A greeting in disguise: Investigating cryptic series of low-frequency vocalizations from the African forest elephant (*Loxodonta cyclotis*)

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Abstract

The social behavior of the African forest elephant (*Loxodonta cyclotis)* still largely remains a mystery. While direct observation of these elephants at forest clearings has offered some insights into their social behaviors, elephants visit clearings infrequently and little is known about their social behavior in the forest. This thesis examines whether we can extract meaningful information about social interactions in the forest by way of passive acoustic monitoring, a reliable method for recording low-frequency elephant vocalizations, or 'rumbles' in a variety of environments. My goal was to locate clusters of rumble vocalizations that might indicate social interaction called 'rumble bouts' in order to 1) determine which environmental factors may predict the distribution of rumble bouts in space and time, and 2) attempt to classify rumble bouts based on their temporal acoustic features. To answer these questions, I analyzed the acoustic features of rumbles sampled over 3963 unique site-date combinations from an ongoing acoustic survey in northern Congo. I found that 1) rumble bouts were 1.69 times more likely to occur in the wet season than the dry season but their frequency was unaffected by habitat type or human activities, and 2) rumble bouts can be reliably grouped into two clusters by the same unique temporal features of social rumble exchanges described in other studies. Further research into additional environmental factors other than season, habitat, and logging status that better predict elephant aggregation and consequently social rumble exchanges may reveal more effective strategies for environmental planning and conservation of forest elephants.

Acknowledgements

I would like to express my deep gratitude to Dr. Peter Wrege and Dr. Daniela Hedwig for providing me with the opportunity to pursue this fulfilling work and guiding me through this process. Dr. Wrege, your provision of a space to ask questions, express my own creativity, and remain curious about what else we might learn from these amazing creatures continues to inspire me. Dr. Hedwig, your consistent willingness to offer support and resources and give your time so generously has been very much appreciated.

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Introduction

The forest elephant, *Loxodonta cyclotis,* lives in various pockets of dense forests, swamps, and streams in sub-Saharan Africa (Blake, 2002, *Table 2.1*). The forest elephant is genetically, ecologically and morphologically distinct from the savannah elephant, *Loxodonta africana*, with whom it shares the continent (Roca et al., 2001, Grubb et al., 2000, Blake, 2002). Forest elephants play an important role in maintaining the forests they dwell in, and occupy a unique ecological niche (Blake et al., 2009, Maisels et al., 2002). Despite their role in increasing plant species diversity by propagating seeds, promoting new growth by consuming herbaceous plants, and in some cases shaping the forest by forming wide trails, recent surveys have revealed that the forest elephant population is declining at an alarming rate due to poaching and habitat loss (Blake et al., 2009, Inogwabini et al., 2013, Turkalo et al., 2017, Poulsen et al., 2017).

The elusive nature of these elephants has led to innovations in camera trapping techniques, acoustic monitoring methods, aerial videography, and dung transects to obtain a better understanding of their ecological role and endangerment status (Wrege et al., 2017, Maisels et al., 2002, Head et al., 2012, Barnes, 1996 Michelmore et al., 1994). Passive acoustic monitoring in particular has emerged as a cost-efficient, consistent, unbiased, non-invasive method for discovering information about animals in their natural habitats (Wrege et al., 2012, Astaras et al., 2017). Passive acoustic monitoring consists of the placement of audio recorders in the desired subjects' environment. In absence of a visual cue for distinguishing the activities of elephants in dense forests, acoustic features of elephant vocalizations are often used to analyze and describe elephant behavior. To do this, scientists employ software that generates spectrograms—visual representations of sound. Using this software, researchers can dissect features of these vocalizations and analyze them based on their acoustic characteristics such as duration, amplitude, and frequency.

Forest elephants use their large vocal tract and uniquely shaped trunk to generate an expansive variety of vocal repertoire for communicating with other elephants (Soltis, 2010). Across all elephant species the most frequently used call is the “rumble”, a low-frequency vocalization used to convey information to another elephant (conspecific) (Langbauer et al., 1991, Poole et al., 1988). While the elephant rumble has proven useful in tracking these elephants, the question still exists as to whether this call can be used to discern any other information about their social interactions. Researchers have recently made advances in understanding the vocal repertoire of the forest elephant (Hedwig et al., 2019), the attenuation of the forest elephant rumble (Hedwig et al., 2018), and social behavior at forest clearings (Turkalo et al., 2013), however there is a lack of information regarding how forest elephants use their rumbles to communicate with conspecifics in the forest.

The goal of this project is to bridge the gap in understanding forest elephant rumble exchanges by using acoustic information extracted from spectrograms. There are three ways in which I will explore this topic. My first focus is to establish criteria for identifying social rumble exchanges from the sound stream alone. My second focus is to gather information about the recording sites themselves to discover which environmental features may predict the occurrence of these rumble exchanges. My third focus is to group these rumble exchanges based on their acoustic characteristics and compare my findings to previous social interaction studies conducted in the field. Ultimately, my goal is to expand the current understanding of how to interpret acoustic information about these rumbles, and in doing so, to establish methods for decoding the elusive social life of the forest elephant.

Review of the Literature

Forest Elephant Ecology

Habitat Use

As large herbivores, forest elephants play an important role in shaping the forest ecosystem by consuming large amounts of vegetation and fruits, dispersing seeds (Blake et al., 2009), and forming wide trails with their large, heavy bodies (Inogwabini et al., 2013). In contrast to the closed-canopy forest where direct observation is limited, forest clearings have facilitated an intimate look into the social behavior of forest elephants (Turkalo and Fay, 1995, Turkalo et al., 2013). It is hypothesized that forest elephants visit these forest clearings, known colloquially as bais, to seek out mineral springs and herbaceous plants (Turkalo and Fay, 1995, Blake, 2002, Sienne, 2014). While most information about elephant movement and diet within the forest has been uncovered through dung transects, camera traps have also revealed that the voracious consumption of fruits by forest elephants leads to competitive exclusion of other species, such as chimpanzee and gorilla (Barnes, 1996, Head et al., 2012).

Group Size

Forest elephants exhibit an average group size of 2.36 elephants; the group typically consists of a mother with one or two dependent offspring, a much smaller group size than that of the savannah elephant (Turkalo et al., 2013, Wittemeyer and Getz, 2007). Other species of elephants exhibit a fission-fusion social structure where individuals form and disband groups in response to environmental factors such as predation and resource availability. Turkalo and Fay (1995) were the first to hypothesize that the consistently patchy distribution of food sources in the forest contributes to the small group size of the forest elephant across seasons. This hypothesis has been supported by recent reports from Turkalo et al. (2013) that document no significant difference in forest elephant group size in the wet or dry season. Fay and Agnagna (1991) have reported that humans remain the main predators of the forest elephant, limiting the need for grouping in response to the threat of predation. These reports regarding forest elephant group size as it relates to ecological competition help to substantiate Turkalo and Fay's (1995) argument that forest elephants do not experience the same amount of fission-fusion as savannah elephants due to consistent levels of increased competition for resources in the forest environment. One of these competitive resources may be seasonal fruit availability (White, 1994a, White, 1994b). White (1994a) has shown that the patchy availability of fruiting trees in the forest corresponds to fluctuations in elephant movement. This study shows how differences in the limited availability of these trees across season can predict forest elephant movement while keeping overall group size low (White, 1994a). While it is generally accepted that these small group sizes reflect the relatively resource-limited environment of the forest elephant, there is still little information about forest elephant aggregation in the dense forest and how these animals might exhibit fission-fusion patterns in their social relationships.

Anthropogenic Pressure

Human activity has led to significant changes in elephant activity, as elephants avoid anthropogenic spaces and become more nocturnal (Blake et al., 2007, Wrege at al., 2012). Researchers have generally reported a low amount of predation against forest elephants other than that sourced from their primary predator: humans (Blake and Inkamba-Nkulu, 2004, Fay and Agnagna, 1991). Ivory poaching has devastated the forest elephant population, with a decline of 78-81% estimated in the population size between 2004 and 2014 (Poulsen et al., 2017). Despite recent efforts to conserve the species, thousands of forest elephants are poached every year (Poulsen et al., 2017). As a result of human hunting pressures, elephants seem to avoid anthropogenic spaces such as roads (Blake et al., 2007) and sites set aside by the local government to allow for the logging of trees, better known as logging concessions (Maisels et al., 2002). Aerial videography reports have shown that forest elephants tend to avoid logging concessions, abandoning nearby forest clearings and reestablishing themselves in protected areas such as national parks (Maisels et al., 2002). While older logging sites may provide attractive new plant growth for forest elephants, there is little data about how elephants respond to these post-anthropogenic spaces.

Bioacoustic Methods in Forest Elephant Conservation

To circumvent the challenges of observing forest elephants directly in their dense rainforest habitat, modern work in forest elephant research uses passive acoustic monitoring (PAM) to track ecologically and behaviorally relevant information for conservation planning in various protected areas (Astaras et al., 2017). PAM has proven to be a useful method for estimating population sizes, identifying locations and hours with high elephant activity (activity cycles), and measuring anthropogenic pressures while remaining non-invasive and cost-effective (Wrege et al., 2017).

How is this done?

Passive acoustic monitoring uses acoustic recording units systematically installed at various sites throughout a desired area (Wrege et al., 2012, Wrege et al., 2017, Thompson et al., 2009). Elephant vocalizations from these recordings are counted at different sites, dates, and locations (Wrege et al., 2017). These counts yield information about elephant movement and behavior that can be incorporated into conservation planning. For example, Wrege et al. (2010) used PAM to observe change in forest elephant activity cycles in response to local oil exploration. Finding that the local elephant population size remained consistent, but that elephants were becoming more nocturnal, this study expanded our understanding of how forest elephants respond to anthropogenic activity. Studies like these open the door for more specific applications of using acoustic cues to determine temporal and spatial elephant movement patterns within a population.

What is an elephant rumble?

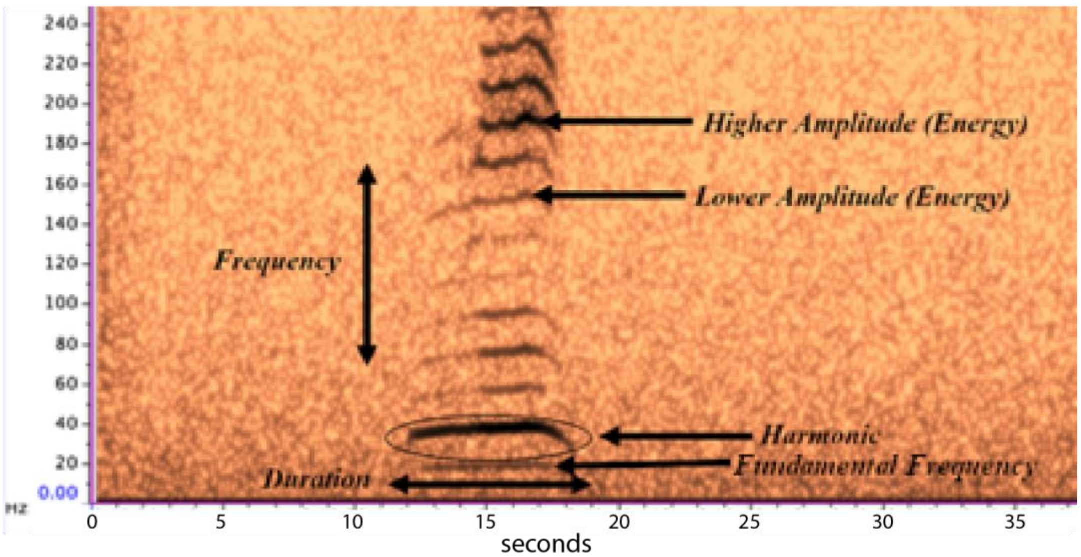


Figure 1: A spectrogram showing an elephant rumble with common acoustic measurements. Darker shades indicate higher energy and grey shades indicate lower energy. The x-axis represents time (1-second ticks). The y-axis represents frequency(10-*Hz* ticks). The lighter shaded areas surrounding the elephant rumble represent background noise according to these three measurements. [Image Description]

While forest elephants have an expansive repertoire of vocalizations for communicating with conspecifics, the vocalization typically used for acoustic monitoring is the elephant 'rumble' (*Figure 1*). These infrasonic rumbles have distinct acoustic signatures resulting from the elephant's large vocal tract and uniquely shaped trunk (Soltis, 2010). Sound analysis software is used to investigate acoustic features such as duration, amplitude, and frequency. Amplitude, measured as "energy" (Soltis et al., 2005b, Wrege et al., 2017), refers to the strength or loudness of the sound, and is often measured in decibels. Frequency, typically measured in Hertz (*Hz*), refers to the pitch of the sound. The fundamental frequency is the lowest discernable base frequency of these tonal vocalizations. While the fundamental frequency of these rumbles is negatively associated with body size and may be useful for assessing age and sex ratios of forest elephant groups (Thompson, 2009, Wrege et al., 2012), this frequency is unlikely to provide specific enough information for researchers to identify individual elephants. At higher frequencies above the fundamental, elephant rumbles have distinct harmonics or acoustic multiples of the fundamental frequency. These harmonics can have more or less energy, potentially allowing elephants to encode different information for the intended recipient of the rumble. Any variation in the pitch across the duration of the fundamental frequency is described as frequency modulation. Elephant rumbles can be modulated or unmodulated, a characteristic that may reflect the animal's level of arousal (Soltis et al., 2009). The elephant rumble is hypothesized to communicate important information such as identity, social status, location, mating availability, and distress through these acoustic features, however most investigation into the social role of these sounds is based on studies of savannah elephants (Poole, 2011, Soltis, 2013, Soltis et al., 2005a).

