ECOLOGICAL AND SOCIAL INFLUENCES ON ORANGUTAN LONG CALL BEHAVIOR AND ACOUSTIC VARIATION

by

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ABSTRACT

Vocalizations are used in multiple contexts for widely different functions. However, the vocalizing individual may convey more information than merely the primary context of the vocalization, including caller identity, dominance status, reproductive status, body condition, etc. Decoding these potential signals could be useful as a noninvasive research tool in conservation. We explore this possibility in the long-distance vocalization of the male orangutan, the long call, and address three questions.

When do males call? Researchers must first understand the temporal call patterns of the targeted species to know when and how to study the species. By using a passive acoustic monitoring (PAM) system and direct observation, we were able to study in an unbiased manner when flanged male orangutans call. We discovered that the diurnal orangutan calls more frequently at night than during the activity period.

What influences the calling behavior of individuals? Understanding if social or environmental factors influence vocal behavior is necessary to be able to disentangle the information content of vocal signals. While multiple social factors, like association with another individual, do result in a higher long call rate of male orangutans, the dominant influence on vocal behavior was food availability. We discuss how local ecology may determine to which degree each factor can influence vocal behavior.

How do vocalizations vary over time? Understanding which aspects of the vocalization remain constant and which vary is key to understanding which acoustic features may encode signals that should not change, such as identity, and signals that may change, such as body condition or dominance status. We found that, while there is inter-individual variation, overall the orangutan long call is not stereotyped, and the most easily measured acoustic features do not allow reliable identification of individuals over long time periods.

With current rates of deforestation around the world, conservation managers seek a less labor intensive and noninvasive method to monitor habitat condition. If researchers are able to decode acoustic signals, vocal behavior may provide a more sensitive method to monitor populations and, potentially, habitat condition. This research shows for the highly endangered orangutan clear limitations in this approach, but also highlights that habitat condition may be reflected in the calling behavior.

To my family for their support, and to Sam for putting up with me.

“Living wild species are like a library of books still unread. Our heedless destruction of them is akin to burning that library without ever having read its books.”
— John Dingell

“This book was written using 100% recycled words.”
— Terry Pratchett, Wyrd Sisters

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CHAPTER 1

INTRODUCTION

Vocalizations play a vital role in animal communication. Vocalizations can function in mate attraction, territory defense, alerting conspecifics to the presence of predators, and other species-specific roles. Additionally, the receiver of the vocal signal may be able to obtain more information from vocalizations than merely the primary contextual information (Taylor et al. 2016). The vocal signal can contain individually-identifiable signatures of the caller and reveal information about other characteristics, such as the age (Reby and McComb 2003; Ey et al. 2007; Mathevon et al. 2010; Benitez et al. 2016), sex (Ey et al. 2007), dominance status (Kitchen et al. 2003; Mathevon et al. 2010; Benitez et al. 2016), reproductive status (Reby and McComb 2003), and current body condition of the caller (Galeotti et al. 1997; Martín-Vivaldi et al. 1998; Poulin and Lefebvre 2003). In many species, conspecifics are able to identify individuals through their vocalizations (Terry et al. 2005; Sliwa et al. 2011; Pfefferle et al. 2013). It is potentially advantageous for receivers to be able to recognize the identity of conspecifics through their vocalizations, allowing them to assess whether or not to approach a calling conspecific (Ehnes and Foote 2014). Furthermore, encoded information about the caller’s reproductive status may play a role in pursuing mating opportunities for both sexes or reducing infanticide (Wich et al. 2003).

Disentangling the functionally relevant features of the vocalization could render vocal communication a vital research tool, especially for conservation applications (Terry et al. 2005; Potamitis et al. 2014), because acoustic signals are easily and noninvasively recorded and allow information to be collected over longer distances. The ability to recognize individuals by their vocalization alone may constitute a more accurate and less time-consuming method for estimating population densities, assessing number and size of territories, and tracking migration patterns (e.g., Celis-Murillo et al. 2009; Blumstein et al. 2011; Mennill 2011). Especially in species where few interactions are observed, changes in dominance status of an individual may be easier to discover by recording and analyzing the vocalizations. Furthermore, if the body condition of an individual can be inferred from acoustic signatures, such features could be used as an early indication of habitat decline (Fischer et al. 1997; Poulin and Lefebvre 2003).

Detecting potential signatures of individual identity, body condition, and social standing within vocalizations requires insight into three central factors:

1) When does the species call? Understanding the daily call patterns of a species allows researchers to know when and how to study the targeted species (Kessel et al. 2013; Sousa-Lima et al. 2013; Kalan et al. 2015). Yet, traditionally vocal behavior of diurnal or nocturnal animals has been studied during the respective active period of the daily cycle, and less attention has been paid to the resting period (Zamma 2013). However, potentially important vocal and social behavior may be occurring during the times of low activity levels. Frequently, during these times observer effort is lowest, thus contributing to our incomplete understanding of vocal behavior during the nonactive period.

2) **What influences the calling behavior of individuals?** Calling rate (the number of calls per unit time) has been used to study group dynamics (Payne et al. 2003; Rogers et al. 2013), reproductive status (McComb 1991; Payne et al. 2003), the internal state of the individual (Fine et al. 1977; Candolin 2003; Scheuber et al. 2005), fighting ability (McComb 1991), and habitat quality (Rogers et al. 2013). Because changes in behavior are frequently the first modification in response to variable or challenging circumstances, call behavior may reflect, for example, changes in dominance status, or body condition.

3) **How do vocalizations vary over time?** Before signatures of age, body condition, dominance status, etc., can be assessed, the variability of the acoustic features of the vocalizations must first be understood. To be able to successfully distinguish individuals by their vocalizations, acoustic features that have greater variation between individuals than within an individual must first be identified (Terry et al. 2005; Fox 2008). Additionally, these acoustic features must exhibit little variation over time (Fox 2008). If individuals can be identified by their vocalizations, conspecifics must be able to reliably recognize individuals over multiple years. Nonetheless, how acoustic features change over time was the focus of relatively few studies (Lengagne 2001; Gilbert et al. 2002; Briefer et al. 2010; Puglisi et al. 2016) and is therefore poorly understood.

To begin to address these three factors, we studied male orangutans in Central Kalimantan, Borneo, Indonesia. Orangutans are semisolitary primates that reside on only two islands in Southeast Asia, Sumatra (Pongo abelii) and Borneo (Pongo pygmaeus) (e.g., Muir et al. 1998, Delgado and Van Schaik 2000; Brandon-Jones et al. 2004). Orangutans are sexually dimorphic and are estimated to live 53-58 years in the wild

(Wich et al. 2004). Males are two-fold larger than females and are sexually mature by 14 years of age (e.g., MacKinnon 1974; Banes et al. 2015). However prominent, male secondary sexual characteristics do not develop until around the age of 20 (Winkler 1989; Delgado and Van Schaik 2000; Wich et al. 2004). The appearance of large subcutaneous connective tissue on the face (flanges) and pendulous laryngeal sacs coincides with the production of the long call (Delgado and Van Schaik 2000; Wich et al. 2004). Orangutan long calls can be heard for over a kilometer (Galdikas 1983; Mitani 1985) and are thought to communicate information about individual identity and call context (Lameira and Wich 2008; Spillmann et al. 2010; van Schaik et al. 2013; Askew and Morrogh-Bernard 2016; Spillmann et al. 2016). Spontaneously produced long calls are thought to indicate the caller's direction of travel, and conspecifics can spatially orient themselves accordingly (van Schaik et al. 2013; Askew and Morrogh-Bernard 2016). For example, Sumatran females typically stay within a limited range of the dominant long calling male, whereas Bornean females typically travel away (Setia and van Schaik 2007; Spillmann et al. 2010). Males on both islands may choose to either pursue or avoid the long calling male (Setia and van Schaik 2007; Buckley 2014).

For several reasons, orangutans are ideally suited for investigating how the various influences affect vocal behavior and the nature of encoded information. First, male orangutans produce a long-distance vocal signal, the long call, which is easy to record, even from a distance (Spillmann et al. 2015). This enables us to monitor orangutans around-the-clock using passive acoustic monitoring (PAM) systems, providing an unbiased sample of both diurnal and nocturnal calling patterns. Second, among the great apes, orangutans are particularly interesting for examining how social and environmental influences affect calling behavior. Orangutans are semisolitary and are the least social great ape (e.g., Marchant and Nishida 1996), which should facilitate dissection of different social factors and their influence on calling behavior. Orangutans appear to experience longer periods of food droughts than the other great apes (Harrison et al. 2010). Interspecies and island comparisons have shown that different environmental conditions and food availability affect orangutan behavior (Knott 1998; Wich et al. 2006; Marshall et al. 2009). In general, Sumatran forests have higher food availability, which permits orangutans to live at higher densities; Sumatran orangutans are also more social (Singleton and Schaik 2001; Husson et al. 2009; Marshall et al. 2009). Lastly, orangutans are a long-lived species (Wich et al. 2004), and males have large home ranges (Delgado and Van Schaik 2000; Singleton and Schaik 2001; Buckley 2014), creating a high degree of spatial separation between individuals, even within a population. Low population densities may have exerted increased selective pressures for the long call to encode identity, age, body condition, and dominance status. If individuals do not come into contact with each other often, then perhaps there is increased selective pressure to encode individual identity in vocalizations so that visual contact is not necessary for recognizing nearby individuals. This provides receiving individuals with more information to decide on whether they should avoid or approach the vocalizing individual. Individual distinction through features of the long call of males has been reported (Spillmann et al. 2010; Askew and Morrogh-Bernard 2016; Spillmann et al. 2016). However, it is unknown if these individual-specific features remain characteristic over months or even years. Furthermore, the secondary sexual characteristics of flanged male orangutans are thought to change with age and body condition (MacKinnon 1974; Delgado and Van

Schaik 2000; Banes et al. 2015), and may be part of the mechanism by which these characters are encoded in the call. Because the acoustic features that comprise this information may vary, the variation of the long call must be examined in detail over sufficiently long periods.

In Chapter 2, we provide the first unbiased observation of the diurnal and nocturnal long call behavior of male orangutans. To do so, we first test the passive acoustic monitoring system with traditional observation methods, to be able to interpret nocturnal long call behavior recorded by the PAM system. Even though the PAM coverage range is limited, the trends were consistent with the trends observed with traditional follow methods. Furthermore, the composition of nocturnal long calls was similar to diurnal long calls. Even though nocturnal long calls have been reported previously, we provide the first evidence that male orangutans are calling more at night than during their normal diurnal activity period.

In Chapter 3, we use a long-term database to investigate the environmental and social influences on long calling behavior of male orangutans in southern Borneo and assess our findings in the context of what is known about other populations in different social and environmental conditions. We show that both social and environmental factors affect call rate (the number of long calls made per hour). However, this is the first study to indicate that food availability is a strong determinant of calling behavior. Unlike in previous studies, we analyzed a long-term database, which allowed us to detect a correlation between calling behavior and seasonal variation in food availability.

