number of seeds found in dung per month, canopy cover, precipitation measured as number of successive dry days after dung deposition, number of boli, proportion of animal visits, substrate, and habitat type (Figure 4.2A; Appendix A). Percent canopy cover had the strongest effect on the rate of decay, with each percent increase in cover increasing the rate (decreasing survival) of dung decay by 50%. Higher average number of seeds and larger proportion of animal visits also increased the rate of decay by 2% and 26%. The number of dry days and number of boli reduced decay rate (increased survival) by 1% and 4% respectively. Compared to dung deposited on dead leaves, decay of dung on dry soil and live vegetation was 100% and 14% slower,

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whereas decay of dung on mud was 42% faster. Compared to forest habitat, dung decay in human disturbed areas was 20% slower, whereas inundated habitat sped up the decay rate by 50%. With cross validation, the model predicted the dung decay of withheld data with a median error of 53%. The top model estimated a decay rate of 33 ± 11 days compared to the observed rate of 39 ± 17 days.

For the Gabon wet season and Gabon dry season datasets, 42 and 13 models, respectively, were in the top model sets (Figure 4.2A; Appendix A). The top wet season model (best pRMSE = 27%) predicted dung decay of the withheld data with a median error of 72% and a decay time of 31 ± 13 days, compared to the observed rate of 35 ± 18 days. The top dry season model (best pRMSE = 24%) predicted the dung decay of withheld data with a median error of 35% and a decay time of 31 ± 12 days compared to the observed rate of 33 ± 12 days.

Table 4.3: Assessment of model quality for field, remote, and combined models. Best pRMSE = percent root mean squared error of the best model from coefficient selection. All other columns report model validation: Median pRMSE = median pRMSE of model validation; R2 = coefficient of determination; Observed decay rate = observed mean number of days (and standard deviation) until dung disappeared for withheld data; Predicted decay rate = modeled mean number of days (and standard deviation) until dung decay for withheld data.

Model Type	Models	Best pRMSE	Median pRMSE	R²	Observed decay rate (SD)	Predicted decay rate (SD)
Field	Gabon	38%	53%	0.20	39 (17)	33 (11)
	Gabon Dry	24%	35%	0.56	33 (12)	31 (12)
	Gabon Wet	27%	72%	0.68	35 (18)	31 (13)
Remotely Sensed	All	50%	60%	0.41	41 (27)	36 (12)
	Gabon	33%	46%	0.39	39 (17)	33 (12)
	Congo	46%	68%	0.37	51 (30)	43 (15)
	Gabon Dry	16%	32%	0.79	31 (11)	31 (9)
	Gabon Wet	18%	53%	0.86	41 (20)	42 (20)
Full	Gabon	31%	45%	0.58	29 (14)	31 (13)

    Model 2: Remotely sensed model. For the Gabon model, a single model was retained (best pRMSE = 33%) including humidity, cumulative precipitation the month of deposition and the month following deposition, and temperature (Figure 4.2B; Appendix A). Increasing humidity and temperature increased the survival time of dung by 50% and 13%. Precipitation decreased survival by 2%. With cross validation, the model predicted dung decay of the withheld data with a median error of 46% and a decay time of 33 ± 12 days compared to the observed rate of 39 ± 17 days.

    For the Gabon wet season and dry season datasets, 116 and 20 models, respectively, were in the top model sets (Figure 4.2B; Appendix A). The top wet season model (best pRMSE = 18%) predicted the dung decay of the withheld data with a

median error of 53% and a decay time of 42 ± 20 days compared to the observed rate of

41 ± 20 days. The top dry season model (best pRMSE = 16%) predicted the dung decay of

withheld data with a median error of 32% and a decay time of 31 ± 9 days compared to

the observed rate of 31 ± 11 days. We report results from the Congo data in Supporting

Information 2 and 3.

Model 3: Combined Data Model. The top model set included 8 models. The top

model (best pRMSE = 31%) included canopy cover, humidity, precipitation measured as

the cumulative precipitation the month of deposition and the month following

deposition, number of boli, substrate, temperature, and habitat type, and excluded

average seed count and proportion of animal visits (Figure 4.2C, Appendix A). All

covariates follow the same trend of increasing or decreasing survival as the field and

remote model types (Appendix A). With cross validation, the model predicted the dung

decay of withheld data with a median error of 45% and a decay rate of 31 ± 13 days