Why is this useful?

Passive acoustic monitoring helps to circumvent the inaccessibility of information outside of the forest clearing. While direct observation is useful, this method is nearly restricted to the highly specific context of forest clearings. Dung transects are the most common method for gathering information about forest elephants and use counts of dung piles across one or more sites to estimate population sizes (Barnes, 1996). Dung transects have provided a wealth of information regarding forest elephant distribution and population size; however transects are expensive and aggregate information over relatively long time periods (Blake and Inkamba-Nkulu, 2004, Inogwabini et al., 2013, Barnes, 1996, Buij et al., 2007, Michelmore et al., 1994). Camera traps have proven useful in monitoring population distribution and habitat use throughout the forest but can also be expensive for the limited survey of activity afforded by their stationary design (Gessner et al., 2014, Head et al., 2012). While these methods are not mutually exclusive, PAM circumvents the potential bias of these methods by collecting acoustic information about forest elephants from otherwise inaccessible and disregarded areas of the forest. This method is also non-invasive and does not require expensive technology to track elephant movements. While using PAM for conservation remains a continuous, non-invasive, cost effective, unbiased method for obtaining dynamic demographic information, the goal of the analysis reported in this thesis is to expand its use to obtain behavioral information about the social life of the forest elephant.

Bioacoustic Research: Savannah Elephant Rumbles

Most research regarding the social structure and acoustic communication system of African elephants comes from studies of the savannah elephant. While differences in group size, bai behavior, morphology, range, and ecology encourage separate study into forest elephant social structure, broad similarities in vocalization structure and social behavior between the African species suggest that models based on savannah elephant studies are a good starting point for investigations of forest elephants (Turkalo et al., 2013, Soltis, 2010, Hedwig et al., 2018, Danquah and Oppong, 2014).

Function of the Elephant Rumble

The elephant rumble serves an important role in allowing savannah elephants to maintain their social relationships. Katy Payne and colleagues (Payne et al., 1986) were the first to document savannah elephants' usage of infrasonic calls, and several studies have since established a 'contact call' function for rumbles, that they might be used to identify as well as locate individuals (Leighty et al., 2008, Langbauer et al., 1991, Poole, 1999). Multiple experiments show that elephants tend to get closer to known elephants or speakers emitting familiar rumbles and distance themselves from unknown elephants or speakers emitting unfamiliar rumbles (Leighty et al., 2008, McComb et al., 2003, McComb et al., 2000). Establishing a perceptible range for these rumbles in savannah elephants has also been a popular area of research. For example, McComb et al. (2003) suggests that savannah elephants respond to rumbles from distances of 2.5 km, but are better at discriminating familiar and unfamiliar rumbles at distances of 1-1.5 km. These studies have contributed to the general consensus that elephants may use these rumbles to mediate social gatherings with conspecifics over long distances.

Elephant Rumble Exchanges

Subcategories of rumble interactions between savannah elephants described in Poole et al. 1988 include the *greeting rumble, contact call and contact answer rumbles, "Let's go" rumble, musth rumble*, *female chorus*, and the *post-copulatory or estrous sequence.* The *"Let's go" rumble, musth rumble, female chorus,* and the *post-copulatory or estrous sequence* are vocalized in concordance with specific behaviors such as grouping or mating that are most easily observed at a bai (Poole et al., 1988). This thesis focuses on classifying examples of *greeting rumbles* and *contact call and contact answer rumbles* as these are the most commonly observed rumble exchanges.

The *greeting rumble* is typically associated with a greeting ceremony, an exchange between two elephants after hours of not seeing each other (Moss and Poole, 1983). These greetings tend to contain higher energy and frequency modulation after longer periods of separation (Poole et al., 1988). *Greeting rumbles* typically overlap each other throughout this high energy meeting in a sort of duet (Poole et al., 1988). Observed *greeting rumbles* are consistently distinct and always occur in this spatial pattern (Poole et al., 1988). These greeting ceremonies between two elephants are also associated with other vocalizations and olfactory signals including elephant roars, gland secretions, urinations, and defecations (Poole et al., 1988).

The *contact call and contact answer rumbles* are one of the most common rumble exchanges, often produced by one individual to localize and meet with other elephants (Poole et al., 1988). These are series of rumbles with less energy that do not overlap and synchronize in the same manner as greeting ceremonies. While it is possible that the rumbles in these exchanges could show some overlap, they typically consist of a rumble with or without a response from a recipient with “listening” and “response” gaps in time between rumbles.

There is little literature exploring how these interactions between elephants could be classified using information solely from the sound stream. To infer the contexts of these rumbles, previous studies have measured various parameters characterizing the acoustic structure of individual rumbles, including frequency modulation, energy, and harmonic spacing (Hedwig et al., 2019, Soltis et al., 2009). As *greeting rumbles* are generally characterized by a relatively large proportion of overlap in the sequence of rumbles between two elephants, whereas the *contact call and contact answer rumbles* are typically found with temporal gaps between each rumble in the exchange (Poole et al., 1988), the recurrent temporal spacing of these unique rumble exchanges suggest that elephant listeners may extract information from these acoustic patterns.

This Study: Interpreting Rumble Exchanges from the Forest

In this thesis, I report on investigations of whether the temporal distribution of rumbles might indicate social rumble exchanges, e.g., *greeting rumbles* and *contact call and contact answer rumbles* (Poole et al., 1988). My goal is to add value to PAM by interpreting behavioral information about the forest elephant solely using the acoustic characteristics of their rumbles.

Information about where these rumble exchanges are found, why they are found there, and how these rumbles might be classified could inform future conservation planning. There are two ways in which I chose to explore these questions.

Hypothesis 1: Rumble bout count data will reveal patterns in forest elephant aggregation

I hypothesize that environmental features of the Nouabalé-Ndoki National Park influence the occurrence of elephant rumble exchanges.

Prediction: If there are environmental features of the Nouabale-Ndoki National Park that promote elephant aggregation, there will be a statistically significant difference in the occurrence of rumble exchanges between subcategories of habitat, season, and logging status covariates.

1. *Season:* Fruit availability is higher in the rainy season (White, 1994b). Since these resources tend to have a clumped distribution, I predict that forest elephant aggregations and consequently rumble exchanges should be more common in the wet season.
2. *Habitat:* I expect that forest elephants will be less likely to gather in swamps, and more likely to gather in the mixed forest rather than the monodominant forest because of higher fruit availability. I predict that this pattern of forest elephant aggregation will contribute to lower counts of rumble exchanges at swamps, and higher counts in the mixed forest.
3. *Logging status:* The study site includes monitoring in three strata: national park, formerly logged areas, and currently logged areas. I predict that forest elephant avoidance of environments with high amounts of human activity will yield lower counts of rumble exchanges in the active logging concession. I also predict that secondary forage growth in the inactive logging concession will promote forest

elephant aggregation and yield the highest counts of rumble exchanges out of these three strata.

Hypothesis 2: Temporal pattern of rumbles relate to type of social interaction

I hypothesize that rumble exchanges can be reliably grouped into distinct classes based on the number of rumbles, the overlap of these rumbles, and their temporal spacing. I hypothesize that these characteristics will generate discrete groups between these rumble exchanges with acoustic features similar to those unique temporal differences found between *greeting rumbles* and *contact call and contact answer rumbles*.

Prediction 1: Cluster analyses performed with these variables will yield a discrete cluster solution with more than one group.

Prediction 2: If these temporal characteristics generate discrete clusters, the rumble exchanges grouped in this study will be distinguished by the degree of overlap and spacing between their rumbles, reflecting the unique temporal characteristics of *greeting rumbles* and *contact call and contact answer rumbles*.

Materials and Methods

Field Site and Acoustic Recording

Forest elephant rumbles were recorded in and around the Nouabalé-Ndoki National Park in the Republic of Congo using 50 Swift model acoustic recording units, custom-designed at the Center for Conservation Bioacoustics at Cornell University. The 50 sites were determined by stratified random sampling such that one recorder was placed within each of 50 grid cells, 25 km^2 in area (*Figure 2*). The detection distance of an average elephant rumble using this recording equipment is about 800m. The recorders ran 24 hours a day for 3-4 months between visits to refresh the power supply and collect recorded sound data. This project used recordings obtained between December 15th, 2017 and August 13th, 2018. The climate in the Republic of the Congo includes a dry season with lower rainfall in November through March, and a wet season in April through October (Cordell, 2019). Four randomly sampled days over 13-week periods in each season were chosen for this analysis, ultimately resulting in 52 days from the wet and dry seasons. Inconsistencies in sampling due to mechanical failures and lack of rumble count data at some of these dates and sites contributed to a final sample size of 52 days from the dry season and 44 days from the wet season when continuous rumble count data was available at 41 sites, creating a total sample size of 3,936 unique site-date combinations.

Rumble Detection

Elephant rumbles were detected in the sound files using an automated algorithm (Keen et al., 2017). These detections were manually reviewed to verify the elephant rumbles and generally the detector tagged about 65% of all rumbles present in the sound file. For the purposes of this study, rumbles were defined as tonal sounds between 10 and 75 *Hz*, greater than or equal to one second in duration (modified from Thompson et al., 2009).