In Chapter 4, we examine the daily, monthly, and yearly variation of the male orangutan long call. We discovered that short and long term variability can decrease the ability to correctly identify a male orangutan by his long call. There is, however, individual variation in how constant certain acoustic features remain over time. Furthermore, we provide evidence of dynamic adjustments of the upper vocal tract, which may allow callers to mask properties of the upper vocal tract that would reflect vocal tract length, and thus, body size.

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CHAPTER 2

NOCTURNAL LONG CALL BEHAVIOR OF THE DIRURNAL ORANGUTAN: A COMPARISON OF TRADITIONAL OBSERVATION AND PASSIVE ACOUSTIC MONITORING (PAM)

Vocalization is a widespread and diverse means of acoustic communication in animals. When and how often an individual vocalizes can be influenced by a complex interplay of factors, including environmental conditions, physiological condition of the sender and behavior of potential receivers (e.g., Cowlishaw 1996; Setia and van Schaik 2007; Buckley 2014; Chapter 2). For example, timing of vocalization could depend on ambient noise levels or competition for acoustic niches (e.g., Schneider et al. 2008; Dominoni et al. 2016). Traditionally vocal behavior of diurnal or nocturnal animals has been studied during the respective active period of the daily cycle, and less attention has been paid to the resting period. However, potentially important vocal and social behavior may be occurring during the times of low activity levels. Frequently, during these times observer effort is lowest, thus contributing to our incomplete understanding of vocal behavior during the nonactive period. In diurnal animals, the reduced observer effort can be attributed in part to the difficulties associated with studying and following any animal at night. In addition, prevailing assumptions about the activity patterns of supposedly diurnal animals equally affect sampling effort (Zamma 2013). Most knowledge of nocturnal activity of diurnal species has been derived from anecdotal observations (La 2011), and detailed studies of nocturnal activities of diurnal animals, including vocalization, are infrequent. In a review of the nocturnal activities of birds, 30% of North American birds (18 of 22 orders) were found to vocalize at night, yet 70% of these species are classified as diurnal (La 2011). Clearly, vocal behavior of 'diurnal' animals is not restricted to daylight hours, and the relationships between diurnal and nocturnal behavior remain understudied.

The majority of primates are diurnal, few are nocturnal (Overdorff and Rasmussen 1995; Fernandez-Duque 2003) and cathemerality (flexible, irregular activity periods) is rare in primates but otherwise common in mammals (Rasmussen 2005; Donati et al. 2013). Prosimian primates (lemurs, lorises, tarsiers) exhibit nocturnal activity (Erkert and Kappeler 2004), and increasing evidence of a cathemeral lifestyle for 'diurnal' lemurs is coming to light (Donati et al. 2013). The 'diurnal' ring-tailed lemur, travels at night (especially on nights illuminated by moonlight), and may also mate at night (Parga 2011). Owl monkeys exhibit a cathemeral lifestyle and increase their nocturnal activity with moonlight (Fernandez-Duque 2003). More evidence is emerging about nocturnal activity in diurnal primates (Drubbel and Gautier 1993; Parga 2011; Krief et al. 2014), opening up the possibility that some species previously classified as diurnal may indeed be cathemeral in the wild (Donati et al. 2013). Video trap studies have shown chimpanzees raiding crops at night, a behavioral adjustment that may afford both lowered predation risk and access to high nutrient foods (Krief et al. 2014). Other diurnal primates have been seen to travel (gelada baboons, Kawai and Iwamoto 1979; Japanese macaques, Nishikawa and Mochida 2010; ring-tailed lemurs Parga 2011), play (rhesus macaques, Vessey 1973), eat (rhesus macaques, Vessey 1973), copulate (rhesus macaques, Vessey 1973), and vocalize (barbary macaques, Hammerschmidt et al. 1994; red howlers, Drubbel and Gautier 1993).

Because direct observational data during the night are often missing, absence of nocturnal activity has been inferred from indirect evidence (Drubbel and Gautier 1993; Zamma 2013). It is thought that nocturnal activity of diurnal primates is unlikely, because individuals can be found in the same night nest or sleeping tree in which they had been seen the evening before (MacKinnon 1974; Riss and Goodall 1976). Not only does this inference not account for the possibility that individuals could be exiting and re-entering these sleeping areas during the night, but it also does not exclude the possibility for vocal behavior in the nest.

Recent technological advances have enhanced our ability to examine nocturnal activity in general and to remotely monitor the presence, movement, and behavior of groups and individuals (Blumstein et al. 2011). Passive acoustic monitoring (PAM) is a remote acoustic recording technology using a microphone array, hydrophones, or other autonomous recording units (Blumstein et al. 2011; Marques et al. 2013; Kalan et al. 2015). PAM systems have become increasingly popular over the past few decades, beginning with the development of autonomous recording units (ARUs) in the 1990s (Sousa-Lima et al. 2013). ARUs are "any electrical recording device or system that acquires and stores data internally without cables, or radio links… or a person to run it" (Sousa-Lima et al. 2013). Commercially available ARUs have reduced the level of technical expertise previously required to build and deploy PAM systems, granting a larger demographic of field researchers the ability to afford and deploy PAM systems

(Sousa-Lima et al. 2013).

The practical and scientific benefits of ARUs and PAM systems explain their increasing popularity. Because advanced technical knowledge is no longer required to obtain and use ARUs, field personnel can be trained to use the system, freeing up resources and time (Sousa-Lima et al. 2013). PAM systems are less labor intensive, because they do not require researchers to actively track and follow their study species (Kalan et al. 2016). As these methods are noninvasive, disturbance to both the habitat and its resident animals is minimal (Kessel et al. 2013; Sousa-Lima et al. 2013; Kalan et al. 2015). With the use of multiple ARUs or connected networks of ARUs, larger areas can be covered (Kessel et al. 2013), affording more flexibility in recording times and configurations than traditional survey methods (Kessel et al. 2013; Sousa-Lima et al. 2013). Increasing coverage means that multiple individuals and species can be tracked simultaneously without concentrated or specific efforts for certain focal targets. Overall, PAM systems are becoming more affordable and have become a cost effective way of determining species presence and abundance (Kessel et al. 2013; Sousa-Lima et al. 2013; Kalan et al. 2015). This is especially true for locations that are either remote or have rough terrain, which makes active following difficult (Sousa-Lima et al. 2013; Kalan et al. 2016). In cases where both methods are feasible, a combination of traditional methods and PAM systems can give a better, more robust estimate of occupancy than either alone (Kalan et al. 2015). Lastly, because acoustic recordings are stored in PAM systems, the data files can be repeatedly accessed and analyzed (Kalan et al. 2015). This could be used to double check analysis, compare methods using the same data, or address different research questions at a later date, none of which are possible with traditional visual and listening survey methods. Furthermore, ARUs can reduce observer bias and minimize error (Celis-Murillo et al. 2009; Hutto and Stutzman 2009), because the same metrics can be verified by other researchers.

Nonetheless, limitations still apply that may prevent ARUs from being used solely or apart from traditional methods (Kalan et al. 2015). To properly deploy ARUs, researchers must already have a good understanding of the target species' behavior – including vocal behavior (Kessel et al. 2013; Sousa-Lima et al. 2013; Kalan et al. 2015). Basic understanding of home range size, seasonality of calling, or travel patterns is important for proper installation of a PAM system, depending upon the biological question of interest (Sousa-Lima et al. 2013). Furthermore, certain vocal metrics dictate the detection range of the ARUs. Detection range itself does not yet have a standardized definition. Kessel et al. (2013) propose to define detection range by the probability of detecting the call on the recording in relation to the distance between the receiver and calling individual. Without proper understanding of the detection range, PAM results could be misinterpreted and lead to the mismanagement of conservation sites (Kessel et al. 2013). However, even knowing the detection distance for vocalizations of a target species, each ARU configuration needs to be tested for each target species, which is typically inadequately considered (Kessel et al. 2013). To further complicate the issue, detection range may change and vary. This is commonly acknowledged in aquatic systems (Kessel et al. 2013), but it also applies to terrestrial environments when atmospheric changes or habitat alteration could dampen sound transmission, for instance through changes in humidity or tree falls (Wiley and Richards 1978; Merchant et al. 2015). Lastly, in PAM systems consisting of ARUs the data need to be manually recovered at regular intervals because they do not rely on cables or other connections (Kalan et al. 2015). This imposes limits on storage or bandwidth capacities and precludes real-time data processing (Kalan et al. 2015). Even though the deployment of these devices is user friendly, data extraction is a time consuming process, which requires more research time and specialized algorithms to properly extract target vocalizations (Kalan et al. 2015). Algorithms and software programs have been developed to speed up data extraction. However, these methods are subject to false negatives and false positives (e.g., Blumstein et al. 2011). Thus, these files still need to be checked manually. Human observers listening or visually searching the acoustic files find more targeted sounds and are more accurate in classifying targeted sound events (Swiston and Mennill 2009).

Before PAM systems can be effectively employed to study nocturnal vocalization, we must compare their performance to traditional methods. Validation should be most effective comparing the PAM system to traditional observational follow data of diurnal vocal behavior. Furthermore, diurnal vocal behavior can be used to normalize and contextualize nocturnal vocal behavior. For instance, if the PAM system does not detect nocturnal vocalizations, it is unclear whether the absence of vocalization is attributed to absence of the behavior or absence of animals in the vicinity. Characterizing local trends in diurnal vocalization can get around presence/absence uncertainty, and may also reveal more crepuscular activity.

ARUs are now enabling researchers to access places, habitats, and times for acoustic monitoring, which would have been difficult otherwise, to the point where ARUs constitute a more viable method than traditional monitoring methods in many locations. With increased use of PAM systems (Piel 2014), it is important to understand how data collected with them compare to traditional observer-based data. For a number of field sites long-term behavioral data are available, which must be put in context before switching to a PAM system or comparing between sites with two methods. Few studies have directly compared traditional methods with ARU systems (Hobson et al. 2002; Celis-Murillo et al. 2009). To start to address this question, I installed three permanent ARUs at a field site on Borneo where behavioral data on Bornean orangutans (Pongo pygmaeus wurmbii) have already been collected for over a decade. Flanged male orangutans produce a long-distance vocalization, the long call, which can travel a kilometer in the forest. ARUs have been tested at another Bornean site and reliably detected them up to 700 m. Thus, we placed three ARUs around our research grid, roughly one kilometer apart to maximize coverage area (Figure 2.1). We then compared this PAM system with traditional behavioral data from follows in the same area to understand whether or not the two methods yield similar data on frequency and timing of orangutan long call behavior.