compared to the observed rate of 29 ± 14 days.
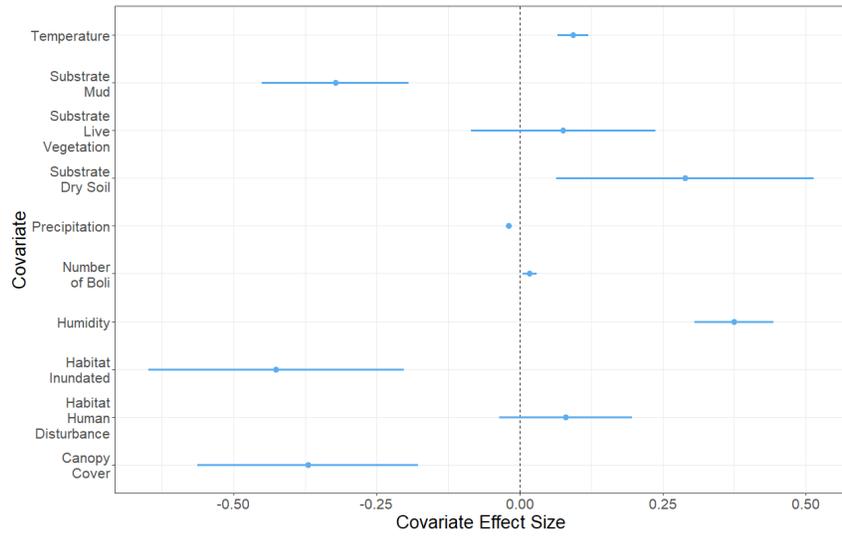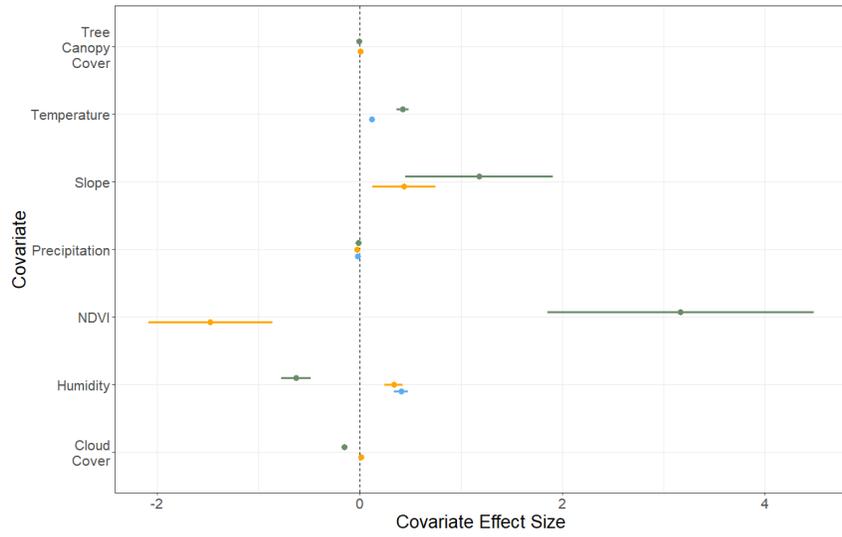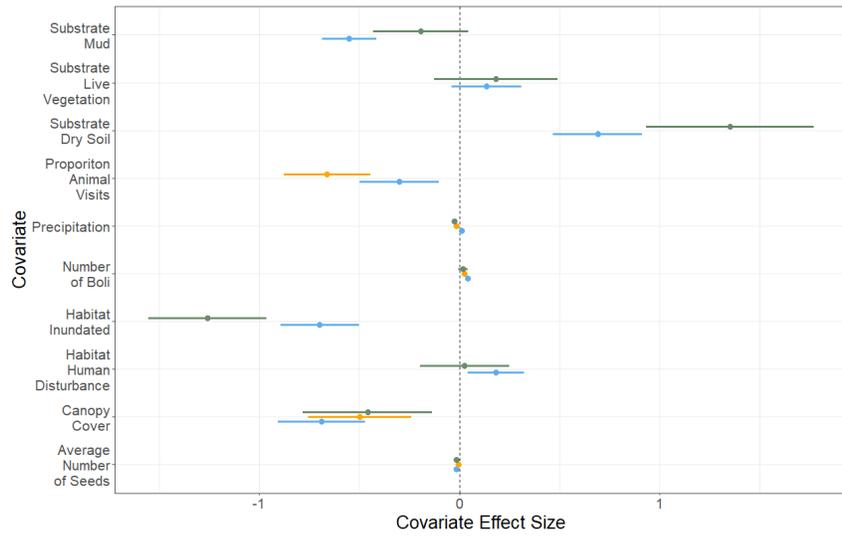
Figure 4.2: Effect size of covariates influencing dung decay. Field Models (A), Remote Models (B), Combined Model (C). Dots = point estimate of effect, line segments = standard errors. Blue = Gabon model, orange = Dry Season model, green = Wet Season model, none = covariate not significant. Precipitation variables differ by model: Gabon = number dry days following deposition; Dry Season = cumulative precipitation the month of deposition plus following month (cm); Wet Season = cumulative precipitation 30 days after deposition (cm). See Tables 4.1 & 4.2 for covariate details.

Population estimation from environmental variation

Failing to account for differences in environmental characteristics caused large variation in the estimated density of elephants (Figures 4.3B & 4.4B). In the spatial variation scenario, we estimated average survival for the protected areas and survival of all random locations (point estimates) within each park (Figure 4.3A): Ivindo National Park (mean = 53 days, range of point estimates = 40-74 days), Minkébé National Park (mean = 44 days, range of point estimates = 34-62 days), Moukalaba Doudou National Park (mean = 43 days, range of point estimates = 27-67 days), and Wonga Wongué Presidential Reserve (mean = 52 days, range of point estimates = 36-80 days). In the temporal variation scenario, we estimated dung degradation times of 53, 44, 43 and 52 days in the dry season and 45, 37, 15, and 26 days in the wet season for Ivindo, Minkébé and Moukalaba Doudou National Parks and the Wonga Wongué Presidential Reserve (Figure 4.4A). Excluding temporal variation resulted in up to a 6.9-fold change in estimated number of elephants.

Population reassessment for Minkébé National Park, Gabon

Using the weighted average of decay times on each transect, we estimated a

decay rate of 42.1 ± 1.4 days in 2014 and 40.5 ± 1.2 days in 2004 (Table 4.4; example R

code in Appendix B), less than half the value used by Poulsen *et al.* (2017). With these

decay rates, we estimated forest elephant population sizes of 73,006 in 2004 and 15,772

elephants in 2014 (unweighted estimates: 81,226 for 2004 and 15,514 for 2014). These

abundances are 214% (2004) and 222% (2014) higher than originally estimated.