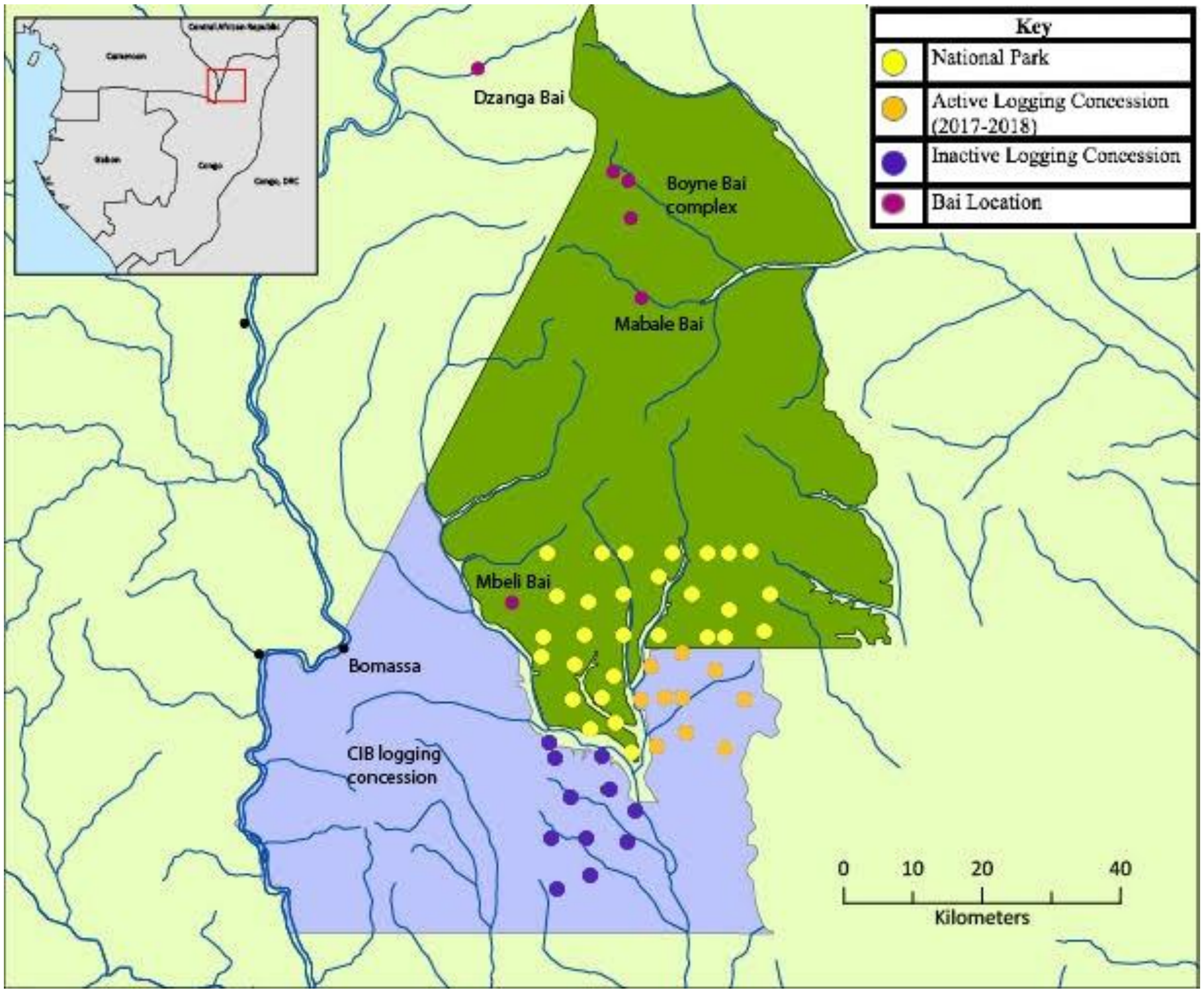


Figure 2: Location of the Nouabalé-Ndoki National Park, the 50 recording sites, and their locations inside or outside of the national park. The blue shaded region of the map represents a logging concession, and the green shaded region the national park.

[Image Description]

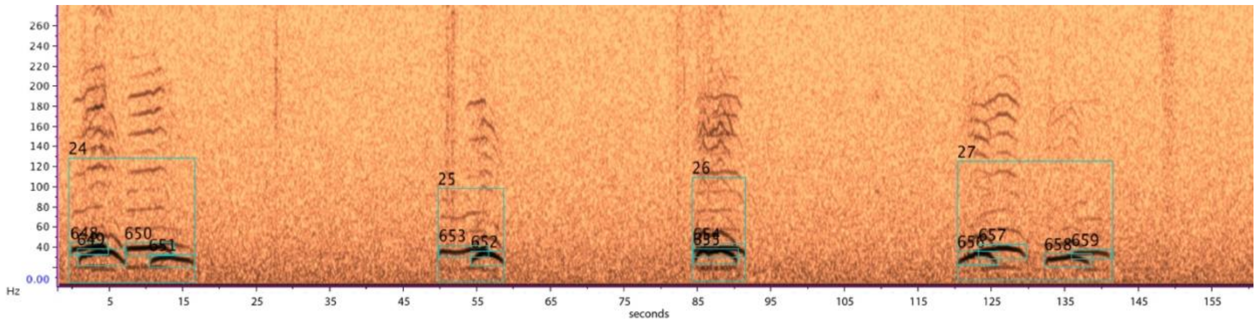


Figure 3: An example of rumble bout coding in the sound stream. Blue rectangles represent selections of rumble bouts and the rumbles within them. This image shows four rumble bouts with at least 20 seconds of space between each new selection. The x-axis represents time (5-second ticks). The y-axis represents frequency (10-*Hz* ticks). *[Image Description]*

Using only algorithmically detected rumbles throughout the sampled days, I coded adjacent rumbles in the sound stream as 'rumble bouts' if they occurred within 20 seconds of each other (*Figure 3*). Then, to reduce the number of missed rumble bout events, I browsed the sound stream manually before and after the originally detected rumble bout, including any additional rumble bouts that satisfied the 20-second criterion until there were 2 minutes without any elephant rumbles. I chose a 20-second criterion based on the duration of a confirmed *contact call and contact answer rumble* exchange between two savannah elephants described in Poole et al. (1988). Since *greeting rumbles* tend to have very little time between individual rumbles, and *contact call and contact a*nswer *rumbles* tend to have a "listening" and "response" time between rumbles, I assumed that either type of exchange would be captured by the 20 seconds it took for the two elephants in this observation to exchange multiple *contact call and contact answer rumbles*. I coded site-date combinations without any algorithmically detected rumbles within 20 seconds of each other as having zero rumble bouts.

Acoustic Measurements

Measurements for all parameters were obtained using Raven Pro Sound Analysis Software ® (version 2.0) on spectrograms generated using a Hann window with a frequency resolution of 0.977 Hz and time resolution of 28 ms. Measurement rectangles extended along the temporal axis from the start to the end of each rumble and rumble bout to generate unique begin and end times (see *Figure 3*).

I took measurements to assess the temporal relationship of the rumbles within each rumble bout by calculating the amount of time between a given rumble and the rumbles before and after it, measuring the seconds of overlap between adjacent rumbles and whether each rumble was completely overlapped, or "contained" between the begin and end time of another rumble (*Table 1*). Using these temporal measurements, I calculated other variables to describe quantitatively how these rumbles within each rumble bout formed what I termed '*stacks*' (clusters), groups of adjacent rumbles that overlapped each other consecutively within a rumble bout (*Table 2*). I used these stacks as well as measurements from each rumble to quantify the overall structure of rumble bouts according to their degree of stacking, their duration, the amount of busy/empty time in the rumble, and other unique characteristics (*Table 2*).

The parameters *DeltaTime*, *Number of Calls,* and *Total of Rumble Durations* represent the temporal size of the rumble bout (*Table 2*). I also generated measurements of *Busy Time* and *Empty Time* to represent the absolute amount of spacing between rumbles in a rumble bout (*Table 2*). The remainder of these characteristics, *Total Number of Stacks, Overlap Time, Total Stack Durations, Number of Rumbles Overlapped,* and *Total Non-Stack Rumble Durations,* represented the amount of stacking in the rumble bout (*Table 2*). These metrics, specifically those concerning the degree of stacking as well as spacing between rumbles, were expected to reflect the unique temporal features of the *greeting rumbles* and *contact call and contact answer rumbles* described in Poole et al. (1988) to discriminate the rumble bouts from this study into similar categories.

To allow for comparability between rumble bouts, I turned these acoustic characteristics into proportions. Measures describing a particular number of rumbles, for example, *Number of Rumbles Overlapped*, were divided by the total number of individual rumbles in the rumble bout, whereas measures describing duration were divided by the total duration of the rumble bout (DeltaTime). I z-scaled these proportions as well as the original *DeltaTime*, *Total Number of Stacks,* and *Total Number of Rumbles* measurements to normalize their distribution before running a cluster analysis on the data (*Table 2*).

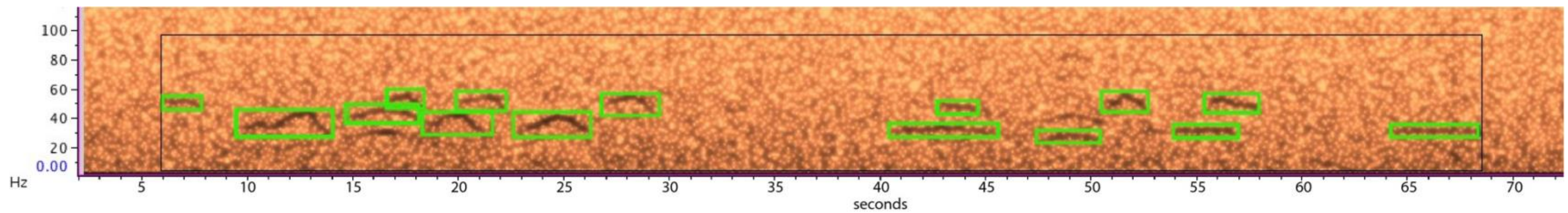
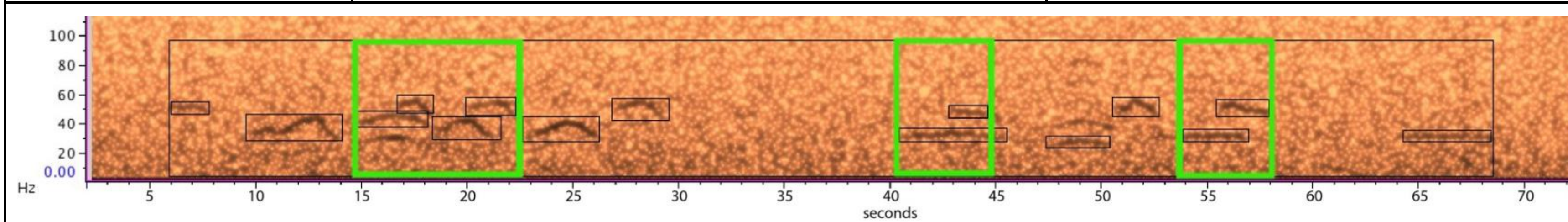
Table 1. Measurements to assess temporal relationship between rumbles within a bout.

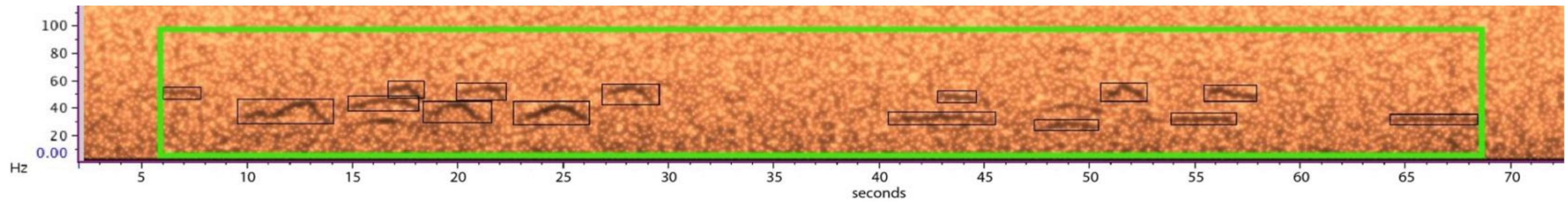
Measurement	**Description**	**Equation**[a]	**If Positive**	**If Negative**
Containment	Whether the current rumble (i) is contained within the rumble that came before it.	Containment= End Time (i) - End Time (i-1)	Rumble is not contained.	Rumble is contained.
AfterTime1	The duration of time between the end time of the current rumble and the begin time of the rumble after it.	AfterTime1= End Time (i) - Begin Time (i+1)	Absolute value of time represents overlap time between rumbles.	Absolute value of time represents gap time between rumbles.
BeforeTime1	The duration of time between the begin time of the current rumble and the end time of the rumble before it.	BeforeTime1= End Time (i-1) - Begin Time (i)	Absolute value of time represents overlap time between rumbles.	Absolute value of time represents gap time between rumbles.
AfterTime2	The duration of time between the end time of the current rumble and the begin time of the rumble two after it.	AfterTime2= End Time (i) - Begin Time (i+2)	Absolute value of time represents overlap time between rumbles.	Absolute value of time represents gap time between rumbles.
BeforeTime2	The duration of time between the begin time of the current rumble and the end time of the rumble before it.	BeforeTime2= End Time (i-2) - Begin Time (i)	Absolute value of time represents overlap time between rumbles.	Absolute value of time represents gap time between rumbles.
AfterTime3	The duration of time between the end time of the current rumble and the begin time of the rumble three after it.	AfterTime3= End Time (i) - Begin Time (i+3)	Absolute value of time represents overlap time between rumbles.	Absolute value of time represents gap time between rumbles.