In this chapter, I present the first direct method comparison between traditional follow data and PAM systems for calling behavior, comparing the long call trends of each method across different time scales. Because these data were collected with both methods simultaneously, it allowed us to examine the detection range of ARUs and the potential directionality of the orangutan long call. The ARUs recorded around-the-clock, allowing us to also examine the frequency and timing of nocturnal long calling. Additionally, we compare nocturnal and diurnal calling and assess whether nocturnal long calls differ in composition or basic acoustic characteristics from those of diurnal long calls.

2.1 Methods

This research was conducted in collaboration with the Borneo Nature Foundation and the Center for International Cooperation in Sustainable Management of Tropical Peatland in the Natural Laboratory of Peat-swamp (NLPS) in the Sabangau forest, in southern Borneo, Central Kalimantan Indonesia. The NLPS is 500 km2 nested within the 5,780 km2 area that constitutes the Sabangau forest. Within the NLPS, the main study grid, where the research was conducted, is 8 km2. The Sabangau forest is a mixed-peat swamp that was concession logged until 1997, but illegal logging continued until 2004. It is estimated that there are around 6,900 individual orangutans, Pongo pygmaeus wurmbii, residing in the Sabangau forest with an average density of 1.12 individuals/ km2 (Morrogh-Bernard et al. 2003; Husson et al. 2009). This research took place from August 2012 to September 2013.

To compare passive acoustic monitoring systems (PAM systems) to traditional observational data (“follows”), flanged male orangutans were followed, and three permanent ARUs from Wildlife Acoustics, model SM2+, were placed triangularly around the research grid. The ARUs were set 1 to 1.25 km apart (Figure 2.1), at a height of about 1.5 m. Because orangutan long calls can travel up to a kilometer in the forest, this distance was chosen to maximize the covered acoustic area. Furthermore, the ARUs were placed near common travel routes of flanged male orangutans (personal correspondence with Ben Buckley). Each recorder was equipped with one SMX-II waterproof microphone (Wildlife Acoustics). Preliminary data were used to establish an acoustic radius of about approximately 500 m for each ARU, providing coverage of a total area of approximately 2.5 km2. Each ARU recorded from 00:01 h to 12:59 h and from 13:01 h to

23:59, providing almost a daily recording time of 24 hours; the 4-minute interval was used to avoid conflicts with recording start and stop times of the ARUs. Recordings were made at 16 bits with a 22.50 kHz sample rate. ARUs were run on 4 D batteries, which lasted for one week. Each week, the batteries and SD cards were replaced, and the files were checked before being downloaded onto an external hard drive.

The recorded files from the ARUs were inspected for long call behavior by visual scanning of spectrograms in Avisoft SASLab Pro (version 5.2.10). Files were initially filtered, Tschebyscheff IIR low pass band filter at 1.2 kHz, before they were searched for the presence of long calls. After a long call was identified, the duration of the total call, the number of pulses, the rate (number of pulses.s-1), and the type of pulses were extracted. Each pulse was classified into one of six categories: volcano, high roar, low roar, intermediate, sigh, and bubbles, as previously described by Ross and Geissmann (2007) and Spillmann et al. (2010). The quality of recording was noted on a scale of 1 to 5, one being poor quality and assumed to be the furthest detectable distance between calling orangutan and the ARU, and five as the highest quality, typically indicated by capture of upper harmonics.

Direct follow observations of orangutan calling behavior were made by follows of focal flanged males. Flanged male orangutans were followed for the extent of their activity period (from night nest to night nest) for multiple consecutive days. During these follows, behavioral data were taken following an established protocol by Morrogh-Bernard (2009). When the focal male produced a long call, a GPS coordinate of the male was taken.

When the male produced a long call, the distance to the nearest ARU was determined, and the direction of his call relative to that ARU was determined. For example, if the focal male was directly south of the closest ARU and he called directly north, the direction of the long call is 0º. If a male was directly south of an ARU and called to the east or west, the direction of the long call was noted as 90º. On days a flanged male was followed, the recordings from all three ARUs were searched for the entire day. To avoid biasing the search of these files for long calls, files were searched without knowing which ARU the male was closest to that day, or if he produced any long calls. This allowed us to test the limitations of the ARU, including distance to the individual and effects of directionality of the long call on the likelihood of being recorded. If a long call was found on an ARU within 6 minutes of the time a long call was observed during a follow, the long call recording on the ARU was assumed to be produced by the male followed (6 minutes was used because different researchers' watches were not synchronized).

To compare methods, diurnal call patterns of male orangutans recorded with traditional follows were compared to the times long calls were found on the ARUs. Files from the ARUs were initially searched on the 15th to the 19th of each month, a total of 60 days, for a random sample throughout the year. The ARU files were searched in their entirety. However only times between 04:00 h and 17:00 h were used to compare with follow data, since this is the time period during which orangutans are typically followed. The total number of long calls heard and produced during a flanged male orangutan follow was compared to the total number of long calls found on the ARU files. Next, to standardize the coverage area of the two methods, only long calls that occurred within the coverage area of the PAM system were used and only from follows where 80% or more of the follow occurred within the PAM coverage area. Initially, the timing of long calls during follows from the long call database was examined over the same time period as the PAM system (August 2012 to September 2013).

For a general trend of daily and seasonal (monthly) calling rates, the PAM system and traditional follow data were compared day to day and month to month over the course of the 13 months. The two methods were compared using Pearson’s correlation analysis in R (v. 3.2.3; R core team (2015)).

The PAM system is ideally suited to record nocturnal calling, and its use allowed us to examine the frequency of nocturnal calling, nocturnal call patterns, and, thus, facilitated the comparison between nocturnal and diurnal calling. With these data, we can also test the hypothesis that nocturnal call behavior is a continuation of diurnal vocal behavior. To do so, we divided the 24-hour period into a 12-hour day (5-16) and a 12-hour night (17-4) period. We then compared the number of diurnal calls recorded on the PAM system to the number of nocturnal calls recorded with a Pearson’s correlation analysis. We also compared the duration of the long call, number of pulses, rate of the call, and the type of pules used (expressed as a percentage of pulse type/total number of pulses) between diurnal and nocturnal long calls with a Welch two-sample t-test. We hypothesized that periods with high diurnal long calls will also be characterized by high nocturnal long call rates, and during periods of few diurnal long calls, there will be no nocturnal long calls. Also, we hypothesize that nocturnal long calls will have the same composition as diurnal long calls.

2.2 Results

2.2.1 Testing the autonomous recording units

By using identified times at which long calls were produced during follows, the detection range of the ARUs could be tested by including the location and the direction the male faced when he called. If the male was within 150 m of an ARU, 100% of the long calls were captured on the nearest ARU (Figure 2.2). At distances greater than 150 m, the proportion of long calls that were recorded on the ARU decreased. Only half of the long calls were captured between 150-200 m, a third of the calls were registered at 350 m, and calls produced 450 m or more from an ARU typically were not captured. However, there were a few exceptions. During one follow 550 m from the nearest ARU, three long calls were produced and all of them were recorded on the ARU. Furthermore, long calls produced up to a kilometer away were occasionally recorded on an ARU.

To test directionality of the long call, we looked at the proportion of calls that were recorded on the nearest ARU in relation to the direction the male faced as he called. If the male was facing directly at the ARU (0º), 75% of the calls were captured on the ARU (Figure 2.3). If the male faced 45º away from the ARU on either side, 57% of the long calls were recorded. Once the male's calling direction was perpendicular (90º) or 135º to the ARU, the number of recorded long calls dropped to only 25% and 37%.

The distance from an ARU and the direction in which the male faced during the call relative to the ARU therefore affected the likelihood of calls being registered. To test this relationship and the significance of each factor, we used a binomial GLM. About half of the calls we examined were recorded on an ARU (20 recorded out of 41 calls examined). In this analysis neither distance of the male from the ARU nor direction reached significance (GLM, AIC = 55, n = 46; direction p = 0.21, slope estimate = -0.009; distance p=0.06, slope estimate = 0.005). This lack of a significant effect was surprising given the data shown in Figures 2.2 and 2.3, but might be explained by the small sample size. When these two factors were examined separately, a significant effect of distance emerged (GLM, AIC = 58, distance p = 0.006, slope estimate = -0.007), but no significant effect of direction was found (GLM, AIC = 59, distance p = 0.1, slope estimate = -0.01).

The recording quality of the PAM system is not comparable to what follow recordings can provide (Figure 2.4). The signal to noise ratio is poor in the PAM recordings, which cannot be overcome by more filtering (Figure 2.4b). The low recording quality seriously jeopardizes the ability to automatically detect long calls on PAM recordings and limits the precision of measurements that can be made using these recordings.

2.2.2 General long call behavior captured on the PAM system compared to traditional observation data

To directly compare the trends of general long call behavior as recorded by traditional observer data and the PAM systems, we collected data on the same day using both methods. Initially, for the most accurate comparison, we only used long calls produced by the focal male during follows that occurred within the range of the PAM system. Using only those follows, the results of the two methods were highly correlated (Pearson’s correlation, p < 0.0001, r = 0.89, n = 42; Figure 2.5).

Next, we compared the long calls produced and heard on follows that occurred within the coverage area of the PAM system. The correlation between the two methods was slightly weaker, but still highly significant (Pearson’s correlation, $p < 0.0001$, $r = 0.77$, $n = 39$). To examine, if both methods show a similar trend overall without being area-limited, we used long calls made and heard during flanged male follows that occurred at any location and compared this number to recorded vocalizations on the PAM system. Both methods showed a similar trend and the numbers were highly correlated, but the PAM system recorded only about half the calls that were directly observed during follows (Pearson’s correlation, $p < 0.0001$, $r = 0.56$, $n = 68$; Figure 2.5). Overall, observers captured more long calls than were found on the ARU files. The only instances where more long calls were found on the ARU files than were recorded during follows occurred when the observers were in a different area of the forest and out of hearing range of calls captured on the PAM system.

The daily calling behavior was then summed into monthly calling rates and used to explore annual trends and to reduce potential noise that could affect the correlation between the two methods. Data from the two methods displayed a similarity that was comparable to the daily comparison, when only considering area-limited follows (Pearson’s correlation, $p = 0.0014$, $r = 0.84$, $n = 11$). But, when follows that occurred at any location were compared to the PAM system, the correlation coefficient for monthly data was higher than that for daily data (Pearson’s correlation, $p = 0.017$, $r = 0.67$, $n = 12$).

2.2.3 Diurnal and nocturnal calling behavior

The diurnal calling patterns of the male orangutan long calls were examined using the same days previously discussed for the follow data and the PAM system. Even though the two methods captured a different number of long calls, these two methods yield similar patterns of calling behavior (Figure 2.6). Both methods showed a call peak in the early morning, a weak peak in the late morning, and a strong evening peak. The morning and evening peaks are likely coincident with leaving and entering the night nest. The two methods yielded slightly different timing of the peaks.