Table 4.4: Estimated elephant population in Minkébé National Park under different dung decay scenarios. Grey shading highlights top model prediction for number of elephants with same defecation rate and modeled dung decay rate. Gabon = overall model used to average decay rate for all transects. Gabon Seasons = incorporated wet and dry seasonal models applying season-specific decay rates to transects walked by season. Gabon Seasons Weighted = "Gabon Seasons" weighted by the proportion of dung found per transect.

Year	Dataset	Defecation Rate	Decay Rate	Predicted abundance
		19	90	7,370
	Poulsen *et al.* (2017)	18.1	45.5	15,328
		18.1	55.6	12,543
2014	Gabon Seasons Weighted	19	42.1	15,772
	Gabon Seasons	19	42.8	15,514
	Gabon	18.1	37.6	18,537
	Gabon Seasons	18.1	42.8	16,285
		19	90	32,851
	Poulsen *et al.* (2017)	18.1	45.5	68,215
		18.1	55.6	55,819
2004	Gabon Seasons Weighted	19	40.5	73,006
	Gabon Seasons	19	36.4	81,229
	Gabon	18.1	66.3	46,814
	Gabon Seasons	18.1	36.4	85,268
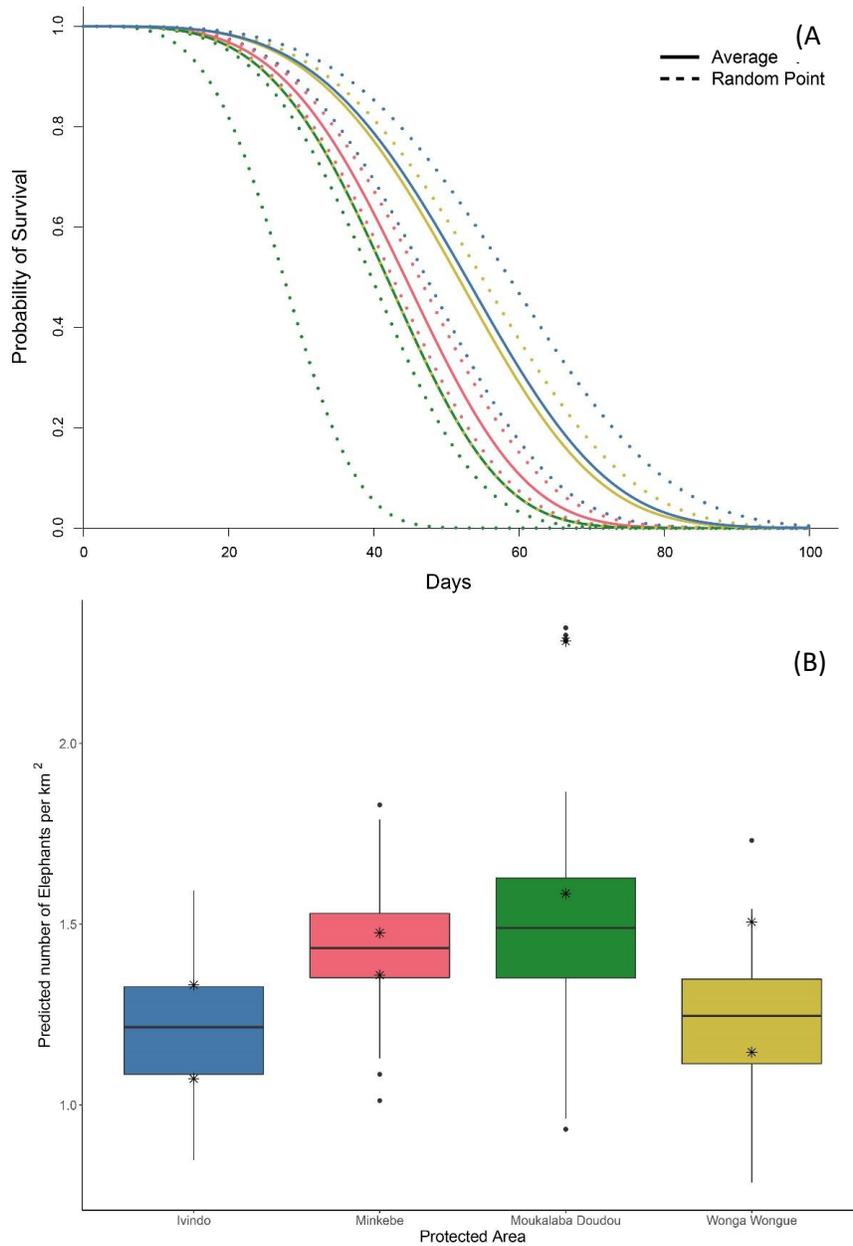
Figure 4.3: Effect of spatially heterogenous environmental variables. (A) Predicted dung survival curve from Gabon Remote Dry Season model for park average and two randomly selected locations within the park. (B) Boxplot including median and interquartile range of point estimates for number of elephants/km2 predicted using the Gabon Remote Dry Season model decay rates and 1,000 dung piles/km2. Dots = outliers, asterisks= estimated number of elephants from random points in (A). Site colors correspond in (A) and (B).
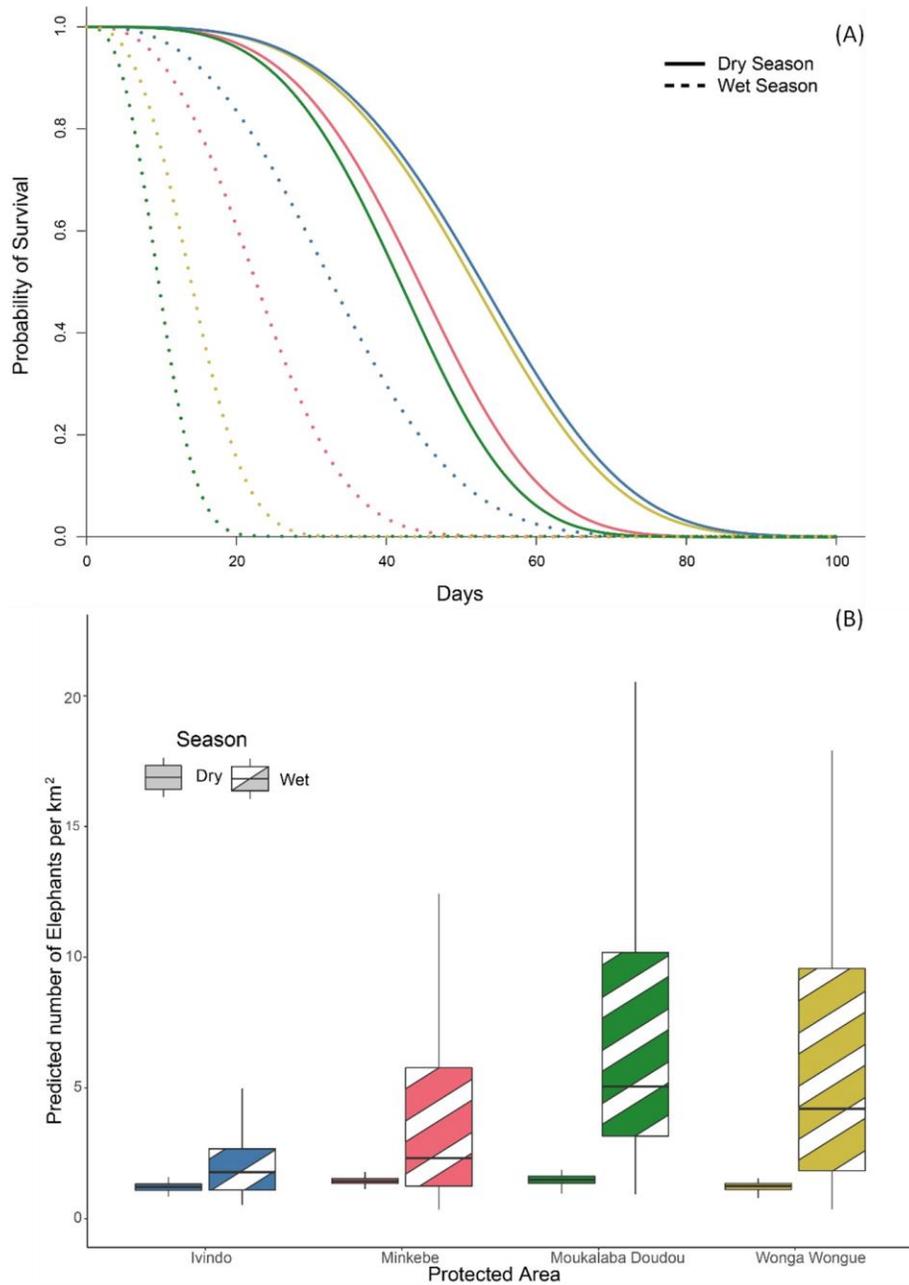
Figure 4.4: Effect of temporally heterogeneous environmental variables. (A) Predicted dung survival curve from Gabon Remotely Sensed Wet and Dry Season models for the average conditions in the rainy and dry seasons. (B) Boxplot including median and interquartile range of point estimates for number of elephants/km2 predicted using each seasonal model's dung decay rate and 1,000 dung piles/km2. Outliers have been excluded from graph; maximum value predicted: 76 elephants/km2 in Wonga Wongué from dung disappearing in one day. Site colors correspond in (A) and (B).