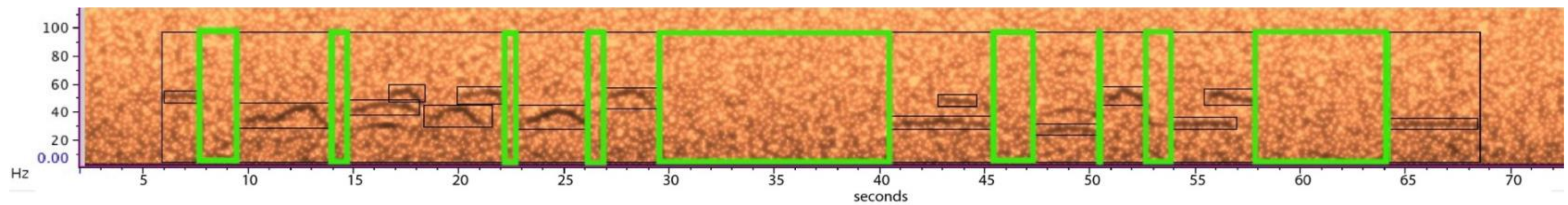
BeforeTime3	The duration of time between the begin time of the current rumble and the end time of the rumble three before it.	BeforeTime3= End Time (*i*-3) - Begin Time (*i*)	Absolute value of time represents overlap time between rumbles.	Absolute value of time represents gap time between rumbles.
AfterTime4	The duration of time between the end time of the current rumble and the begin time of the rumble four after it.	AfterTime4= End Time (*i*) - Begin Time (*i*+4)	Absolute value of time represents overlap time between rumbles.	Absolute value of time represents gap time between rumbles.
BeforeTime4	The duration of time between the begin time of the current rumble and the end time of the rumble four before it.	BeforeTime4= End Time (*i*-4) - Begin Time (*i*)	Absolute value of time represents overlap time between rumbles.	Absolute value of time represents gap time between rumbles.

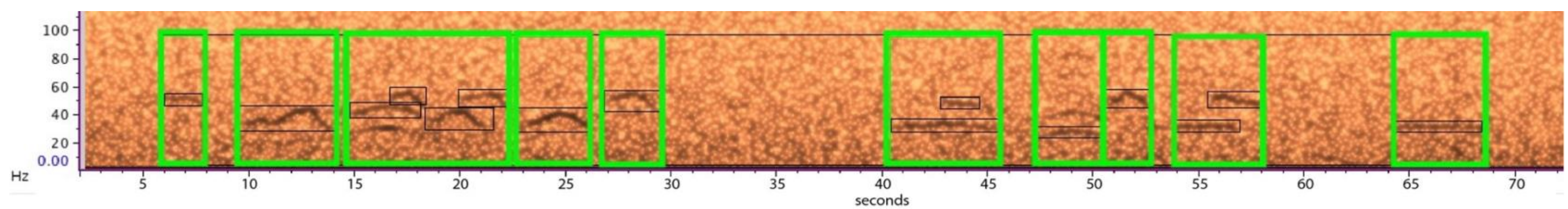
[a] *i* indicates the current rumble, rumbles were ordered in sequence of detection

Table 2: Parameters calculated to describe rumbles within a rumble bout according to their temporal distribution.

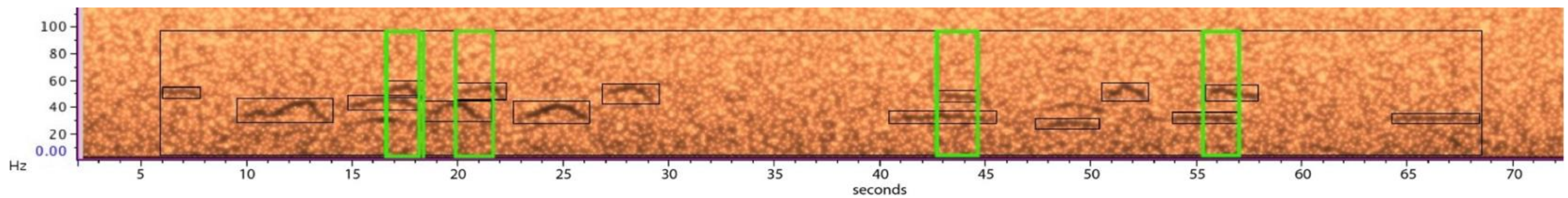
Parameter	**Description**[a]	**Equation**
Total Number of Rumbles	Total number of rumbles within a rumble bout (area enclosed by narrow black box). Example= 15 rumbles	NA
 [Image Description]		
Total Number of Stacks	Total number of unique stacks within a rumble bout (area enclosed by narrow black box). Example= 3 stacks	NA
 [Image Description]		

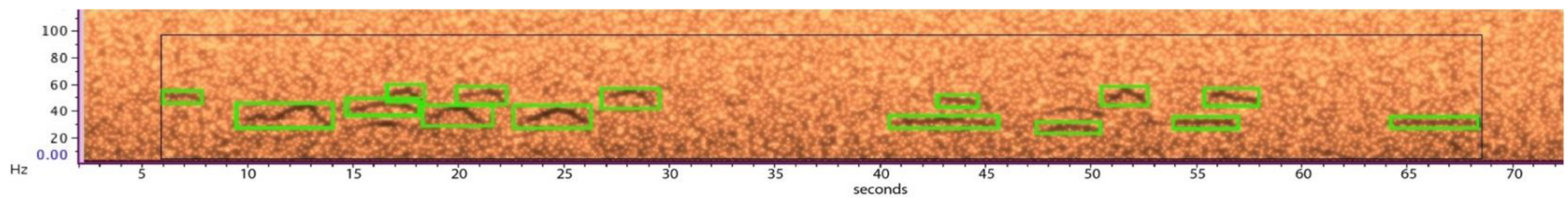
<table>
<tr><td>DeltaTime</td><td>Total time in rumble bout (area enclosed by narrow black box). Example= 62.72 seconds</td><td>DeltaTime= End Time of Rumble Bout- Begin Time of Rumble Bout</td></tr>
<tr><td colspan="3">

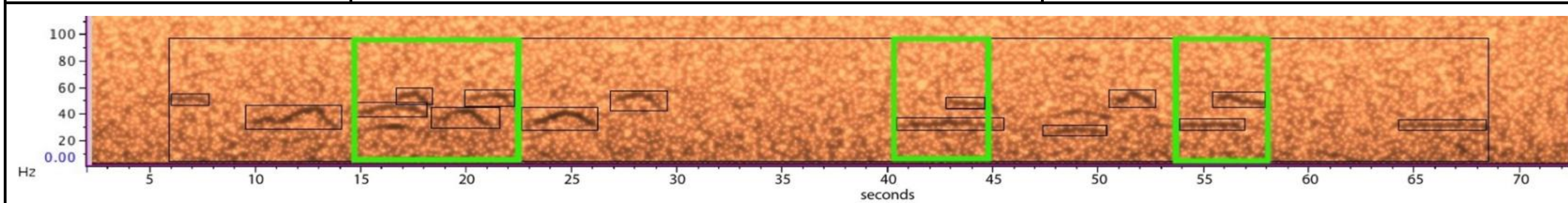
[Image Description]</td></tr>
<tr><td>Empty Time</td><td>Amount of time in seconds within a rumble bout (area enclosed by narrow black box) when there are no rumbles. Example= 24.78 seconds</td><td>Empty Time= DeltaTime - (Total Stack Durations + Non-Stack Rumble Durations)</td></tr>
<tr><td colspan="3">

[Image Description]</td></tr>
<tr><td>Busy Time</td><td>Amount of time in seconds within a rumble bout (area enclosed by narrow black box) when there is a rumble. Example= 37.94 seconds</td><td>Busy Time= Total Stack Durations + Non-Stack Rumble Durations</td></tr>
<tr><td colspan="3">

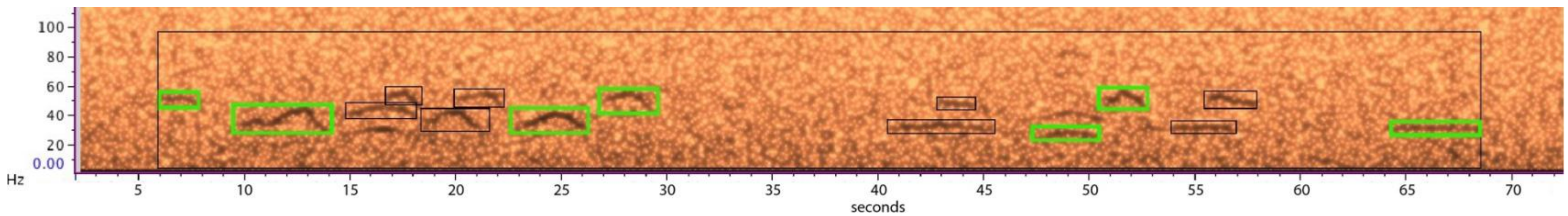
[Image Description]</td></tr>
</table>

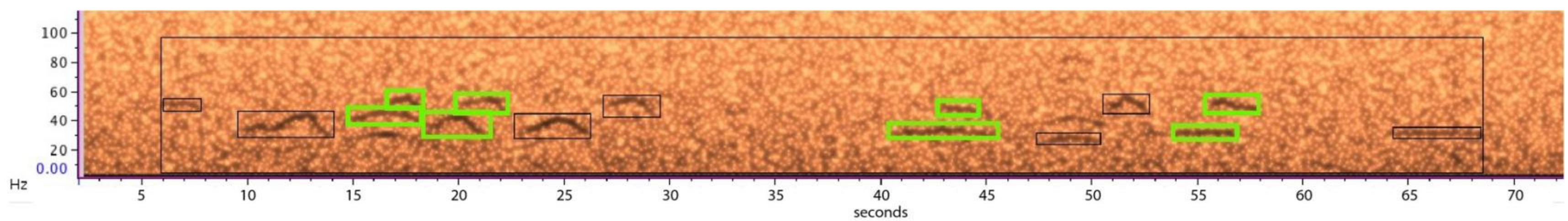
<table>
<tr><td>Overlap Time</td><td>Amount of time in seconds within a rumble bout (area enclosed by narrow black box) when rumbles are overlapping. Example= 6.56 seconds</td><td>Overlap Time= Measure A + |Neg Measure B|</td></tr>
<tr><td colspan="3">

[Image Description]</td></tr>
<tr><td>Total Rumble Durations</td><td>Sum of length in seconds of each rumble within a rumble bout (area enclosed by narrow black box). Example= 45.49 seconds</td><td>Total Rumble Durations= sum(deltatime of rumble 1, deltatime of rumble 2, deltatime of rumble 3, ...)</td></tr>
<tr><td colspan="3">

[Image Description]</td></tr>
<tr><td>Total Stack Durations</td><td>Sum of length in seconds of each stack within a rumble bout (area enclosed by narrow black box). Example= 15.80 seconds</td><td>Total Stack Durations= sum(end time of last rumble in stack-begin time of first rumble in stack)</td></tr>
<tr><td colspan="3">

[Image Description]</td></tr>
</table>

<table>
<tr><td>Total Non-Stack Rumble Durations</td><td>Sum of rumble lengths in a rumble bout (area enclosed by narrow black box) in seconds that do not occur in a stack.
Example= 22.14 seconds</td><td>Total Non-Stack Rumble Durations= sum(deltatime of non-overlapped rumble 1, deltatime of non-overlapped rumble 2, deltatime of non-overlapped rumble 3, ...)</td></tr>
<tr><td colspan="3">

[Image Description]</td></tr>
<tr><td>Number of Rumbles Overlapped</td><td>Number of rumbles that overlap with another rumble within a rumble bout (area enclosed by narrow black box). Example= 8 rumbles</td><td>NA</td></tr>
<tr><td colspan="3">

[Image Description]</td></tr>
</table>

[a] spectrograms: green boxes indicate the focus of a particular measurement, x-axis represents time (1-second ticks), y-axis represents frequency(10-*Hz* ticks).

Covariates

Average Abundance of Elephants- To test whether the occurrence of rumble bouts i.e., social exchanges, is driven by environmental factors, I needed to control for the general amount of elephant calling detected at each site-date combination. This effect would determine how much of the variation in rumble bout counts could be better predicted by the number of elephants at a particular location rather than the environmental features of each recording unit across the acoustic grid. While a relationship between detected rumble counts and the distribution of rumble bouts was expected, this density covariate was incorporated to control for this effect and show the extent to which this variable contributed to the results of this study. While evaluating an ideal window of time based on the pattern of call frequency across days, I settled on a 13-day average of daily call counts as a proxy for overall elephant activity at each site-date combination. In order to normalize the distribution of the means I used z-score normalization. The daily counts were based on automated detector output, which was only available for 94% of site-days in my sample, reducing the original data set of 3963 site-date combinations sampled to 3701 site-date combinations.