We increased the sample size of both methods to include additional days over the same time period, not limited to dates that directly overlap, to test if a larger sample size of both methods confirmed the daily pattern of calling activity. We used the entire behavioral database of long calls produced during male follows and heard during male and female follows for the time period of PAM system use (i.e., August 2012 – July 2013) and compared it to the remotely recorded data. Data from both monitoring methods showed strong morning and evening peaks of calling activity (Figure 2.6; follow hours = 2047, PAM hours = 1236; LCs during follows = 111, LCs recorded on PAM = 463 total (154 diurnal)).

Night calling was only monitored with PAM systems. Surprisingly, more long calls were found on the ARU recordings at night than during the day, 309 nocturnal long calls compared to 154 diurnal long calls. It is unlikely that this difference was a result of a slightly higher sampling effort at night (7 more nights were surveyed than days for a total of 110 night and 103 diurnal sample days). Nocturnal call behavior was significantly correlated with diurnal calling, during nights both preceding and following the monitored diurnal calling activity (Pearson’s correlation; previous night to following day $p < 0.0001$, $r = 0.51$, $n = 74$; night behavior following day behavior $p < 0.0001$, $r = 0.62$, $n = 75$; Figure 2.7).

There was a clear nocturnal long call pattern with low calling rates early during the night, presumably right after the male built a night nest and the onset of sleep (Figure 2.8). Males were most likely to call at night during the period from just before midnight until early morning. The pattern of calling activity during the night was similar to that found for daytime calling (Figure 2.9). However, there were nocturnal calls recorded during certain periods when no diurnal calls were recorded (March-April). The absence of diurnal and nocturnal calls recorded on the ARU, however, may merely be an indication of absence of male orangutans in the study area, rather than indicative of a lack of vocal behavior.

2.2.4 Composition of nocturnal long calls compared to diurnal long calls

The structure and composition of diurnal and nocturnal long calls were similar. Nocturnal long calls used the same pulse types in a similar order, i.e., higher energy pulses (huitus and high roars) preceded lower energy pulses (sighs and bubbles; Figure 2.10). However, nocturnal calls had fewer pulses (mean number of diurnal pulses = 25.1, mean number of nocturnal pulses = 18.4; Welch two-sample t-test, $p = 0.005$, $t = 2.92$, $n = 64$; Figure 2.11a) and were consistently produced at a slower pulse repetition rate (mean diurnal rate = 0.55, mean nocturnal rate = 0.46; t-test, $p = 0.002$, $t = 3.35$, $n = 64$, Figure 2.11b). The total duration of nocturnal and diurnal long calls did not differ (mean diurnal duration = 46.52 s, mean nocturnal duration = 40.61 s; t-test, $p = 0.20$, $t = 1.29$, n

$= 64$). There was no significant difference between the composition of diurnal and nocturnal long calls. Only one pulse type, the huitus, showed a trend toward more frequent use in nocturnal calls, but this trend was not significant (t-test, $p = 0.066$, $t = -1.87$, $n = 64$).

Recording quality influenced the duration measurements of the long call and the counting of the number of included pulses, especially for soft pulse types. The duration and the number of pulses was highly dependent on the recording quality (lm of duration, $p = 0.001$, $R2 = 0.16$, $n = 64$; lm of number of pulses, $p = 0.002$, $R2 = 0.13$, $n = 64$), and, as expected, the number of pulses is highly dependent on duration ($p < 0.001$, $R2 = 0.78$, $n = 64$). However, the measurements of pulse rate within a long call (number of pulses.s-1) were not influenced by recording quality (lm, $p = 0.44$, $R2 = -0.006$, $n = 64$). The assessment of which type of pulse is present can also somewhat depend on recording quality. Even though pulse type was verified by visual inspection and listening, at low recording quality it can be difficult to determine the subtle differences between certain pulse types. Lastly, there was a significant difference of recording quality between the diurnal and nocturnal long calls. The diurnal recordings had a higher mean quality (mean diurnal recording quality = 3.17, mean nocturnal recording quality = 2.53; t-test, $p = 0.05$, $t = 2.02$, $n = 64$).

2.3 Discussion

2.3.1 Detection of long calls on the PAM system

The detection range for long calls by the ARUs shows substantial variation. Overall, long call detection is negatively correlated with increasing distance and not significantly related to the angle of the calling male relative to the ARU. If these two factors are simultaneously considered, neither factor reached significance in our data set. However, this lack of significance for distance is most likely a result of sample size and the fact that distance was limited by the proximity of another ARU, thus excluding data clearly outside the detection range. Because sound attenuates with distance (e.g., Marten et al. 1977; Maciej et al. 2011), detection range must be limited. It is interesting, however, that considerable variability existed in whether or not a call at greater distance could be detected. Microhabitat differences may account for this difference in sound transmission as well as the height at which the orangutan vocalizes (Marten et al. 1977). In regard to the direction in which the male faces relative to the location of the ARU, identification of individuals by call features becomes more difficult with increasing angle away from the ARU (Spillmann et al. 2015). This result also suggests detection distance may not be severely affected, but recording quality may suffer from additional scattering of sound.

The detection range of the ARUs in the Sabangau forest was lower than in a previous orangutan study using the same device (Spillmann et al. 2015). There was 100% detection of long calls up to 150 m away from the ARU, after which the proportion of long calls captured on ARU recordings dropped significantly. By 250 m, only half of the long calls were captured, and beyond 450 m, most calls were not captured. This steep drop in detection range after a certain distance is similar to that found in previous studies (Kessel et al. 2013; Spillmann et al. 2015). However, Spillmann et al. (2015), who studied the same subspecies of Bornean orangutans in a similar habitat type, had a 100% detection range up to about 350 m and 50% detection up around 800 m, more than double the detection range found in this study. There are several possible explanations for the discrepancy between our two studies. First, the placement of the ARUs in the forests differed. We placed our ARUs within arm's reach to easily change batteries weekly, whereas Spillmann et al. (2015), had placed the microphones 10 m above ground. This difference generates slightly longer paths for sound transmission in our study, but this change is small and therefore cannot account for the two-fold change in detection range. Alternatively, the effects of scattering and reflection through foliage may differ substantially between horizontal and horizontal as well as vertical sound transmission paths (Marten et al. 1977). Furthermore, notable differences in habitat quality exist between the two study sites, even though both are categorized as mixed peat-swamps (Vogel et al. 2015). Detection range can also change within a study site as weather and forest conditions vary (Kessel et al. 2013). It is therefore not surprising that two similar forests can have different detection ranges. Second, we used different methods to search for the presence of long calls on the ARU recordings. We visually inspected spectrograms to search for the presence of calls. In contrast, Spillmann et al. (2015) used algorithms in the program Song Scope to locate calls. These two data extraction methods are not likely to account for the difference in detection ranges of long calls because previous studies have found human observers manually scanning sound recordings were significantly more accurate and detected more targeted sounds than automated methods (Swiston and Mennill 2009). These two studies highlight the importance of testing the detection range for each ARU in every forest to avoid misleading conclusions (Kessel et al. 2013).

Before PAM systems can be fully utilized or replace traditional methods, detection of targeted vocalizations on the PAM files needs to be made less labor intensive and more accurate. As previously mentioned, two methods have been used for detecting targeted vocalizations, visual inspection and batch processing algorithms. Even with filtering, vocalizations are difficult to detect with visual inspection (Figure 2.4) because of the poor signal to noise ratio. The signal to noise ratio may be improved somewhat by deploying more ARUs in a smaller area and placing the microphones higher in the canopy as previously discussed. However, this may not completely remedy the problem, and visual inspection of the sound files will remain time consuming. Using an algorithm and batch processing the files still produces many false negatives, and thus finding targeted vocalizations still remains a time consuming process (pers. correspondence with Spillmann). Researchers are striving to improve these algorithms, but the long call of male orangutans is particularly difficult to detect. Algorithms work best on short, stereotyped vocalizations, unlike orangutan long calls which are long vocalizations consisting of multiple different pulses. Further, orangutans can call at any time of day and therefore do not make it possible to temporally restrict the inspection of recordings. In contrast, gibbons predominantly great call at dawn, allowing researchers to limit their search on recordings to a few hours a day. Even in the case of gibbons, however, researchers need to first establish with unbiased PAM sampling methods that they do in fact predominantly call only at dawn. Depending upon the research question or application, not every vocal event needs to be found or recorded. For example, if researchers are trying to estimate the population densities of gibbons, it is not vital that every great call recorded is discovered; only a limited number of each group is necessary to map out their territories. Also, searching recordings for great calls can be limited to a few hours each day, which greatly reduces the time required to find the vocalizations on the PAM recordings. Because not every vocal event needs to be discovered and few recordings of each group are required, a few ARUs could be constantly moved in the forest to best map out gibbon group territories. By moving the ARUs, they will eventually get placed near the core territory of each group, providing better recording quality, which may be sufficiently high to perform some acoustic analysis on the vocalizations. In contrast, more effort is required to detect orangutan long calls, because they call infrequently, not during specified hours and they have vast home ranges. The larger and more fluid home range size of the male orangutan makes it more difficult to place enough ARUs in the forest to gain recordings with a better signal to noise ratio.

2.3.2 Comparison between PAM system and traditional follow data

To assess nocturnal behavior recorded by the PAM system correctly, we first must understand how reliably the PAM system allows detection. This can be done by comparing PAM system data to the traditional follow data for diurnal call activity. Overall, the PAM system showed the same trends as traditional follow data, but typically, the PAM system recorded fewer calls. Unsurprisingly, in a direct comparison on individual days, the best correlation between the two methods was found when only the long calls produced by the focal male that occurred within the coverage area of the PAM system were used. If all long calls produced and heard during follows are used, the location of male generating the calls classified as heard (i.e., not produced by the focal male) is unknown and may fall outside the PAM coverage area. Furthermore, observers can hear calls over twice the distance of the PAM system detection range (1 km compared to about 450 m) and therefore will register more calls.

When we looked at the number of long calls recorded by follow data compared to the PAM system on a monthly basis, the correlation coefficient was slightly higher than for the comparisons on individual days. The monthly comparison did not reduce the noise difference between the two systems when only using area-limited follows, but did increase the correlation (and reduce the noise) with the non-area-limited follows. These results show that the detection rate of the PAM system consistently underestimates the actual calling rate, but that a consistent relationship exists between the detection rates of the two methods.

Overall, if years or decades of follow data are available for a field site, PAM system data can yield useful comparative data with minimal “calibration” of the two methods. However, depending on the specific research questions, PAM system data may or may not provide an alternative methodology to the time-consuming traditional follow approach.

2.3.3 Diurnal and nocturnal long call behavior and composition

The analysis of the timing of long calls during the 24-hour period revealed some very interesting findings. Flanged male orangutans produce long calls most frequently during the night until they exit their night nest in the morning. The second highest peak occurred during the late afternoon, around the time they build and enter a night nest.