Discussion

Ideally, dung decay would be assessed in the field at the spatial scale and time of the survey to account for the multiple variables that influence the rate of decomposition. Doing so would account for much more nuance in decay rate that cannot be modeled with remotely sensed data – e.g., influence of animal disturbance and critical microhabitat features. However, this would be costly, time consuming, and logistically infeasible at the scale of most forest mammal transect surveys. Our results demonstrate that adaptive models incorporating remotely sensed variables to assess decay of animal sign are an alternative approach to using previously observed rates of sign decay. While we focused on forest elephants, these methods could improve indirect transect surveys for other difficult to observe species (e.g. deer, duikers, great apes; Koster & Hart, 1988; Rovero & Marshall, 2004) and could be applied to other types of degrading sign, such as ape nests (Stokes et al., 2010).

Our suite of models builds on efforts to improve the accuracy of estimating dung decay while reducing the cost of field observations. For the full Gabon dataset, the field, remote, and combined models accounted for 20%, 39%, and 58% of the variation in dung decay times. Seasonal models tended to perform better than combining data over seasons: seasonal remote models accounted for 79% (dry season) and 86% (wet season) of the variation, and seasonal field models accounted for 56% (dry season) and 68% (wet season) of the variation. Comparatively, previous dung decay models based on rainfall

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accounted for 56% and 69% of variation in the data (Barnes et al., 1997; Barnes & Dunn, 2002). The ability of the remote models to explain more of the variation than field models suggests that broad scale environmental conditions might be more important than microhabitat variables. Barnes *et al.* (2006) also demonstrated that variables measured at a broad scale (e.g., canopy cover) performed better than microhabitat variables (e.g., slope).