Habitat- Forest type was assessed by field researchers at the location of each recorder. These forest types included swamp forest, Gilbertiodendron forest (a monodominant forest), and mixed species forest.

Logging status- Each recording unit was situated within one of three strata representing logging activity: currently active logging, inactive logging, or national park (never logged). Active logging areas had high amounts of human activity and road construction, while inactive logging areas had more second-growth vegetation due to tree removal and construction six years prior to the beginning of this study.

Statistical Tests

I used generalized linear mixed models (GLMMs, Brooks et al., 2017b) to investigate how environmental characteristics influence the occurrence of rumble bouts in the acoustic survey area. GLMMs allow testing for the effects of various covariates (fixed effects) on a response variable simultaneously, while controlling for the random variation of rumble bout counts as predicted by sampling location and date (random effects).

Rumble bout events in this study were relatively rare, and only occurred at 8% of all site-date combinations. To account for excess zeroes in the data set I used a hurdle model approach, which breaks down the analysis into two different tests to assess the effects of covariates without letting the high number of zeroes neutralize differences in the number of events (rumble bouts) at each observation (site-date combination) (Hofstetter et al., 2016). While a zero-inflated model is also helpful for modeling data with excess zeroes, the site-date combinations with zero rumble bouts included in the data set only consisted of sampling zeroes (each observation was at an equal risk for an event) without structural zeroes (an observation was not at risk for an event). Zero-inflated models are most appropriate for data with excess structural and sampling zeroes, whereas hurdle models are most appropriate for data with excess sampling zeroes only (Rose et al. 2006). For this reason, this study uses the hurdle model approach. A first GLMM with a binomial error distribution included observations with zeroes to assess the effect of the metadata on the occurrence of rumble bouts. A second GLMM with a truncated Poisson distribution only included observations with rumble bout detections to assess the effect of the metadata on the number of rumble bouts detected. For both models I used habitat, logging status, season, and rumble density as covariates. I included site and date as random effects to control for their potential influence on elephant vocal behavior. A qqplot was used to assess the dispersion of rumble bout detections and determine that the dispersion of the data met model assumptions.

I implemented the two models using the R package *glmmTMB* (Brooks et al., 2017a). This package fits GLMMs with a maximum likelihood estimation that maximizes the probability of obtaining the observed results. For each part of the model, I first tested the overall significance of the predictors by comparing the full model with all predictor variables, to a null model only including the random effects, using a likelihood ratio test and the R function "anova".

To derive p-values for the categorical predictor variables as a whole (e.g. habitat, season) I used the R package *car* (Fox, 2019) to produce an ANOVA table with a series of Wald chi square tests that use 'dummy' parameterization to determine the statistical significance of categorical predictor variables as compared to a reference (intercept) value. I interpreted the results of both GLMMs using the R package *emmeans* (Lenth, 2020) to determine the probability of a rumble bout detection in each environment. For the binomial model, this package compares each categorical variable to each other by converting the log odds of success into odds ratios and derives p-values for comparisons from these odds ratios (e.g. Mixed Forest/Swamp, Monodominant Forest/Swamp, Mixed Forest/Monodominant Forest). For the truncated Poisson model, this package compares categorical variables by converting the log mean count into rate ratios for each comparison and derives p-values for comparisons from these rate ratios. These rate ratios represent the likelihood of a higher rate of rumble bout detections and serve to compare differences in the number of rumble bouts detected at each site-date combination with one or more rumble bouts. For the purposes of this study, I accepted a p-value of less than 0.01 as statistically significant.

I conducted cluster analyses to classify rumble bouts based on the temporal distribution of the rumbles within them. All rumble bouts found from the original sample of all 50 sites in the acoustic grid and 52 dates from each season were included in the cluster analyses (n=1061 rumble bouts). I used the kmeans cluster algorithm implemented in the R package *NbClust* (Malika Charrad et al., 2014) to assign rumble bouts to clusters and to subsequently assess the discreteness of different cluster solutions ranging from 2 to 15 clusters. Kmeans allocates each rumble bout event to a given number of clusters (k) based on the vector distance of each rumble bout event to the means of those clusters, called centroids.

Twenty-three standard indices from this package were calculated to determine the most appropriate cluster solution (number of centroids) based on within and between cluster similarity (see *Appendix 1*). While the majority rule across all of those indices determined which cluster solution was most appropriate for fitting these data, one of the indices, the silhouette validity index, was used to assess how discrete the clusters were. The silhouette index (SI) is based on a measure of clustering discreteness called silhouette coefficients. Silhouette coefficients for each cluster quantify how similar and dissimilar events are within and between clusters (Rousseeuw, 1987). These coefficients range in value from -1 to +1 with events that are highly matched to their own clusters and poorly matched to other clusters scoring a high value close to ± 1. SI of <0.25 indicates highly assimilated clusters, $0.25 \leq SI < 0.5$ weak clustering, $0.5 \leq SI < 0.7$ moderate clustering and $SI \geq 0.7$ strong clustering (Rousseeuw, 1987).

I performed a series of pairwise t-tests to assess the statistical significance of differences in the temporal acoustic characteristics between the two clusters (see *Table 5*). In order to control for multiple comparisons of rumble bout events in each cluster, I applied a post hoc Bonferroni correction to adjust the p-value results from the pairwise t-tests using the R function “pairwise.t.test”. I mapped the number of rumble bouts as well as the proportions of each rumble bout cluster type at each site sampled to illustrate the relative distribution of these rumble bout detections at each recording unit.

Results

Environmental Influences on Occurrence and Number of Rumble Bouts

The binomial model including habitat, season, logging status, and rumble density was statistically significant (model p-value <0.0001, *Table 3*). The effect of season on the occurrence of rumble bouts at a given site was found to be statistically significant (p=0.0001, *Table 3*) with rumble bouts 1.69 times more likely to occur in the wet season than the dry season (p=0.0001, *Table 3*). The effect of the density covariate was also found to be statistically significant (p<0.0001, *Table 3*), revealing that rumble bout detections were significantly more likely to occur during periods of time with higher rates of detected rumble counts. The truncated Poisson model including habitat, season, logging status, and a density covariate was statistically significant (model p-value <0.0001, *Table 4*). Site-date combinations with higher rumble density, according to the density covariate, had a significantly higher number of rumble bouts (p<0.01, *Table 4*); however the effects of season, habitat and logging status, as well as their rate ratios, were not statistically significant.

Table 3: Environmental influences on the likelihood of a rumble bout detection.[a]

Effect[b]	**Likelihood Chi Square**	**Degrees of Freedom**	**Odds Ratio**	**SE**	**P Value**
(Intercept)	**123.5191**	**1**	**-**	**0.285**	**< 0.0001**
Season	**15.0593**	**1**	**-**	**-**	**0.0001**
Wet compared to Dry	**-**	**3692**	**1.69**	**0.0802**	**0.0001**
Habitat	4.0109	2	-	-	0.1345
Mixed Forest compared to Monodominant Forest	-	3692	1.08	0.235	0.9361
Mixed Forest compared to Swamp	-	3692	2.44	1.086	0.1118
Monodominant Forest compared to Swamp	-	3692	2.26	1.054	0.1861
Logging Status	2.8919	2	-	-	0.2355
Active Logging Concession compared to Inactive Logging Concession	-	3692	0.590	0.192	0.2363
Active Logging Concession compared to National Park	-	3692	0.791	0.229	0.6983
Inactive Logging Concession compared to National Park	-	3692	1.342	0.314	0.4196
Density Covariate	**97.3669**	**1**	-	-	**< 0.0001**

[a] binomial GLMM (n=3701) Likelihood Chi Square=149.6 P-Value<0.0001, Degrees of Freedom=6
[b] site and date included as random effects.

Table 4: Environmental influences on the number of rumble bout detections.[a]

Effect[b]	**Likelihood Chi Square**	**Degrees of Freedom**	**Rate Ratio**	**SE**	**P Value**
(Intercept)	2.2894	1	-	0.267	0.1303
Season	0.6081	1	-	-	0.4355
Wet compared to Dry	-	287	0.87	0.207	0.4362
Habitat	0.1364	2	-	-	0.9341
Mixed Forest compared to Monodominant Forest	-	287	0.935	0.180	0.9349
Mixed Forest compared to Swamp	-	287	0.941	0.319	0.9823
Monodominant Forest compared to Swamp	-	287	1.006	0.362	0.9998
Logging Status	0.3679	2	-	-	0.8320
Active Logging Concession compared to Inactive Logging Concession	-	287	0.933	0.263	0.9676
Active Logging Concession compared to National Park	-	287	1.056	0.274	0.9762
Inactive Logging Concession compared to National Park	-	287	1.131	0.230	0.8175
Density Covariate	**59.8348**	**1**	**-**	**-**	**<0.0001**

[a] truncated Poisson GLMM (n=296) Likelihood Chi Square=68.703, P-Value<0.0001, Degrees of Freedom=6
[b] site and date included as random effects.

Clustering of Rumble Bouts from Temporal Measurements

Figure 4 shows the result of the kmeans cluster analysis, suggesting that rumble bouts fall optimally into two clusters (see also *Appendix 1*). According to the silhouette index, these two clusters were weakly integrated with a best fit value of 0.488. Rumble bouts in Cluster1 were the most common (N=853) and consisted of 80% of the total number of rumble bouts. The means and ranges presented in *Table* 5 show that the biggest differences between rumble bouts in the two clusters largely consisted of differences in rumble overlap and stacking. Rumble bouts in Cluster2 had a relatively higher *Proportion of Stack Durations, Proportion of Rumbles Overlapped, Total Number of Stacks, Proportion of Overlap Time, and Proportion of Rumble Durations* compared to rumble bouts in Cluster1. Rumble bouts in Cluster2 also had a higher average *Proportion of Busy Time to Empty Time* compared to Cluster1 (3:1 as opposed to 1:1, *Table 5*). In contrast, rumble bouts in Cluster1 had a higher *Proportion of Non-Stack Rumble Durations*. The number of rumble bouts as well as the proportions of each cluster type are shown in *Figures 5/6*. The spatial distribution of rumble bout frequency and cluster type is relatively uniform across the acoustic grid.