An initial study examining the circadian distribution of the long call of male orangutans found a difference between Sumatran and Bornean orangutans (MacKinnon 1974). Sumatran orangutans were found to have peaks in long call production in the early morning (4 h) and in the late afternoon (17 h), while in Bornean orangutans only a broad, mid-morning call peak around 9 h was found. MacKinnon (1974) explained this inter-island difference by what Ross and Geissmann (2009) termed “calling time competition hypothesis.” Borneo has a lower primate density, specifically siamangs and Thomas’s leaf-monkeys, and therefore orangutans encounter less competition for acoustic space. Galdikas (1983), in Borneo, also observed a calling peak between 9 and 11 h. However, the Batang Ai orangutan population on Borneo was described to have a calling pattern similar to the one described for Sumatran orangutans (Ross and Geissmann 2009). Mitani (1985) found that dominant males in Borneo call at all times during the night, and lastly Samson et al. (2014) also found high call rates in captive orangutans from 1 - 7 a.m. However, these studies are based on very limited nocturnal observation hours, and as Galdikas (1983) noted, probably more nocturnal vocal behavior occurs than has been observed.

The ARU recordings and the observer data both have morning and evening peaks, irrespective of whether the dates examined directly overlapped or not. The timing of these morning and evening peaks differed by an hour (observer morning peak 6 vs. ARU morning peak at 5; observer evening peak at 15 vs ARU evening peak at 16). The sampling effort was not standardized or limited to full day follows. Therefore, there could be a bias of sampling effort in the observer-based data sets. One major benefit of using PAM systems to study this aspect of calling behavior is an unbiased sampling effort.

This is the first study with unbiased sampling, and we found that the diurnal orangutans produced more calls during the night than during the day. The number of calls during the night was twice that found over the same time period during the day with similar sampling effort. Furthermore, nocturnal long calls also occurred during periods when long calls were not produced during the photophase. However, it is possible that on the PAM recordings long calls produced at night were easier to identify than during the day. In general, the ARU recordings had less background noise at night than during the day, with the exception of cicada calls, which could be mostly filtered out before examining the file for long calls. During the day, gibbons and several bird species, especially during dawn chorus, dominate the acoustic space and their frequency ranges overlap with that of the orangutan long call. Although this factor could have caused a slight underestimate of call production during the day, it is unlikely that it will reverse the observed trend in higher rates of night-time call production. Red howlers have a higher long call rate at night as well, while during the day they use short calls more frequently (Drubbel and Gautier 1993). The long calls in red howlers are for intergroup communication, but why these are produced at night is unclear.

Nocturnal long calls are compositionally similar to diurnal long calls in that all of the seven pulse types were seen in nocturnal long calls, and they were used in a similar order as during daytime long calls. Male orangutans also produce a fast call, which is similar to the long call but has a faster rate (Galdikas and Insley 1988). Furthermore, spontaneously produced long calls compared to long calls produced in different contexts, i.e., in response to another long call or following a snag crash, for example, are also distinguishable by different pulse repetition rates (Spillmann et al. 2010; Askew and Morrogh-Bernard 2016). The fact that pulse rates in nocturnal calls are lower may therefore be significant in communication. The mean rate of the diurnal PAM recordings is the same as the follow recordings files, (mean follow pulse rate = 0.54, mean diurnal

PAM pulse rate = 0.55). The nocturnal long call pulse rate is 0.46 pulses/sec, which falls within the first quartile of the long calls recorded on follows. The mean fast call rate is 0.63 pulses/sec, which falls within the third quartile of the long calls recorded on follows. Both the nocturnal and fast long call rates fall within the range of spontaneously produced long calls, but lie on opposite ends of this spectrum. If higher pulse rates indicate a more excited state, then the low pulse rates of the nocturnal long calls indicate a low level of excitement.

2.3.4 Why vocalize at night?

Why male orangutans call more frequently during the night, especially during periods when there are no diurnal long calls is still unknown. Because we did not follow and observe behavior of males after they entered their night nest, we can only speculate. We hypothesize three potential reasons for these night vocalizations, which are not mutually exclusive. First, potentially it is less ‘risky’ to call at night. A male could advertise his current location and travel plans for the next morning with night-time long calls (van Schaik et al. 2013; Askew and Morrogh-Bernard 2016) and reduce the risk of being chased by a nearby male. This may allow a male to advertise his position to receptive females with less chance of being engaged in a fight or chased by a nearby male, because males may be less likely to exit their night nest to pursue the vocalizing male. Second, because there is a predawn nocturnal calling peak, male orangutans may be calling before the dawn chorus to avoid acoustic competition. As previously mentioned, several bird species and gibbons have overlapping frequency ranges and show peak vocal behavior during the dawn chorus. Orangutans may therefore emit their long-distance signal when there is less masking noise in the environment. Lastly, males have been observed to long call in response to disturbances, namely noises from other species (pig, deer, etc.), anthropogenic noises (gunshots), tree falls or breaking of branches, and even to abiotic noises (wind and thunder; MacKinnon 1974). Disturbances that wake males up at night could provoke them into producing a long call. For example, male orangutans call frequently when observers pass by and disturb them in their night nest before dawn (personal obs.). Thus, with limited risk of another male engaging in a chase or fight, biotic and abiotic disturbances may cause a male to long call during the night.

This is the first evidence that the diurnal orangutan produces more long calls during the night than during the day. However, the diurnal red howler monkey has also been observed to produce more nocturnal calls than during the day, but an explanation is lacking (Drubbel and Gautier 1993). As more evidence accumulates that diurnal animals display vocal behavior during the night, thorough investigation of the social and ecological relevance is required for revealing the potentially different selective pressures leading to this behavior.

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Figure 2.1 Map of study site.
Map of the trail grid with the location and coverage area (500 m radius) of the ARUs.

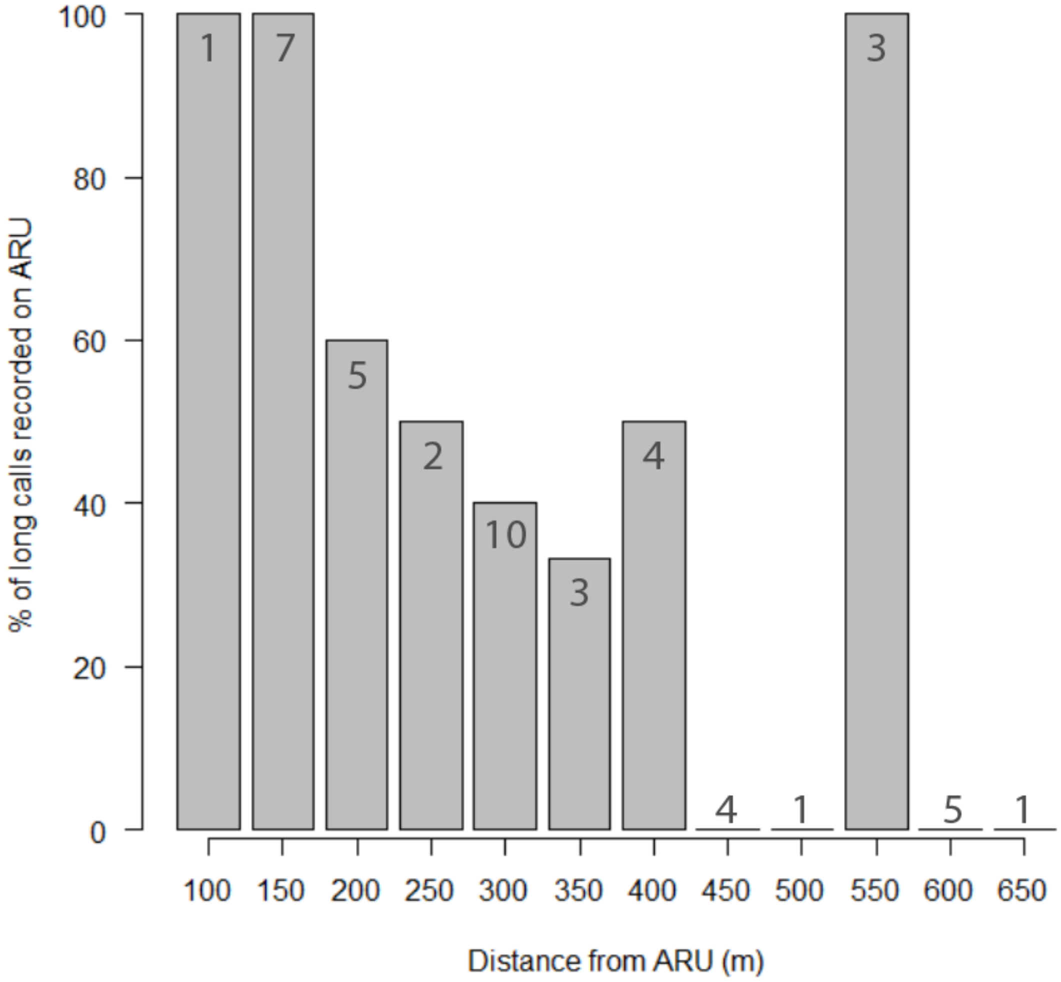

Figure 2.2 ARU recording percentage of long calls as a function of distance.
The percentages of long calls that were recorded on the nearest ARU in relationship to the distance the calling male were from the ARU. A total of 46 long calls based on observers on follows of flanged male orangutans, distributed over the distance range, or sample size, is indicated in each bar.