Despite the high pRMSE (range 32% - 72%), all models estimated a dung survival time within 17% (max 7 days) of the observed mean decay of the withheld datasets. This error is much lower than choosing from one of several previously published, but not spatiotemporally relevant values. For example, our study suggests that by using 90 days, Poulsen *et al.'s* (2017) decay time was 2.2 times longer than our environmentally estimated decay (40.5 vs 90 days). Additionally, compared to other techniques (e.g., retrospective dung decay surveys; Laing et al., 2003), our models do not require additional field observations and our results are not biased by return frequency, which potentially leads to overestimation of dung survival time. However, high pRMSE values suggest that model-based estimates of dung decay can be biased by small study areas or small numbers of transects. Increased environmental heterogeneity improved model averages and accounted for layers that have relatively large pixels (Table 4.2). Thus, our models are best suited for large-scale, regional or national level studies.

Of all models, seasonal field and remote models had the lowest error and explained the highest amount of variation in the data, greatly improving model predictive ability. Seasons in the tropics are defined by precipitation (Liebmann et al., 2007), which has been shown to strongly affect decay rates (Breuer & Hockemba, 2007). Despite unanimous agreement on the importance of precipitation, there is little agreement as to which measurement of precipitation best explains dung decay (Barnes & Dunn, 2002; Nchanji & Plumptre, 2001). In our study, we observed site- and model-dependent differences in rainfall variables that best explained dung decay. Of the eight precipitation variables tested, four received support under model selection, with cumulative precipitation the month of deposition and the following month most frequently retained, followed by cumulated precipitation in the 30 days after discovery. Rainfall in the 30 days after discovery was also the best predictor of dung decay in southwestern Cameroon, though cumulative rainfall during the deposition month and the following month was also statistically significant (Nchanji & Plumptre, 2001).

All the variables we tested, except for slope, were retained in most top models. Our study confirmed that canopy cover, habitat type, and the size of dung piles affect rates of dung decay (Nchanji & Plumptre, 2001; L. J. T. White, 1995), but also showed that previously untested variables – substrate type, seed abundance, and animal visitation – significantly influence decay rates. Contrary to Barnes et al., (2006), we found that increasing slope improved dung survival. This might be explained by the

scale of measurement: in our study the resolution was 30 m^2, whereas field-measured slope would be at the microhabitat level. Hilly areas likely aid dung survival because rain washes away rather than soaking the dung pile and accelerating decomposition. Overall, and in agreement with Breuer and Hockemba (2007), our results suggest that drier areas (e.g., open canopy) increase survival time, whereas wetter environments (e.g., muddy substrate, inundated forests, closed canopy) decrease survival time.

We demonstrate that ignoring spatial or temporal environmental heterogeneity can lead to gross over- or underestimation of elephant populations. In the four protected areas, assuming that dung decay in a single location represents the entire park resulted in density estimates that varied by 0.35-0.79 elephants/km^2. For the 9,973 km^2 Minkébé National Park, the observed difference of 0.43 elephants per km^2 underestimates the population by 4,988 elephants – about 5% of the estimated global forest elephant population (Maisels et al., 2013). Or, if the dung decay estimates from Ivindo were used in Minkébé, a seemingly reasonable assumption as the parks are only 65 km apart, elephant densities would be underestimated by 0.2 elephants/km^2 – about 2% of the global population.

Ignoring temporal variation biased elephant population estimates more than ignoring spatial variation. The high variability of temporally fluctuating factors (e.g., precipitation, humidity) may be, on average, more important than temporally static variables (e.g., NDVI, slope). In our dry versus wet seasons simulation, we estimated

elephant populations to be 1.8-6.9 times larger using rainy season decay rates compared to dry season rates (Figure 4.4B). Using decay rates from inappropriate seasons and/or sites risks substantially over- or underestimating abundance or, worse, risk inability to detect population change (Plumptre, 2000).

Recently, Poulsen *et al.* (2017) estimated a 78% decline in elephant abundance in Minkébé National Park, from 32,851-35,404 in 2004 to 6,483-7,370, based on a 90 day dung decay rate and a rainfall model (Barnes & Dunn, 2002). Our remotely sensed seasonal models estimated 73,006 elephants in 2004 and 15,772 in 2014, 2.1-2.4 times more elephants than estimated by the 90 day dung decay rate. We recommend weighting decay times by the abundance of dung on transects for both future field and model-based decay studies due to the heterogeneous and dynamic distribution of elephants (Beirne et al., 2020). Though Poulsen *et al.* (2017) purposefully used conservative decay rates, the estimated difference reinforces the need for study-specific dung decay rates (Hedges, 2012), whether modeled or observed *in-situ.* While representing the same devastating 78% loss of elephants, the larger population sizes provide more optimism for the future of forest elephants.

Within sites, we observed dung piles in relatively small areas (4-6 km^2) but increased environmental variation by observing dung in three widely separated parks. Small spatial distribution of dung samples is likely one of the reasons that predictions for Congo dung decay, on its own or combined with Gabon data (median pRMSE

ranged 52- 68%), were less accurate (Table 4. 3, Appendix A). The Congo dung

observations were on a 2.6 km trail (Breuer & Hockemba, 2007). The resolution of

remotely sensed layers varied from 30 m^2 - 28 km^2; thus, remotely sensed data were too

spatially coarse to capture environmental variation at the level of dung observations.

Remote sensing is rapidly evolving with improved quality, frequency, and accessibility

of imagery: decreasing pixel size is improving resolution of spatial variables (J. Zhang,

2010) and hyper-spectral imagery is enabling differentiation of finer spectral signatures

(Khan et al., 2018). Following this trend, environmental variables currently measure or

modeled at coarse scale (e.g., soil moisture) will be publicly available at finer scales and

over broader geographical areas in the future.

This is the first study to incorporate remotely sensed with field collected data,

reducing the need for costly field studies to obtain site-specific decay rates. However,

our models could be improved by increasing the spatial extent and duration of the field

dung decay observations and by incorporating untested habitats (e.g., savanna).