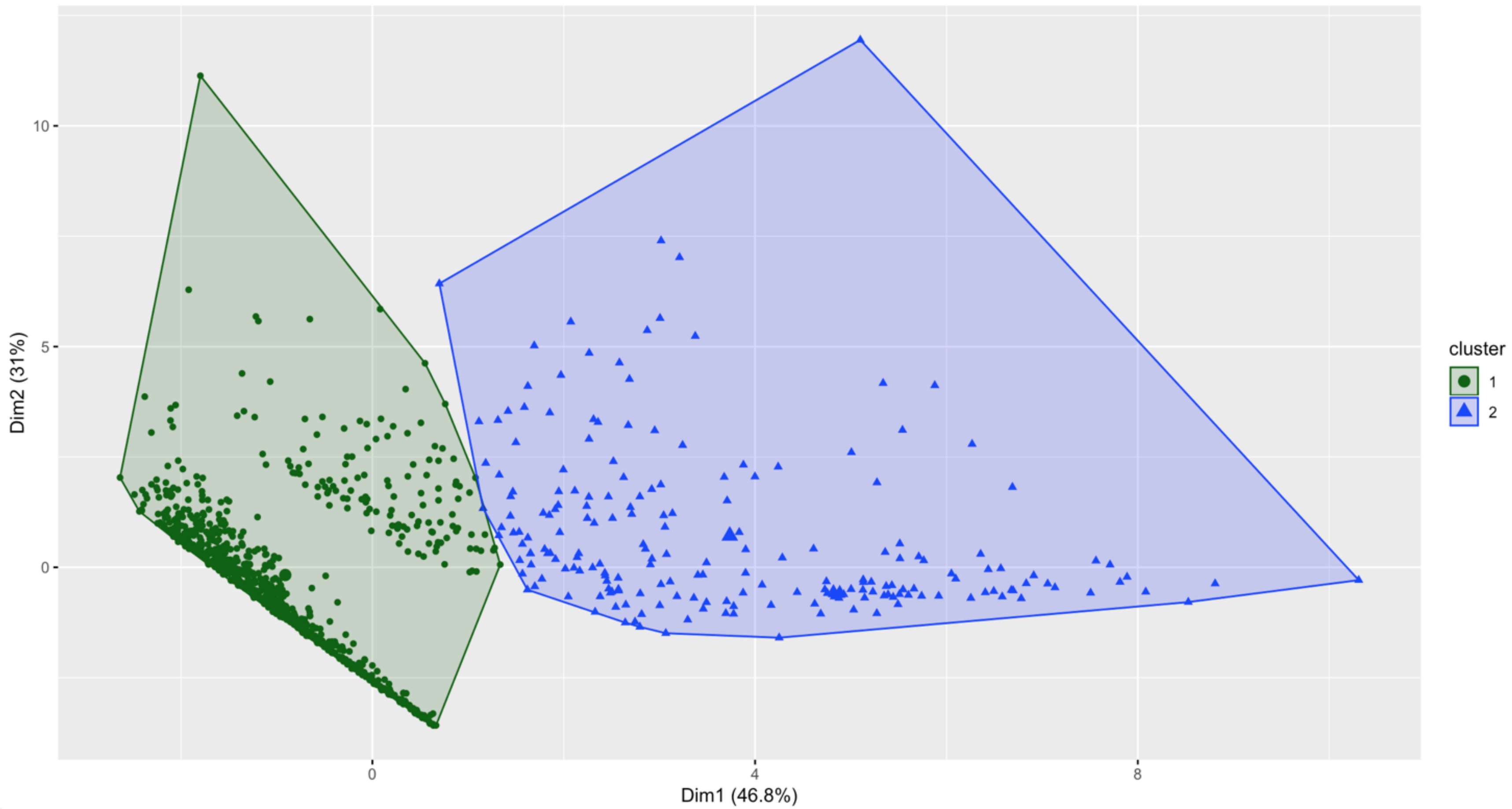


Figure 4: Kmeans clustering results of rumble bouts along two principal components, based on temporal acoustic parameters described in Table 5. [*Image Description*]

Table 5: Average values of acoustic parameters and their influence on differentiating rumble bouts into two clusters[a].

Parameter	**Cluster1 Mean (range)**	**Cluster2 Mean (range)**	**Standard Deviation**	**P-value[b]**
Number of Rumbles	**3.594 (2-23)**	**5.731 (2-46)**	**3.576**	**<0.0001**
Delta Time (s)	30.366 (3.43-478.09)	27.012 (3.08-209.52)	30.087	0.15
Proportion of Busy Time	**0.519 (0.15-0.98)**	**0.751 (0.25-1.18)**	**0.202**	**<0.0001**
Proportion of Empty Time	**0.481 (0.02-0.85)**	**0.250 (0.00-0.75)**	**0.201**	**<0.0001**
Proportion of Rumble Durations	**0.528 (0.15-0.98)**	**0.979 (0.47-1.95)**	**0.273**	**<0.0001**
Proportion of Non-Stack Rumble Durations	**0.494 (0.08-0.98)**	**0.179 (0.00-0.59)**	**0.228**	**<0.0001**
Total Number of Stacks	**0.183 (0-3)**	**1.683 (1-10)**	**0.923**	**<0.0001**
Proportion of Stack Durations	**0.024 (0.00-0.39)**	**0.571 (0.10-0.99)**	**0.253**	**<0.0001**
Proportion of Rumbles Overlapped	**0.066 (0.00-0.67)**	**0.772 (0.4-1.0)**	**0.237**	**<0.0001**
Proportion of Overlap Time	**0.008 (0.00-0.21)**	**0.218 (0.01-1.43)**	**0.124**	**<0.0001**

[a] k-means cluster analysis (n=1061 bouts, 835 scored Cluster1, 208 scored Cluster2).

[b] statistics of pairwise t-tests

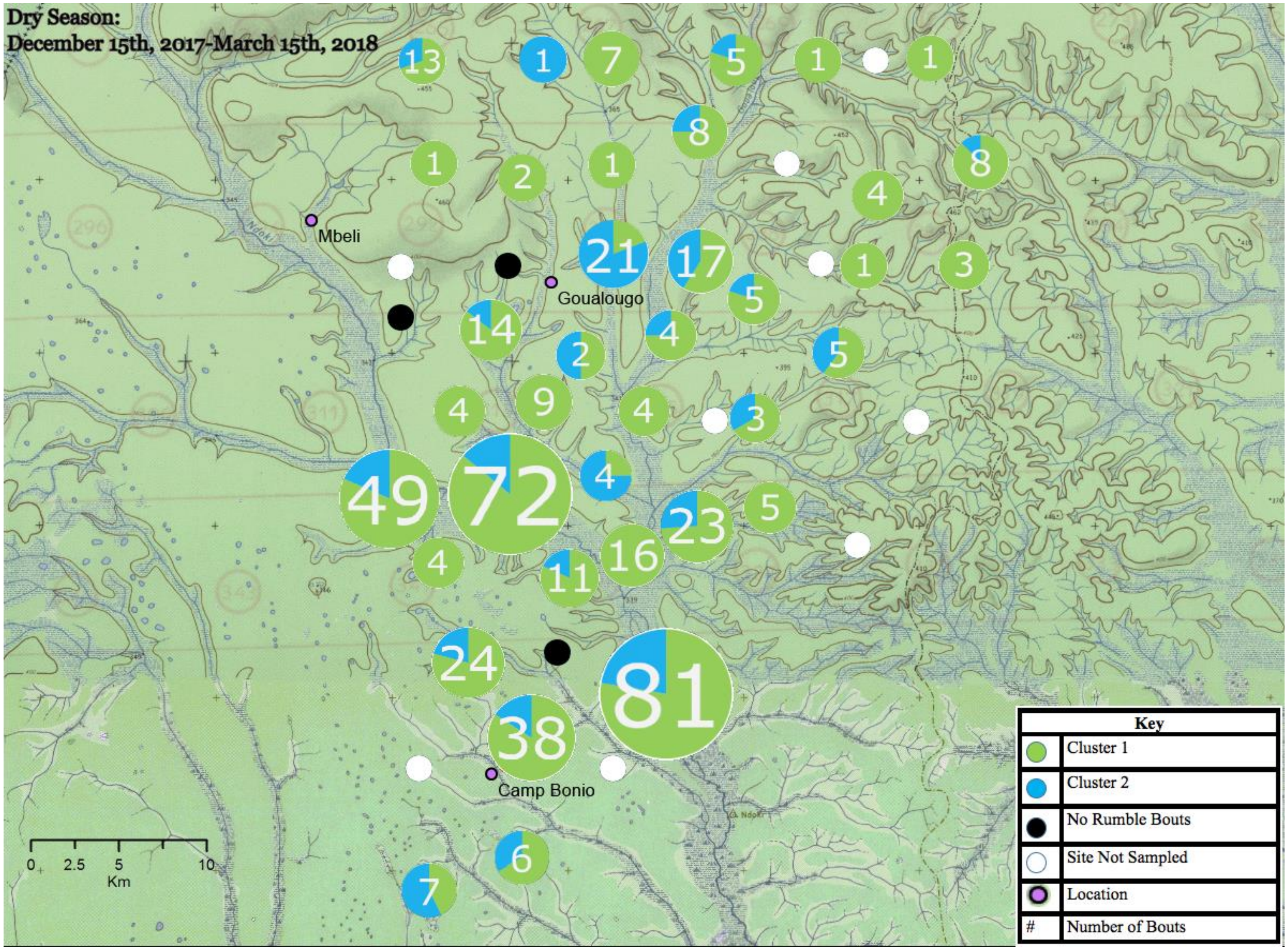


Figure 5: Number of rumble bouts by site and the proportion of those bouts in each designated cluster for all sampled site-date combinations in the dry season. *[Image Description]*

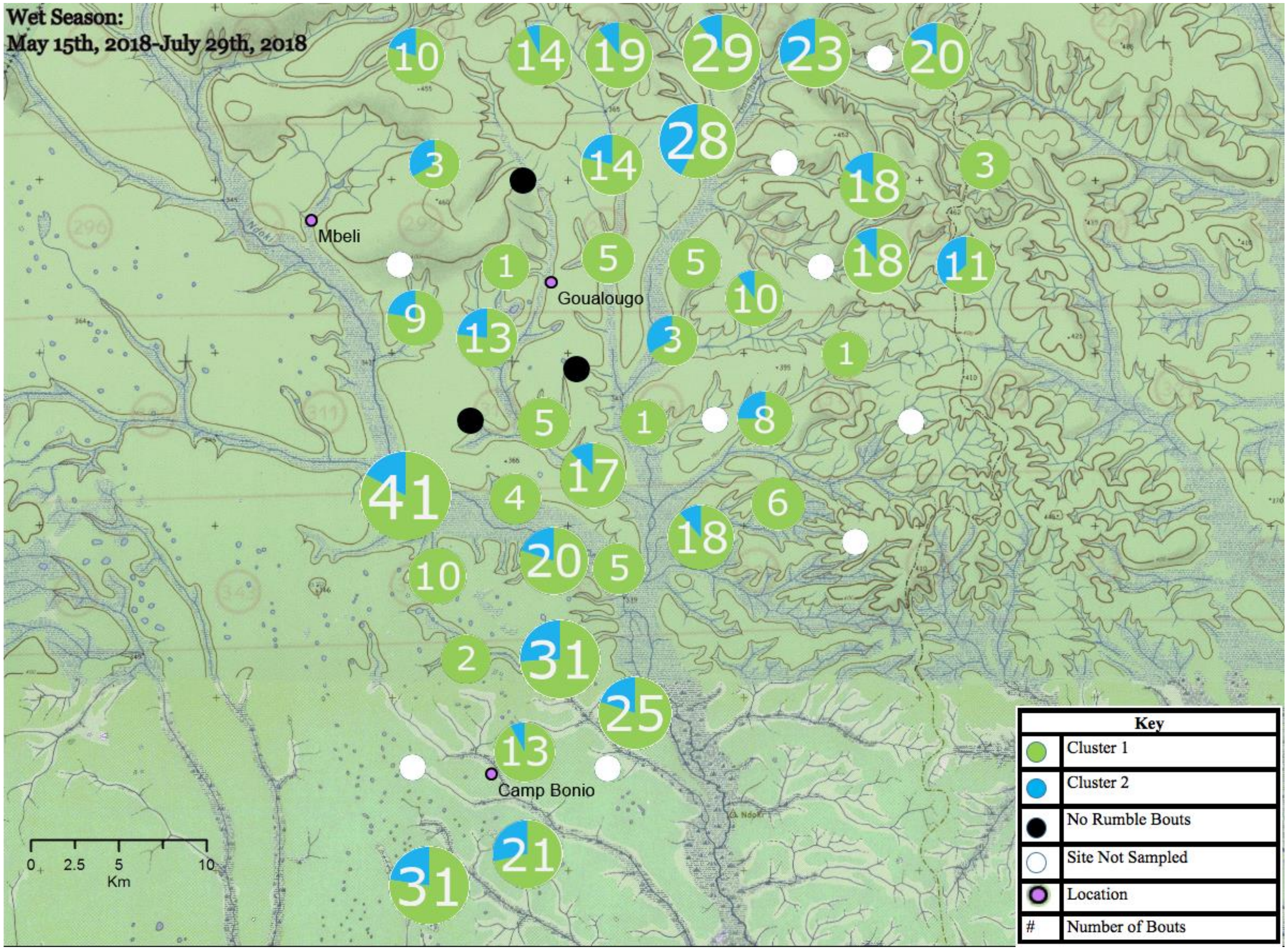


Figure 6: Number of rumble bouts by site and the proportion of those bouts in each designated cluster for all sampled site-date combinations in the wet season. [Image Description]

Discussion

The goal of this study was to better understand the social implications of the rumble bout by 1) predicting the occurrence of these rumble bouts across the acoustic grid according to the environmental features surrounding each acoustic recording unit, and 2) classifying these rumble bouts based on the temporal spacing between their rumbles. The results of this study revealed a significant density covariate and weak season effect with no statistically significant effect of habitat or logging status in predicting rumble bout occurrence or the number of rumble bout detections. My results also show a weak kmeans clustering that clustered the rumble bouts in this study into two groups. The results of this thesis support my predictions that 1) environmental features of the Nouabalé-Ndoki National Park influence the occurrence of rumble bouts and 2) rumble bouts can be discretely clustered into more than one group based on the temporal spacing of the rumbles within them, consistent with representing both greeting ceremony interactions and contact calling interactions.