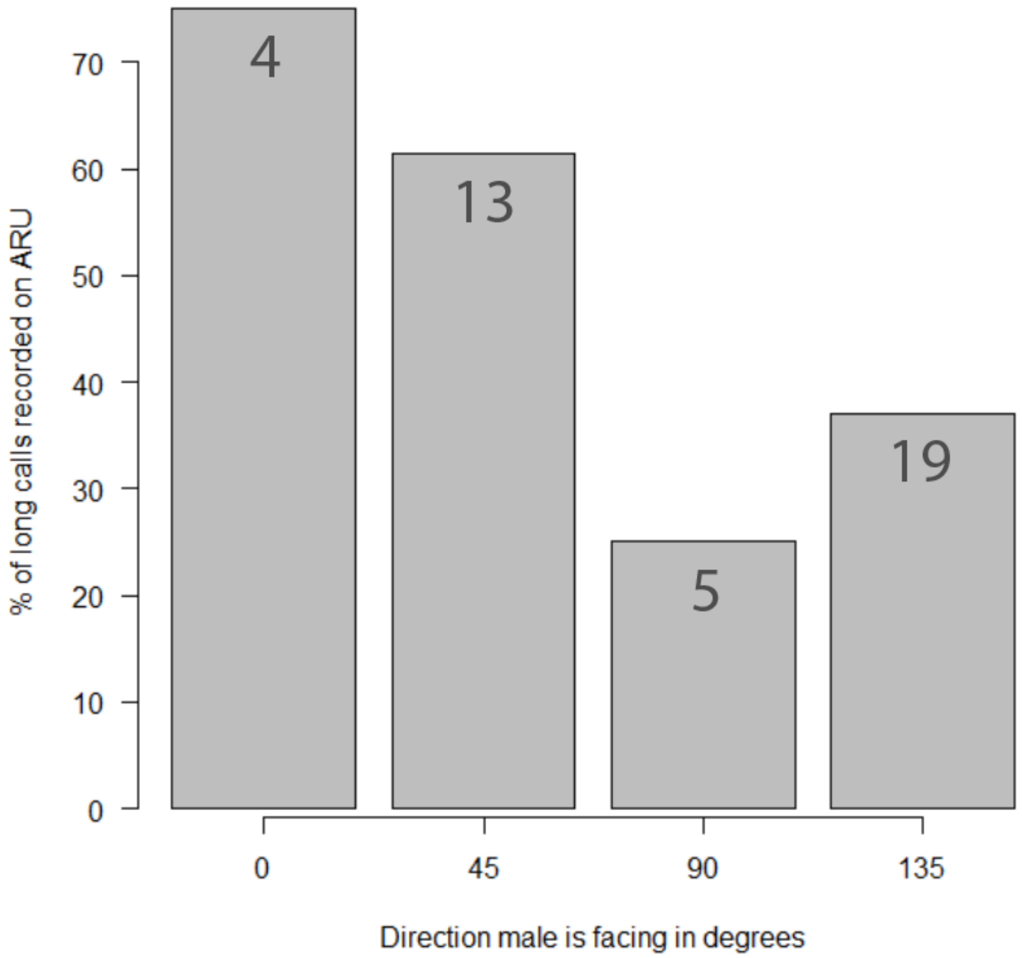

Figure 2.3 ARU recording percentage of long calls as a function of directionality. The percentages of long calls that were recorded on the nearest ARU in relationship to the direction the male was facing as he called. The direction is normalized to each ARU. Therefore when the male is calling directly at the ARU, it is 0º and so forth. A total of 41 calls were sampled, and sample size for each direction is indicated in each bar.

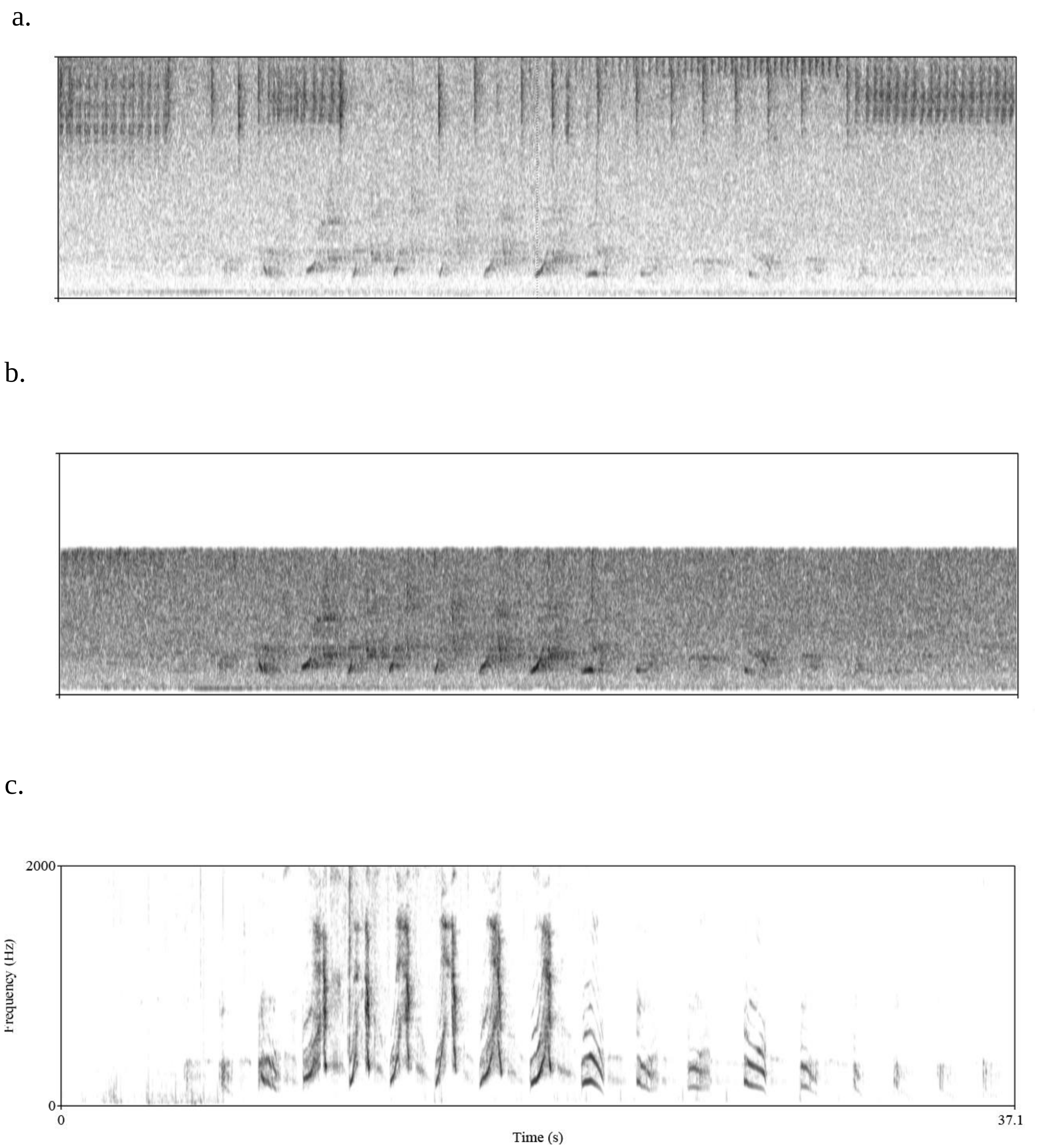

Figure 2.4 Comparison of call quality between follow recording and PAM systems. Example of a PAM recording low-pass filtered at 2000 Hz (a) and 1200 Hz (b) and a comparison with the recording of the same call made during the follow (c) without any filtering. Aside from differential filtering, the parameters for displaying the three spectrograms were kept the same to illustrate the different signal to noise ratios and definition of acoustic features.

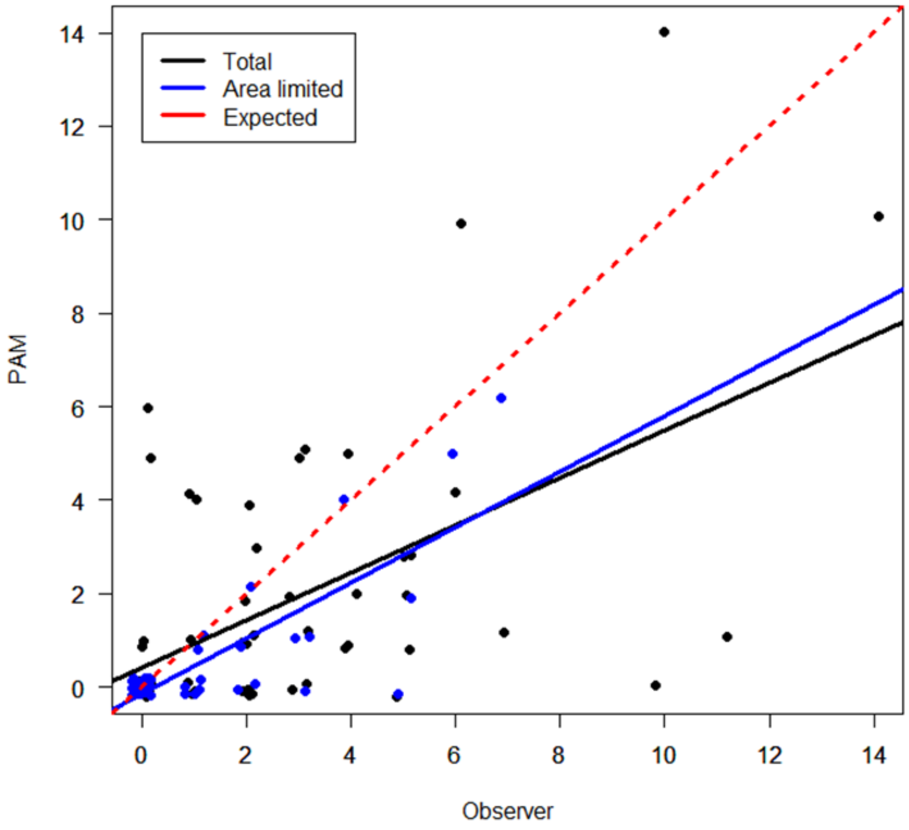

Figure 2.5 Direct comparison of long calls from follow data compared to PAM systems. Daily direct comparison of traditional observer data compared to PAM system shows that data from the remote recordings generally underestimate the frequency of calling. These trends are similar for long calls produced by flanged males within the range of the PAM systems (blue dots and slope) and all flanged male orangutans that were followed, regardless of location (black dots and slope). The red line indicates equal numbers for comparison.

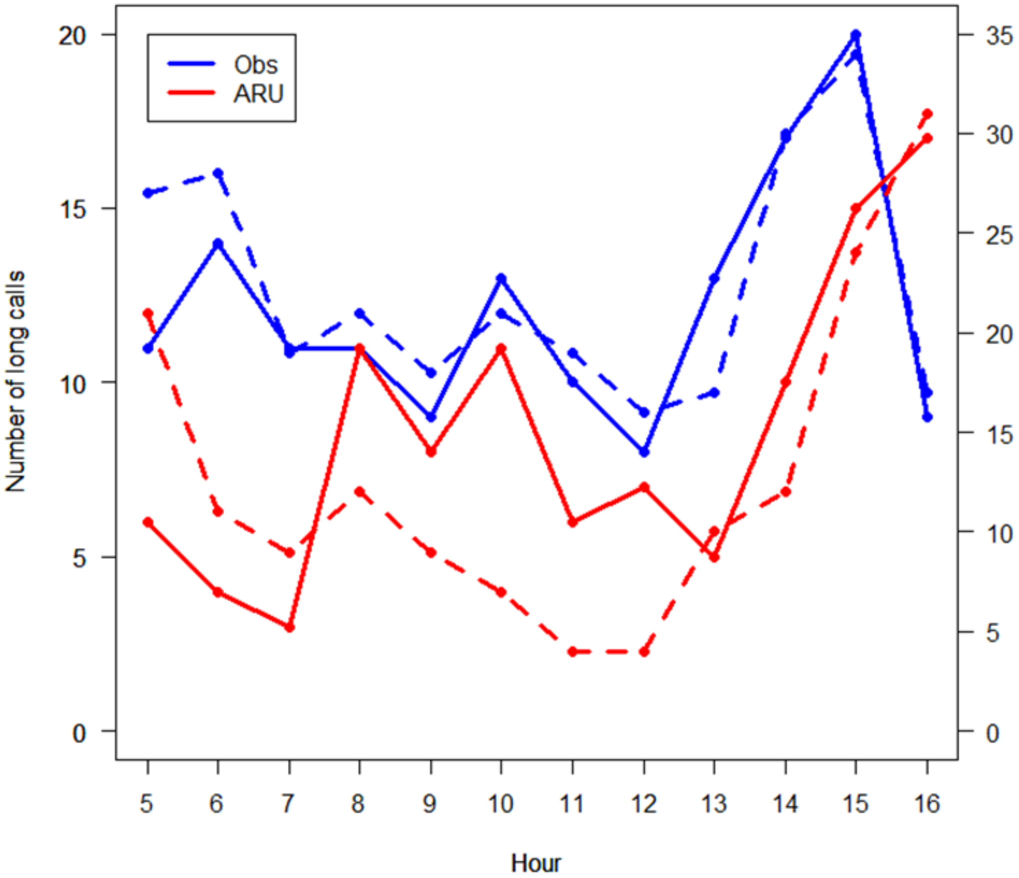

Figure 2.6 Temporal pattern of long call behavior: follow data compared to PAM systems.