Incorporation of recent, unpublished dung observations from throughout the forest

elephant range (Maisels et al., 2013; Maisels & Strindberg, 2012) would likely drastically

improve future models. Additionally, increased sample size would enable us to test

seasonal combined models. These would likely perform better than the individual field

data or remotely sensed models as was observed with the Gabon field, remote and

combined models.

The use of remotely sensed data to predict sign decay times enables researchers to calculate spatially and temporally relevant decay rates when *in situ*, scale-relevant studies are not possible. Moreover, even as camera traps and other *in situ* sensors become more economical and practical for measuring animal populations, accurate sign decay estimates will be important for reevaluating past population estimates of forest species based on dung counts. Remotely sensed variables are typically available from 2000, making reassessment of numbers possible for the past two decades. Knowing population numbers is important for conservation of elephants and other keystone species, and our understanding of their effect on the environment (Poulsen et al., 2018). Accurate population estimates are the foundation of IUCN Red List assessments and CITES Appendix listings that document the global conservation status of species, raise awareness of their plight, and enable wildlife management decisions.

5. Conclusions

This dissertation combined genetic analysis of dung and satellite technology with novel computational methods to provide greater insights into forest elephant group dynamics and social interactions, and improve population monitoring methods. By effectively observing elephants across their home-range, I was able to expand on previous research conducted exclusively in baïs or savannas in forest clearings, providing a more generalized understanding of forest elephant behavior across complex landscapes. In the first research chapter, I showed that forest elephants consistently displayed fission-fusion behavior regardless of habitat or presence in social arenas. I further demonstrated that fruit resource availability and, to a lesser degree, human disturbance influence forest elephant group size. In the second research chapter, I showed that social factors (i.e., number of mutual associations and sex composition), but not environmental factors (e.g., preferred resource availability and human disturbance), were associated with increased probability that two forest elephants interact. I also described the surprising phenomenon that male forest elephants are more social than expected from previous observations of solitary males entering baïs and the group segregation based on sex observed in Asian and savanna elephants (Chiyo et al., 2011; Keerthipriya et al., 2018; Turkalo et al., 2013). This dissertation described aspects of fission-fusion behavior and group composition unique to forest elephants among the

elephantids and furthered our understanding of the ecological constraints on fission-fusion systems and how the environment drives social group composition.

Complementing the more theoretical nature of the first two chapters, the third chapter was highly applied to forest elephant management. I improved upon traditional line transects with distance sampling for indirect sign (e.g., dung) by addressing a key assumption relating to the rate of sign decay. I developed a suite of Weibull survival models to adaptively predict dung decay rates for new and historical studies in the region. The models incorporated field or remotely sensed variables, enabling researchers to calculate spatially and temporally relevant decay rates when *in situ*, scale-relevant studies are not possible and provide an ecological context essential for accurate surveys. While forest elephants were the focus of this study, the combination of remote sensing data and flexible Weibull models to determine sign decay can be developed for any elusive tropical forest species that leave distinctive sign.

Rigorous, evidence-based approaches are necessary for the development and effective implementation of sustainable conservation strategies. While the first two chapters are heavily focused on the social behavior and ecology of forest elephants, the results can be adapted to mitigate human elephant conflict and inform anti-poaching or translocation strategies. The resource availability and human disturbance factors known to influence elephant group size can be mapped seasonally to predict likely hotspots of human-elephant conflict. Determining areas of increased potential human contact with

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large elephant groups could inform antipoaching strategies, indicating areas where elephants are at risk or where negative interactions with farmers can be better mitigated. In these ways, insights into forest elephant fission-fusion dynamics can be highly informative for forest elephant management. Additionally, studies have shown that species in sub-optimal groups are stressed, with individuals displaying higher levels of glucocorticoids (Markham et al., 2015; Pride, 2005). As potential habitat is dwindling, more and more elephants are coming into contact with humans and becoming "problem animals" that need to be translocated. Translocation efforts for elephants may be more successful in the future if actors take into account forest elephant social dimensions, like group size and composition, to promote individual health and integration. Understanding the ecological and social factors that underpin animal societies is now more important than ever as we are faced with the determining the consequences of human disturbance on animal behavior and how to preserve wildlife.

Epilogue

After years of studying pandas, George Schaller wrote the following imaginary monolog from a panda:

> *"Honorable scientists: I want to compliment you on your effort to study my kind. It takes dedication of the highest order to measure so many droppings. Day after day you follow my tracks with admirable persistence if not technique: I can hear and smell you from far away. Actually, I'm not certain what you expect to gain from invading my privacy. You generate numbing statistics about the number of stems I eat in a day and the number of hours I sleep… it merely shows that you have discovered some easy facts about me; most aspects of my life cannot be written in the language of mathematics. How can you understand me? We may seem to share certain moods, but you cannot*

comprehend mine. After all, it's not your perception that really matters… Another point: you study my diet, you study how many times I sent mark, and mate, and how far I travel. Remember, you cannot divide me into independent fragments of existence. At best you might perceive an approximation of a panda, not the reality of one. I am, like any other being, infinite in complexity, invisible, a harmonious whole… we shall always remain of two worlds. Humans can never know the truth about pandas. Therefore, enjoy the mystery - and help us endure."

Schaller's panda entertainingly argues that we can never know the true essence of an animal and poignantly points out our bias as scientists. Through intensive field and lab work, I have been afforded a glimpse into forest elephant social behavior across a variety of habitats in Gabon. I recognize my bias not only as a human asking questions of animal sociality, but also as a privileged western researcher working in Central Africa. As I continue in my career as a researcher, I hope to reduce my biases and promote equity and capacity in the field of tropical ecology. While forest elephant life cannot be written into the language of mathematics, hopefully the statistical models created here will contribute to helping forest elephants endure, for I have greatly enjoyed the mystery of studying them.