These data showed a statistically significant difference in the likelihood of rumble bouts between season. This weak season effect revealed that rumble bouts were more likely to occur in the wet season when compared to the dry (*Table 3)*. While these results do substantiate my prediction that elephant aggregations and consequently rumble exchanges should be more common in the wet season, this weak season effect was the only statistically significant environmental feature. The increased likelihood of rumble bouts in the wet season is likely due to the increased abundance of fruiting trees (White 1994b). The patchy distribution in this attractive resource brings elephants into proximity, promoting elephant aggregation and consequently rumble bouts of a social nature. The habitat covariate was limited to a brief assessment of the area immediately surrounding the acoustic recording units and may not have offered an accurate measure of other environmental features in the 800-meter perceptible range for detecting rumble bouts at each recording site. Future covariates including additional information about the locations of these recording sites such as their proximity to scarce mineral sources and the relative abundance and types of herbaceous plants and fruits found within their range of detection may yield more statistical significance in predicting the frequency of rumbles. The lack of statistically significant results from the logging status covariate in this study was surprising. Since poaching may be a more significant source of anthropogenic pressure, an additional covariate that describes the proximity of these recording units to acoustic detections of gunshots may better predict the absence of elephant aggregation in areas of the acoustic grid where elephants are exposed to human hunting.

My predictions regarding the classification of rumble bouts according to their temporal acoustic features were substantiated by the cluster analysis, which separated bouts into two clusters. The relative distribution of temporal features (*Table 5*) showed that differences in stacking and overlap of the rumbles within rumble bouts were statistically significant and acoustically distinct. Based on these measurements, Cluster2 (*Figure 4* and *Table 5*) likely reflects the unique temporal organization of *greeting rumbles*, rumbles with high stacking and overlap that signify a meeting between two forest elephants. Similarly, Cluster1 (*Figure 4* and *Table 5*) likely reflects *contact call and contact answer rumbles*, rumbles with "listening" and "response" gaps that may function to help forest elephants localize one another. These findings support my second prediction that the rumble exchanges grouped in this study would be distinguished by the same unique temporal acoustic features that make up *greeting rumbles* and *contact call and contact answer rumbles*.

There are several ways that cluster analysis could be improved to yield more relevant social information. Additional studies exploring correlations between temporal acoustic characteristics of rumble bouts and confirmed visual behaviors are necessary for understanding the behavioral significance of these measurements and the types of rumble bouts that they classify. The patterns of rumble bout detection discovered in this thesis could be used to inform placement of cameras in conjunction with audio recorders for a higher likelihood of capturing both. Another potential area for exploring social correlates of these rumble bouts include a cluster analysis with other acoustic measures (frequency modulation, energy, number of harmonics) for the specific rumbles within a bout. For example, rumbles with higher energy and frequency modulation may be correlated with increased arousal and emotion (Soltis et al., 2009, Soltis, 2013), thus indicating more clearly an affiliative social interaction. In this thesis, I chose to focus on temporal measurements for the cluster analysis in order to identify rumble exchanges related to greeting and long-distance social coordination events. However, elephants have an expansive call repertoire, including call types associated with various other social contexts. Including other call types, for instance those associated with agonistic interactions, may also reveal a subtype of these rumble bouts that consists of interactions with unfamiliar forest elephants.

Overall, the mapped distribution of these rumble bout events (see *Figures 5/6*) suggests that these rumble bouts, although relatively sparse in the data, occur across areas of the landscape without the concentrated attractive resource of a forest clearing. Determining whether or not these data reflect busy social gatherings in the forest ultimately depends on whether these rumble bout events can be considered social behavior. Elephant rumbles in this habitat have been shown to travel, on average, about 0.8 km, and, under quiet ambient conditions, to over 3 km (Hedwig et al., 2018). Distances to the source of rumble vocalizations measured in this study were unknown, with some vocalizations likely produced by elephants in close proximity but others potentially at some considerable distance. Information like this could help to confirm that rumble bouts in Cluster2 are in fact familial social interactions at close distance. Localizing rumbles with the help of acoustic arrays could reveal with greater certainty whether these bouts are socially inconsequential or vocalized by elephants that are within perceptible range of a listening conspecific (Blumstein et al., 2011). My study provides the initial step towards a conclusive assessment of the biological significance of rumble bouts in audio recordings and what they could contribute to PAM studies. While I only partially succeeded in meeting the goals of this study, a more complete idea of the social implications of these rumble bouts is clearly within a reasonable grasp.

While the social system of forest elephants is regularly equated to that of more easily observable species of elephants living in grasslands and savannahs, African forest elephants are ecologically, morphologically, and genetically distinct from these species (Roca et al., 2001, Grubb et al., 2000, Blake, 2002). Recent studies have revealed potential differences in forest elephant communication (Hedwig et al., 2018) and PAM is already beginning to improve conservation planning in these areas (Astaras et al., 2017, Wrege et al., 2010, Wrege et al., 2017). Extending the scope of PAM data to deduce patterns in forest elephant social behavior is not only important for more specific conservation planning and management of forest resources, but also allows us to learn more about the behavior of these endangered creatures. As human activity continues to encroach on these unique ecosystems, behavioral research that incorporates PAM could be the key to a more accurate understanding of how environmental disturbances may affect the status of future forest elephant populations.

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Appendix 1

Table A1: Best cluster solutions according to 24 standard validity indices from the *NbClust package* and their corresponding values.

Standard Validity Index	**Number of Clusters**	**Value[a]**
Silhouette Index	2	0.488
Duda Index	2	0.936
Pseudo t_2	2	17.023
Beale Index	2	0.461
McClain Index	2	0.214
Dunn Index	2	0.028
Trcovw Index	3	6.363e+5
Ratkowsky Index	3	0.396
Ball Index	3	1.601e+3
Ptbiserial Index	3	0.669
Scott Index	4	2.013e+3
Marriot Index	4	8.180e+17
Tracew Index	4	714.516
Friedman Index	4	9.535e+3
SD Index	4	3.819
Calinski and Harabasz (CH) Index	5	635.121
KL Index	12	342.419
Rubin Index	12	-0.855
C-Index	12	0.075
Hartigan Index	15	188.686
Cubic Clustering Criterion (CCC) Index	15	17.585
Davies and Bouldin (1979) Index	15	1.00
SDbw Index	15	0.411

[a] n=1071 rumble bouts

Appendix 2

Image Descriptions

Figure 1: An image of a spectrogram generated using Raven Pro Sound Analysis Software ® (version 2.0). The spectrogram itself is bright orange and is speckled with gray. There is a vertical axis with a ruler representing 10 Hertz with each tick mark, ranging from 0.00 to 240 Hertz. There is a horizontal axis with a ruler representing 1 second with each tick mark, ranging from 0 to 37 seconds. There is an elephant rumble in the middle of this spectrogram, that looks like 13 black lines of various shades and widths (from light gray to black), one on top of the other with space in between. There is a vertical arrow with an arrowhead on both sides, and next to it there is a label that says "Frequency". There is a horizontal arrow with an arrowhead on both sides, and next to it there is a label that says "Duration". There is a horizontal arrow pointing to the lowest, barely visible line of the elephant rumble, and next to it there is a label that says "Fundamental Frequency". The elephant rumble line above the Fundamental Frequency has a thin black circle around it, and pointing to this thin black circle is a black arrow with one head, with a label that says "Harmonic". There are two horizontal arrows higher up in the picture that are pointing to the 10th and 8th black line. The first arrow has a label that says "Higher Amplitude (Energy)", and points to a very dark, bold line. The second arrow has a label that says "Lower Amplitude (Energy)" and points to a lighter gray, thinner line.

Figure 2: A map of the area surrounding the Nouabalé-Ndoki National Park in Northern Congo. There are many branching rivers surrounding the national park. The map is a very pale green and the rivers are blue, but there are two sections of the map highlighted. A dark green section of the

map designates the national park, whereas a periwinkle section below that designates the logging concession areas. There are small hot pink circles on the map designating locations of forest clearings. From top to bottom they are named "Dzanga Bai", "Boune Bai complex"-the complex has three locations, "Mabale Bai", and Mbeli Bai. All of the bais are located within the national park except for the "Dzanga Bai". The map also has small black circles designating cities, but the only city labeled is Bomassa, that resides on the north-western border of the logging concession. There is a distance ruler in the bottom right corner that ranges from 0 to 40 km, with tickmarks at every 10 km. There is a key in the upper right hand corner, showing that small yellow circles designate recording sites in the National Park, small orange circles designate recording sites in the Active Logging Concession-a concession that was active between 2017 and 2018, and small dark purple circles designate recording sites in the Inactive Logging Concession. The small orange circles are to the right of the periwinkle logging concession area, whereas the small dark purple circles are central to the periwinkle logging concession area. There is a smaller square gray map of West Africa on the top left corner of the map. This smaller map uses a red square to designate the location of the National Park and its surrounding areas. The gray map features the borders of Gabon, Republic of the Congo, Democratic Republic of the Congo, Cameroon, and the Central African Republic.

Figure 3: An image of a spectrogram generated using Raven Pro Sound Analysis Software ® (version 2.0). The spectrogram itself is bright orange and is speckled with gray. There is a vertical axis with a ruler representing 10 Hertz with each tick mark, ranging from 0.00 to 300 Hertz. There is a horizontal axis with a ruler representing 1 second with each tick mark, ranging from 0 to 160 seconds. There are 12 elephant rumbles total on this spectrogram. The first four are close in time

to one another, as are the next two, the two after that, and the next four. Horizontally, in between each of these clusters of rumbles is the bright orange, gray-speckled background of the spectrogram, representing the time between each of these clusters, termed rumble bouts for the purposes of this study. Each of these rumble bouts are separated by at least twenty seconds without a rumble. Although each of these rumbles have many harmonics, only the boldest harmonic in these rumbles is enclosed by a thin light blue line, and they all have black number labels numbered from 648 to 659. The rumble bouts are also enclosed by 4 much larger light blue boxes, that each have black number labels numbered from 24 to 27.

"Total Number of Rumbles" Image: An image of a spectrogram generated using Raven Pro Sound Analysis Software ® (version 2.0). The spectrogram itself is bright orange and is speckled with gray. There is a vertical axis with a ruler representing 10 Hertz with each tick mark, ranging from 0.00 to 120 Hertz. There is a horizontal axis with a ruler representing 1 second with each tick mark, ranging from 0 to 72 seconds. There are 15 elephant rumbles enclosed by a box with a thin black line. This thin black box designates that these are all individual rumbles within one rumble bout, because each rumble is not more than 20 seconds apart from each other. Almost all of these elephant rumbles do not have any harmonics, except for one with 2 clear harmonics. Because of this, each rumble looks like one single bold black line against the orange, gray-speckled background of the spectrogram. Each of these lines have different shapes, lengths, and boldness. Some overlap each other, and others do not. In this first image representing the "Total Number of Rumbles", there are bright green boxes enclosing each of the elephant rumbles, for a total of fifteen bright green boxes. None of the boxes are labeled.

"Total Number of Stacks" Image: An image of a spectrogram generated using Raven Pro Sound Analysis Software ® (version 2.0). The spectrogram itself is bright orange and is speckled with gray. There is a vertical axis with a ruler representing 10 Hertz with each tick mark, ranging from 0.00 to 120 Hertz. There is a horizontal axis with a ruler representing 1 second with each tick mark, ranging from 0 to 72 seconds. There are 15 elephant rumbles enclosed by a box with a thin black line. This thin black box designates that these are all individual rumbles within one rumble bout, because each rumble is less than 20 seconds apart from its adjacent rumbles. Almost all of these elephant rumbles do not have any harmonics, except for one with 2 clear harmonics. Because of this, each rumble looks like one single bold black line against the orange, gray-speckled background of the spectrogram. Each of these lines have different shapes, lengths, and boldness. Some overlap each other, and others do not. In this second image representing the "Total Number of Stacks", there are bright green boxes enclosing sequences of adjacent rumbles that are overlapping each other. These do not include any rumbles that have gaps in time between them. There are three bright green boxes total, and none of the boxes are labeled.