The distribution of long calls of male orangutans using traditional follow data (blue line) shows a similar daytime pattern to PAM system data (red line) from the same days (solid lines, left vertical axis) and if all the data from both methods are used over the same time span, August 2012 – July 2013 (dotted lines; the right vertical axis).

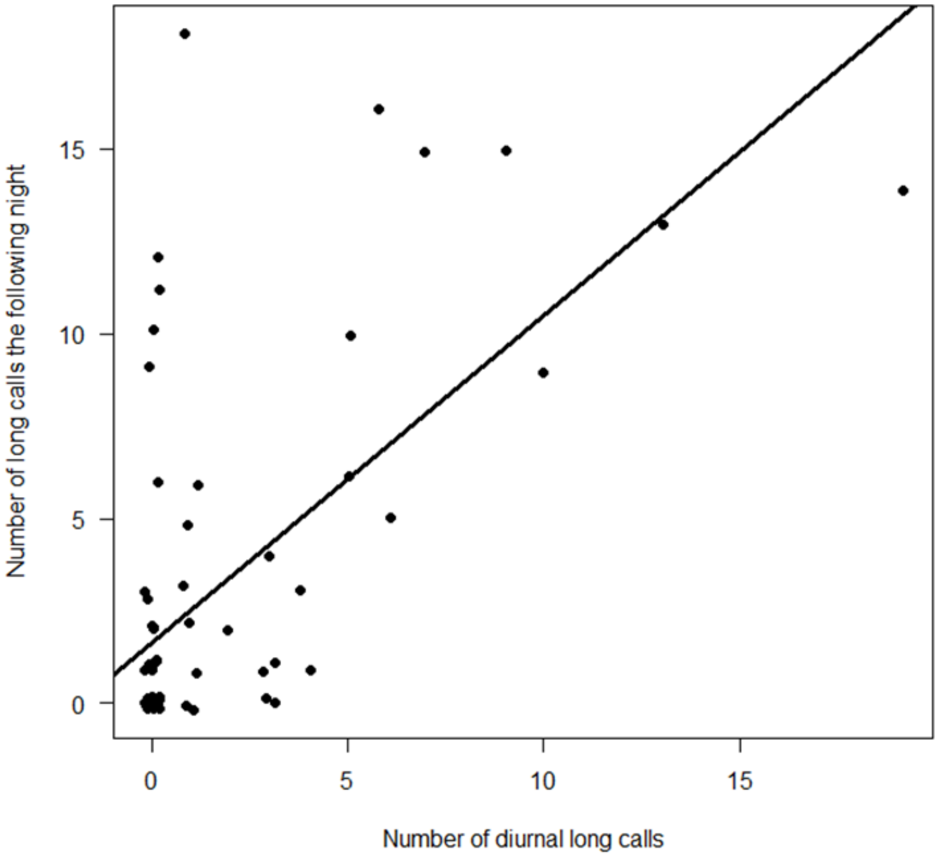

Figure 2.7 Number of diurnal compared to nocturnal long calls.
The relationship between diurnal long call behavior and the long call behavior of the following night.

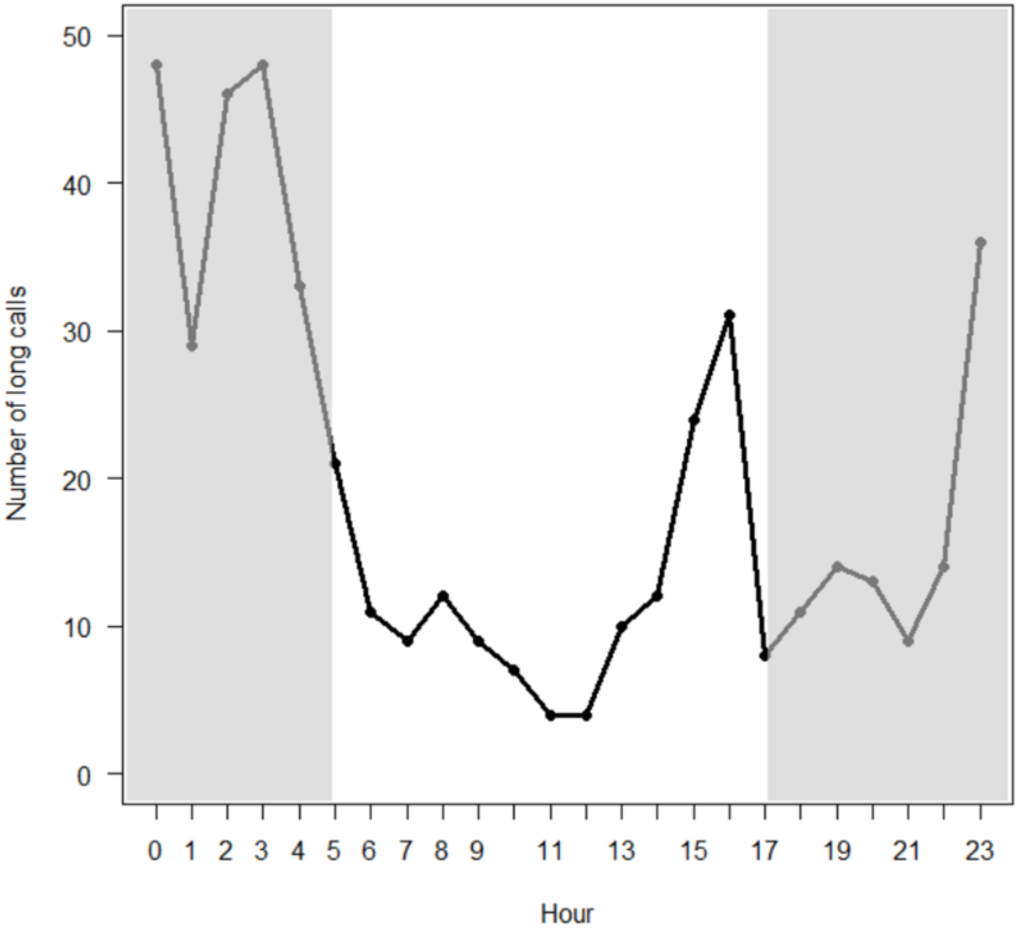

Figure 2.8 24-hour temporal pattern of long call behavior.
Nocturnal and diurnal long calls recorded on the PAM system for all dates sampled for a total of 2556 hours, 103 days and 110 nights.

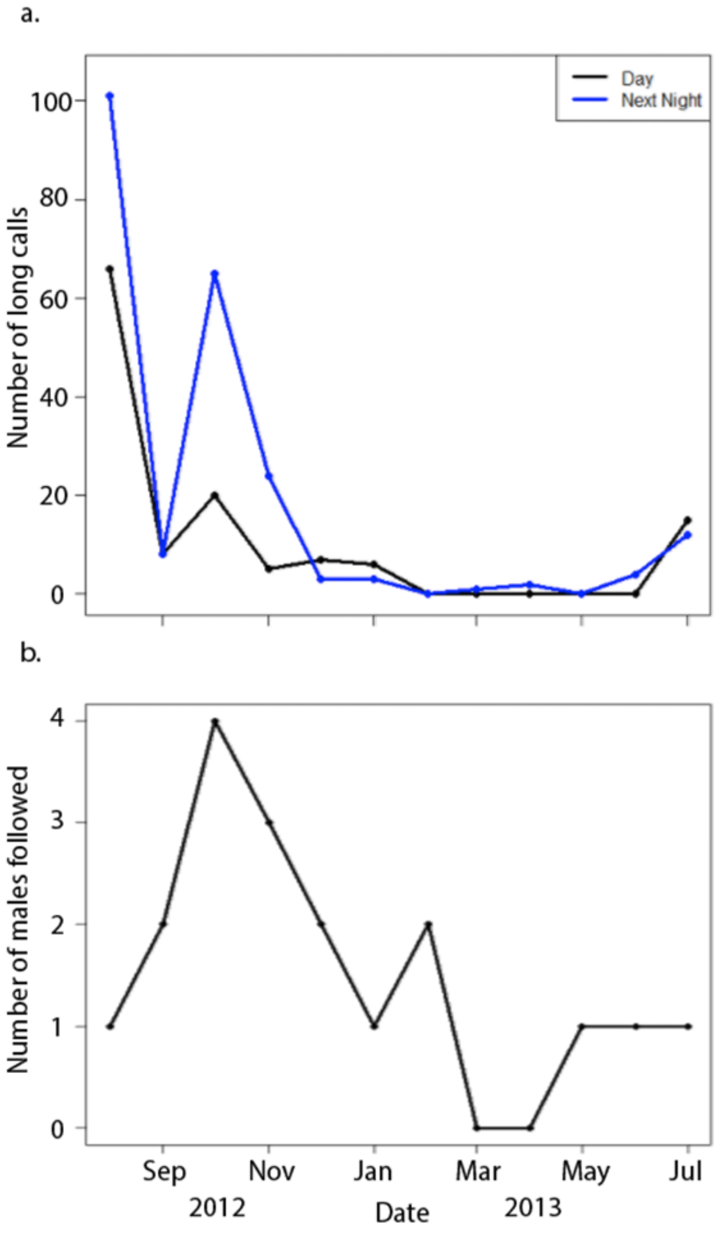

Figure 2.9 Nocturnal and diurnal seasonal long call behavior.
Diurnal long call behavior compared to vocalizations recorded during the following night (a) shows a correspondence to the number of males followed each month (b). Because unknown flanged males that were followed could not be reliably identified, we counted these follows as one present individual during each month.