Appendix A: Chapter 4 Model Coefficients

Table A.1: Coefficients for the field model. Precip. Variable = precipitation variable retained in final model (Dry Days = Number of consecutive dry days after deposition, Month + MF1 = cumulative precipitation the month of deposition and the month following deposition in cm, and Cumulative 30 days = cumulative rainfall in the 30 days following deposition in cm); Int = intercept; Ave Seed = average number of seeds in a dung pile per month; Canopy Cover measured as proportion of cells in densiometer covered by leaves; Precip = precipitation; No. Boli = number of boli in a dung pile; Prop. Anim. Visits = proportion of animal visits over life of dung; Live Veg. = live vegetation; Human Dist. = Human disturbance; Inun. = inundated; Scale = shape parameter in Weibull survival equation. Negative coefficients decrease survival time and positive coefficients increase survival time.

| Model | Precip. Variable | Int. | Ave. Seed | Canopy Cover | Precip. | No. Boli | Prop. Anim. Visits | Substrate | | | Habitat Type | | Scale |
								Dry Soil	Live Veg.	Mud	Human Dist.	Inun.	
Gabon	Dry Days	4.288	-0.017	-0.688	0.011	0.041	-0.301	0.691	0.134	-0.551	0.183	-0.698	0.402
Dry Season	Month +MF1	4.322	-0.007	-0.499	-0.015	0.025	-0.662						0.327
Wet Season	Cumulative 30 days	4.796	-0.017	-0.459	-0.026	0.018		1.351	0.181	-0.193	0.026	-1.259	0.432

Table A.2: Coefficients for the remote models. Precip. Variable = precipitation variable retained in final model (Month + MF1 = cumulative precipitation the month of deposition and the month following deposition in cm, Cumulative 30 days = cumulative rainfall in the 30 days following deposition in cm, and MP1 + MP2 = cumulative rainfall in the two months prior to the month of deposition in cm); Int = intercept; Canopy Cover = Percent of each pixel covered by wood vegetation greater than 5m high; Cloud Cover = monthly average frequency of cloud cover; Hum = humidity as g of water vapor/ kg of air; NDVI = normalized difference vegetation index; Precip = precipitation; Slope = slope in radians; Temp. = temperature in degrees Celsius. Scale = shape parameter in Weibull survival equation. Negative coefficients decrease survival time and positive coefficients increase survival time.

Dataset	Precip. Variable	Int.	Canopy Cover	Cloud Cover	Hum.	NDVI	Precip.	Slope	Temp.	Scale
All	Month +MF1	2.133		-0.029	0.223	-0.519	-0.019		0.042	0.496
Gabon	Month +MF1	-5.676			0.407		-0.023		0.120	0.399
Congo	Month +MF1	3.543		-0.046	0.286		-0.029			0.541
All Dry Season	Month +MF1	0.494	0.018		0.186	-2.820	-0.020		0.058	0.385
All Wet Season	Cumulative 30 days	0.423	-0.008		0.289		-0.054			0.562
Gabon Dry Season	Month +MF1	-1.681	0.007	0.013	0.335	-1.477	-0.026	0.438		0.259
Gabon Wet Season	MP1 + MP2	12.612	-0.007	-0.155	-0.630	3.170	-0.014	1.179	0.423	0.364

Table A.3: Coefficients for the combined model. Int = intercept; Canopy Cover = canopy cover measured as proportion of cells in densiometer covered by leaves; Hum = humidity as g of water vapor/ kg of air; Precip. Month + MF1 = cumulative precipitation the month of deposition and the month following deposition in cm; No. Boli = number of boli per dung pile Temp. = temperature in degrees celsius; Live Veg. = live vegetation; Inun. = inundated; Scale = shape parameter in Weibull survival equation. Negative coefficients decrease survival time and positive coefficients increase survival time.

| Int. | Canopy Cover | Hum. | Precip. Month + MF1 | No. Boli | Temp. | Substrate | | | Habitat Type | | Scale |
						Dry Soil	Live Veg.	Mud	Human Dist.	Inun.	
-4.255	-0.370	0.375	-0.019	0.017	0.093	0.289	0.076	-0.322	0.080	-0.426	0.354