"DeltaTime" Image: An image of a spectrogram generated using Raven Pro Sound Analysis Software ® (version 2.0). The spectrogram itself is bright orange and is speckled with gray. There is a vertical axis with a ruler representing 10 Hertz with each tick mark, ranging from 0.00 to 120 Hertz. There is a horizontal axis with a ruler representing 1 second with each tick mark, ranging from 0 to 72 seconds. Almost all of these elephant rumbles do not have any harmonics, except for one with 2 clear harmonics. Because of this, each rumble looks like one single bold black line against the orange, gray-speckled background of the spectrogram. Each of these lines have different shapes, lengths, and boldness, and each rumble occurs less than 20 seconds apart from

its adjacent rumble. Some overlap each other, and others do not. In this third image representing the "DeltaTime", there are 15 elephant rumbles enclosed by a box with a bright green line. There is one bright green box, and it is not labeled.

"Empty Time" Image: An image of a spectrogram generated using Raven Pro Sound Analysis Software ® (version 2.0). The spectrogram itself is bright orange and is speckled with gray. There is a vertical axis with a ruler representing 10 Hertz with each tick mark, ranging from 0.00 to 120 Hertz. There is a horizontal axis with a ruler representing 1 second with each tick mark, ranging from 0 to 72 seconds. There are 15 elephant rumbles enclosed by a box with a thin black line. This thin black box designates that these are all individual rumbles within one rumble bout, because each rumble is less than 20 seconds apart from its adjacent rumbles. Almost all of these elephant rumbles do not have any harmonics, except for one with 2 clear harmonics. Because of this, each rumble looks like one single bold black line against the orange, gray-speckled background of the spectrogram. Each of these lines have different shapes, lengths, and boldness. Some overlap each other, and others do not. In this fourth image representing the "Empty Time", there are 9 bright green boxes of various sizes that enclose the orange, gray-speckled background of the spectrogram-the time between each of the individual rumbles and adjacent, overlapping series of rumbles. None of these boxes are labeled.

"Busy Time" Image: An image of a spectrogram generated using Raven Pro Sound Analysis Software ® (version 2.0). The spectrogram itself is bright orange and is speckled with gray. There is a vertical axis with a ruler representing 10 Hertz with each tick mark, ranging from 0.00 to 120 Hertz. There is a horizontal axis with a ruler representing 1 second with each tick mark, ranging

from 0 to 72 seconds. There are 15 elephant rumbles enclosed by a box with a thin black line. This thin black box designates that these are all individual rumbles within one rumble bout, because each rumble is less than 20 seconds apart from its adjacent rumbles. Almost all of these elephant rumbles do not have any harmonics, except for one with 2 clear harmonics. Because of this, each rumble looks like one single bold black line against the orange, speckled background of the spectrogram. Each of these lines have different shapes, lengths, and boldness. Some overlap each other, and others do not. In this fifth image representing the "Busy Time", there are bright green boxes enclosing individual rumbles, as well as series of rumbles. These boxes do not include gaps in time between adjacent rumbles There are 10 bright green boxes total, and none of these boxes are labeled.

"Overlap Time" Image: An image of a spectrogram generated using Raven Pro Sound Analysis Software ® (version 2.0). The spectrogram itself is bright orange and is speckled with gray. There is a horizontal axis with a ruler representing 1 second with each tick mark, ranging from 0 to 72 seconds. There are 15 elephant rumbles enclosed by a box with a thin black line. This thin black box designates that these are all individual rumbles within one rumble bout, because each rumble is less than 20 seconds apart from its adjacent rumbles. Almost all of these elephant rumbles do not have any harmonics, except for one with 2 clear harmonics. Because of this, each rumble looks like one single bold black line against the orange, gray-speckled background of the spectrogram. Each of these lines have different shapes, lengths, and boldness. Some overlap each other, and others do not. In this sixth image representing the "Overlap Time", there are bright green boxes enclosing only sections of time when the individual rumbles are overlapping. These do not include

any sections of rumbles that are not overlapping with another rumble. There are four bright green boxes total, and none of the boxes are labeled.

“Total Rumble Durations” Image: An image of a spectrogram generated using Raven Pro Sound Analysis Software ® (version 2.0). The spectrogram itself is bright orange and is speckled with gray. There is a vertical axis with a ruler representing 10 Hertz with each tick mark, ranging from 0.00 to 120 Hertz. There is a horizontal axis with a ruler representing 1 second with each tick mark, ranging from 0 to 72 seconds. There are 15 elephant rumbles enclosed by a box with a thin black line. This thin black box designates that these are all individual rumbles within one rumble bout, because each rumble is less than 20 seconds apart from its adjacent rumbles. Almost all of these elephant rumbles do not have any harmonics, except for one with 2 clear harmonics. Because of this, each rumble looks like one single bold black line against the orange, gray-speckled background of the spectrogram. Each of these lines have different shapes, lengths, and boldness. Some overlap each other, and others do not. In this seventh image representing the "Total Rumble Durations", there are bright green boxes enclosing each of the elephant rumbles, for a total of fifteen bright green boxes. None of the boxes are labeled.

“Total Stack Durations” Image: An image of a spectrogram generated using Raven Pro Sound Analysis Software ® (version 2.0). The spectrogram itself is bright orange and is speckled with gray. There is a vertical axis with a ruler representing 10 Hertz with each tick mark, ranging from 0.00 to 120 Hertz. There is a horizontal axis with a ruler representing 1 second with each tick mark, ranging from 0 to 72 seconds. There are 15 elephant rumbles enclosed by a box with a thin black line. This thin black box designates that these are all individual rumbles within one rumble bout,

because each rumble is less than 20 seconds apart from its adjacent rumbles. Almost all of these elephant rumbles do not have any harmonics, except for one with 2 clear harmonics. Because of this, each rumble looks like one single bold black line against the orange, gray-speckled background of the spectrogram. Each of these lines have different shapes, lengths, and boldness. Some overlap each other, and others do not. In this eighth image representing the "Total Stack Durations", there are bright green boxes enclosing sequences of adjacent rumbles that are overlapping each other. These do not include any rumbles that have gaps in time between them. There are three bright green boxes total, and none of the boxes are labeled.

“Total Non-Stack Rumble Durations” Image: An image of a spectrogram generated using Raven Pro Sound Analysis Software ® (version 2.0). The spectrogram itself is bright orange and is speckled with gray. There is a vertical axis with a ruler representing 10 Hertz with each tick mark, ranging from 0.00 to 120 Hertz. There is a horizontal axis with a ruler representing 1 second with each tick mark, ranging from 0 to 72 seconds. There are 15 elephant rumbles enclosed by a box with a thin black line. This thin black box designates that these are all individual rumbles within one rumble bout, because each rumble is less than 20 seconds apart from its adjacent rumbles. Almost all of these elephant rumbles do not have any harmonics, except for one with 2 clear harmonics. Because of this, each rumble looks like one single bold black line against the orange, gray-speckled background of the spectrogram. Each of these lines have different shapes, lengths, and boldness. Some overlap each other, and others do not. In this ninth image representing the "Total Non-Stack Rumble Durations", 8 rumbles are enclosed by individual boxes with thin black lines, and the rest are enclosed by individual boxes with bright green lines. The bright green boxes

designate individual rumbles that are not overlapping with another rumble. There are 7 bright green boxes total, and none of the boxes are labeled.

"Number of Rumbles Overlapped" Image: An image of a spectrogram generated using Raven Pro Sound Analysis Software ® (version 2.0). The spectrogram itself is bright orange and is speckled with gray.There is a vertical axis with a ruler representing 10 Hertz with each tick mark, ranging from 0.00 to 120 Hertz. There is a horizontal axis with a ruler representing 1 second with each tick mark, ranging from 0 to 72 seconds. There are 15 elephant rumbles enclosed by a box with a thin black line. This thin black box designates that these are all individual rumbles within one rumble bout, because each rumble is less than 20 seconds apart from its adjacent rumbles. Almost all of these elephant rumbles do not have any harmonics, except for one with 2 clear harmonics. Because of this, each rumble looks like one single bold black line against the orange, gray-speckled background of the spectrogram. Each of these lines have different shapes, lengths, and boldness. Some overlap each other, and others do not. In this tenth image representing the "Number of Rumbles Overlapped", 7 rumbles are enclosed by individual boxes with thin black lines, and the rest are enclosed by individual boxes with bright green lines. The bright green boxes designate individual rumbles that are overlapping with another rumble. There are 8 bright green boxes total, and none of the boxes are labeled.

Figure 4: This image shows two geometric objects consisting of observations plotted on a grid represented by two axes (principal components). The geometric shape to the left is green, and the shape to the right is blue. The horizontal axis is labeled Dim1 (46.8%) and provides a ruler with three tick marks each labled 0, 4, and 8 from left to right. Based on the grid the horizontal axis

spans from values of -4 to +9.5, but there are no units provided. The vertical axis is labeled Dim2 (31%) and provides a ruler with three tick marks each labeled 0, 5, and 10 from bottom to top. Based on the grid the vertical axis spans from values of -5 to +16, but there are no units provided. Small symbols representing rumble bout observations are plotted on this grid, and connections between the outliers belonging to each cluster designation form the borders of the geometric objects. Cluster 1 is to the left, is a slanted diamond shape, and has hundreds of small green circles representing rumble bout observations. There are many of these on the bottom left side of this slanted diamond shape, and some of them blend together. Cluster 2 is to the right, and is a much wider, more rectangle-shaped diamond than Cluster 1. It is made up of hundreds of small blue triangles representing rumble bout observations. There is a key to the right that says "cluster". Under it there is a green box with a dark green circle, and to the right it is labeled "1". Under that green box there is a blue box with a dark blue triangle, and to the right it is labeled "2".

Figure 5: A map of all fifty recording sites surrounding the Nouabale-Ndokí National Park in the Dry season. There are many bodies of water in blue that are branching into the land in green. The edges of the land are soft and curvy, and there are very small bodies of water speckling the land masses. Some areas of the map have more water cutting into the land, especially on the right side of the map. There are three locations on the map represented by small pink circles with black borders. From top to bottom they are labeled "Mbeli", "Goualougo", and "Camp Bonio". There are small black circles that represent recording sites with no rumble bouts, and small white circles that represent recording sites that were not sampled for this thesis. There is a bold, black title on the top left of the image that reads "Dry Season: December 15th, 2017-March 15th, 2018". The rest of the recording sites have pie charts with green and blue shading, representing the relative

proportion of types of rumble bouts at each site. The sizes of the pie charts are proportional to the number of rumble bouts at each recording site. There are numbers in bold white font on each of the circles, showing the number of rumble bouts at that recording site. These numbers range from 1to 81. There is a distance ruler in the bottom left corner that ranges from 0 to 10 km, with tick marks at every 2.5 km. There is a key in the bottom right corner showing that the green proportion of the pie charts designates Cluster1, the blue proportion of the pie charts designates Cluster2, a small black circle designates no rumble bouts, a small white circle designates site not sampled, a small pink circle with a black border designates a location, and the numbers in the pie charts (represented in the key using a hashtag), designate the number of rumble bouts at that location.

Figure 6: A map of all fifty recording sites surrounding the Nouabale-Ndokí National Park in the Dry season. There are many bodies of water in light blue that are branching into the land in light green. The edges of the land are soft and curvy, and there are very small bodies of water speckling the land masses. Some areas of the map have more water cutting into the land, especially on the right side of the map. There are three locations on the map represented by small pink circles with black borders. From top to bottom they are labeled "Mbeli", "Goualougo", and "Camp Bonio". There are small black circles that represent recording sites with no rumble bouts, and small white circles that represent recording sites that were not sampled for this thesis. There is a bold, black title on the top left of the image that reads "Wet Season: May 15th, 2018-July 29th, 2018". The rest of the recording sites have pie charts with lime green and bright blue shading, representing the relative proportion of types of rumble bouts at each site. The sizes of the pie charts are proportional to the number of rumble bouts at each recording site. There are numbers in bold white font on each of the circles, showing the number of rumble bouts at that recording site. These numbers range

from 1 to 41. There is a distance ruler in the bottom left corner that ranges from 0 to 10 km, with tick marks at every 2.5 km. There is a key in the bottom right corner showing that the lime green proportion of the pie charts designates Cluster1, the bright blue proportion of the pie charts designates Cluster2, a small black circle designates no rumble bouts, a small white circle designates site not sampled, a small pink circle with a black border designates a location, and the numbers in the pie charts (represented in the key using a hashtag), designate the number of rumble bouts at that location.