Appendix B: Chapter 4 Example Code

```
# required packages
library(tidyverse)

# Building an example dataframe, includes columns for any model subset, value mean & sd from observed
Gabon data
set.seed(123)
ex.dat<- data.frame(ID = c(1:10),
            ave.seed = c(rpois(10, 26)),
            canopy.cover.field = c(0.87, 0.94, 0.87, 0.89, 0.93, 0.83, 0.88, 0.86, 0.92, 0.82),
            number.boli = c(rnorm(10, 5.761261, 3.463022)),
            prop.animal.visits = c(0.13, 0.18, 0.08, 0.28, 0.17, 0.21, 0.13, 0.18, 0.12, 0.17),
            substrate = c(rep(c("live.vegetation","mud","dry.soil", "dead.leaves"), each = 2), "dead.leaves",
"dead.leaves"),
            habitat.type = c(rep(c("forest", "inundated", "human.zone"), times =3), "forest"),
            canopy.cover.RS = c(rnorm(10, 50.09009, 12.06997)),
            cloud.cover = c(rnorm(10, 82.20584, 5.820789)),
            humidity = c(rnorm(10, 16.09993, 1.072978)),
            ndvi = c(rnorm(10, 0.7463306, 0.05617946)),
            slope = c(rnorm(10, mean = 0.124,sd = 0.094)),
            temperature = c(rnorm(10, 28.24151, 1.812022)),
            ppt.m.mf1 = c(runif(10, 0, 91)),
            ppt.cum.30 = c(runif(10, 0, 48)),
            ppt.mp1.mp2 = c(runif(10, 0, 87)),
            ppt.dry.days = c(runif(10, 0, 76)))%>%
  mutate_if(is.factor, as.character)


# Creates a dataframe with coefficients from the Gabon model in table in S3.2. User can incorporate
coefficients from desired model subset. If using a different model match the following naming
conventions:
coefs<- data.frame(Intercept = -5.676, humidity = 0.407, temperature = 0.120, Precip = -0.023, Scale =
0.399, ppt.measure = "ppt.m.mf1")%>%
  mutate_if(is.factor, as.character)

# Function whose output saves the ID of the dung pile and predicted number of days for decay.
PredRS<- function(dat, coefs){
 # 1) a = Shape
 a<- 1/ coefs$Scale

 # 2) Categorical Variables
 dat$dry.soil<- ifelse(dat$substrate == "dry.soil", 1, 0)
 dat$live.vegetation<- ifelse(dat$substrate == "live.vegetation", 1, 0)
 dat$mud<- ifelse(dat$substrate == "mud", 1, 0)
 dat$inundated<- ifelse(dat$habitat.type == "inundated", 1, 0)
 dat$human.zone<- ifelse(dat$habitat.type == "human.zone", 1, 0)
```

```
# 3) b = Scale: create e^(x*beta) w. intercept
dat<- dat%>%
  dplyr::rename(ppt = noquote(coefs$ppt.measure))
covs<- names(coefs)

for (n in 1:nrow(dat)){
  dat$b[n]<- exp((coefs$Intercept)+
          ifelse("ave.seed" %in% covs, coefs$ave.seed*dat$ave.seed[n],0) +
          ifelse("canopy.cover.field" %in% covs, coefs$canopy.cover.field*dat$canopy.cover.field[n],0)
+
          ifelse("prop.animal.visits" %in% covs, coefs$prop.animal.visits*dat$prop.animal.visits[n],0) +
          ifelse("number.boli" %in% covs, coefs$number.boli*dat$number.boli[n],0) +
          ifelse("dry.soil" %in% covs & dat$dry.soil[n] ==1, coefs$dry.soil*dat$dry.soil[n],0) +
          ifelse("live.vegetation" %in% covs & dat$live.vegetation[n] ==1,
coefs$live.vegetation*dat$live.vegetation[n], 0)+
          ifelse("mud" %in% covs & dat$mud[n] ==1, coefs$mud*dat$mud[n], 0)+
          ifelse("human.zone" %in% covs & dat$human.zone[n] ==1,
coefs$human.zone*dat$human.zone[n], 0)+
          ifelse("inundated" %in% covs & dat$inundated[n] ==1, coefs$inundated*dat$inundated[n],
0)+
          ifelse("cloud.cover" %in% covs, coefs$cloud.cover* dat$cloud.cover[n], 0) +
          ifelse("humidity" %in% covs, coefs$humidity* dat$humidity[n], 0)+
          ifelse("ndvi" %in% covs, coefs$ndvi* dat$ndvi[n], 0)+
          ifelse("slope" %in% covs, coefs$slope* dat$slope[n], 0)+
          ifelse("canopy.cover.RS" %in% covs, coefs$canopy.cover.RS* dat$canopy.cover.RS[n], 0)+
          ifelse("temperature" %in% covs, coefs$temperature* dat$temperature[n], 0)+
          ifelse("Precip" %in% covs, coefs$Precip*dat$ppt[n], 0))
}
# 4) Calculates survival in days based on : S(t) = exp(-(t/b)^a) ==> t = (-log(S(t))^(1/a))*b
dat$days<- dat$b*((-log(.5))^(1/a))

# 5) save output select ID and number of days
datresults<- dat%>% dplyr::select(ID, days)
}

# Prediction results
Prediction<- PredRS(ex.dat, coefs)
```

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Biography

      Amelia C. Meier discovered the field of conservation biology through the San

Diego Zoo Safari Park's Conservation Corps as a freshman in high school. In 2012,

Amelia received her B.A. in Integrative Biology, graduating with high distinction from

the University of California Berkeley. While at Berkeley, she conducted her first field

research projects during a study abroad program in Costa Rica. Armed with the desire

to explore field-based animal behavior research, Amelia worked for the Max-Planck

Institute for Evolutionary Anthropology. Based first in Cote d'Ivoire and then the

Republic of Congo, she studied chimpanzee behavior and the biological anthropology of

the Ba'Aka forest peoples. Amelia began her PhD at Duke University in 2015. She is the

grateful recipient of several grants, fellowships, and academic awards. She was awarded

the National Science Foundation's Graduate Research Fellowship, the James B. Duke

International Research Travel Fellowship, and funding from International Elephant

Foundation's African Elephant Conservation Fund, National Geographic Society's Early

Careers Grant, Cleveland Metroparks Zoo's Africa Seed Grant, Riverbanks Zoo and

Garden's Satch Krantz Conservation Fund, the Animal Behavior Society's Student

Research Grant, the Elephant Managers Association's Small Grant, IDEA WILD, Duke

University's Center for International and Global Studies Graduate Award for Research

and Training four years consecutively, and Duke University's Office of Interdisciplinary

Studies' Graduate Research and Training Enhancement Grant, the Nicholas PhD

Advisory Council Small Grant, the Duke Network Analysis Center, the Duke

International Dissertation Travel Award, and the Office of the Vice Provost for

Interdisciplinary Studies. Amelia was nominated as a Preparing Future Faculty Fellow

and received a Certificate in Collage Teaching and Certificate in Geospatial Analysis

from Duke University.

Publications:

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