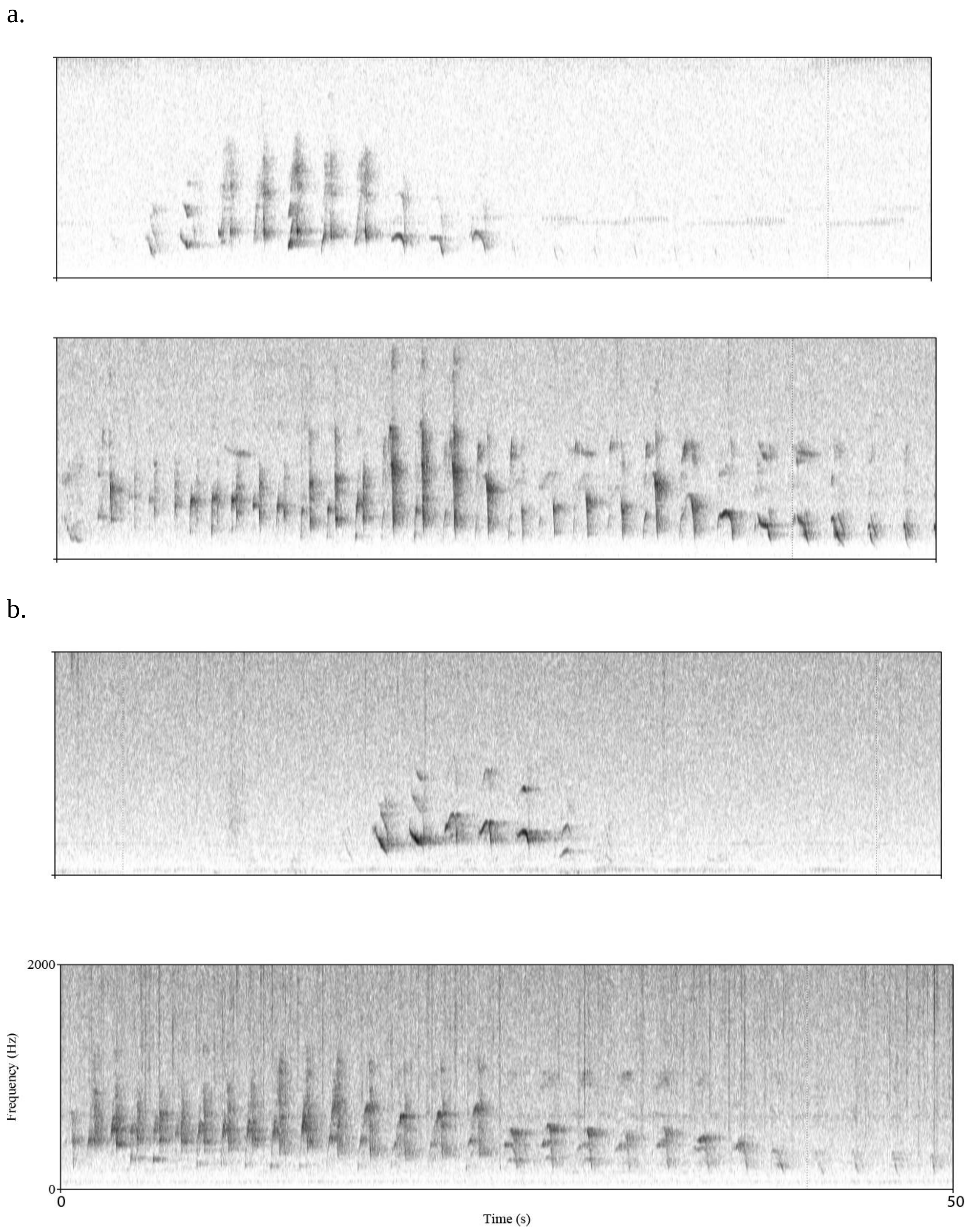

Figure 2.10 Nocturnal and diurnal long call recordings from PAM system. Examples of diurnal long calls (a) and nocturnal long calls (b) recorded on ARUs illustrate the difference in pulse rate.

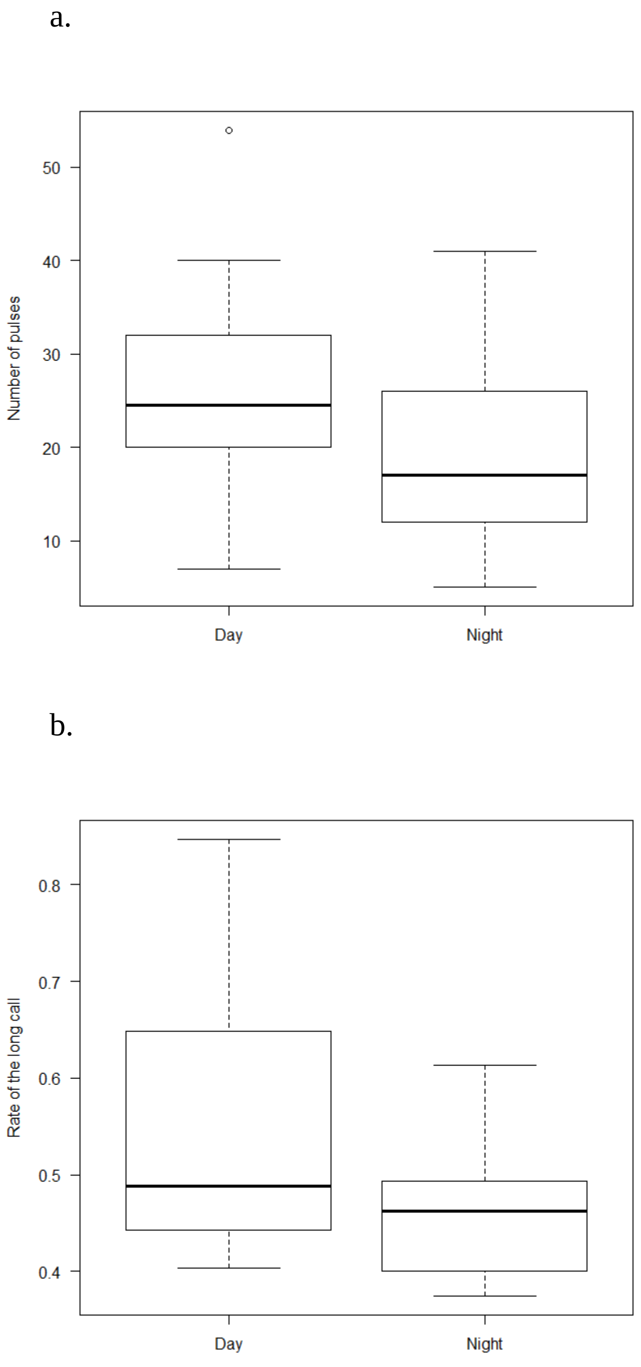

Figure 2.11 Diurnal vs. nocturnal long call characteristics.
Comparison of diurnal and nocturnal long calls shows a decreased number of pulses (a) and slower pulse repetition rate (b) during the night.

CHAPTER 3

ENVIRONMENTAL AND SOCIAL INFLUENCES ON THE LONG CALL BEHAVIOR OF MALE ORANGUTANS *PONGO PYGMAEUS WURMBII*

Animal vocalizations can contain acoustic properties that are "dynamic" and altered by the vocalizing individual as well as "static" features that are relatively unalterable through physiological constraints (e.g.; Gerhardt 1991; Bosch & Marquez 1996; Candolin 2003; Hebets & Papaj 2005). Static properties include features such as fundamental frequency and pulse duration, both of which are limited by morphological and physiological characteristics. In contrast, dynamic properties of vocalizations are highly variable and can be actively modified by the individual, and are thus more susceptible to external influences and stimuli (Gerhardt 1991; Bosch and Marquez 1996). One of the most prominent dynamic properties is the rate at which an individual vocalizes. Our understanding of how different factors interact to influence vocal production is still limited, because the network of influences is complex and incorporates a multitude of internal, social, and ecological driving forces.

Calling rate has been used to study group dynamics (Payne et al. 2003; Rogers et al. 2013), reproductive status (McComb 1991; Payne et al. 2003), internal state of an animal (Fine et al. 1977; Candolin 2003; Scheuber et al. 2005), fighting ability (McComb 1991), and habitat quality (Rogers et al. 2013). Some anuran species even compensate for limitations in static properties of their vocalizations, such as sound frequency, by increasing their call rate to attract females (Bosch and Marquez 1996). However, increasing call rate can be costly, ranging from the energetic costs associated with production to increased risks of predation (Eberhardt 1994; Searcy and Nowicki 2005). With every vocalization, especially loud calls, the sender is taking a risk of notifying potentially aggressive conspecifics or predators of its location (e.g.; Manson 1996; Searcy and Nowicki 2005; Setia and van Schaik 2007; Spillmann et al. 2017). The frequent release of information about the sender's location increases the potential of an antagonistic encounter with conspecifics, which could lead to a chase or fight, and ultimately a potential drop in social status, injury, or even death. In addition, the likelihood of alerting a predator to one's location also increases. Due to these inherent costs of vocalizing, individuals must balance the costs against the benefits of calling, based on a variety of social and environmental factors.

However, differences in life history features and mating strategies exert complex influences on how environmental factors affect call rate. Whereas the temporal dynamics of seasonal breeding systems facilitate the study of calling behavior, dissecting this complexity in the context of prolonged breeding systems is difficult. Socially, elevated calling rate could lead to increased mating opportunities or more effective defense of one's territory. Multiple social factors may influence male calling rate including dominance (Kitchen et al. 2003), population density (Payne et al. 2003), and proximity to cycling females (Spillmann et al. 2017). However, individuals must first meet their basic metabolic needs to be able to endure the costs associated with vocalizing (Cowlishaw 1996). Since the physical condition of an individual is dependent on food availability and thus habitat condition (Knott 1998; Pettorelli et al. 2002; Shochat et al. 2002; Harrison et al. 2010), environmental factors may play a large role in determining if an individual can afford to call. After basal metabolic needs are met, social factors may predominantly determine calling behavior. Thus, social and environmental factors need to be examined simultaneously to understand their respective influences on variable vocal behavior.

Orangutans are semisolitary primates that reside on only two islands in Southeast Asia, Sumatra (*Pongo abelii*) and Borneo (*Pongo pygmaeus*) (e.g., Xu and Anason 1996, Delgado and Van Schaik 2000; Brandon-Jones et al. 2004). Orangutans are sexually dimorphic, and male orangutans produce a long-distance vocalization, the long call (LC), which is believed to communicate diverse information about the sender, such as individual identity and direction of travel (Spillmann et al. 2010; van Schaik et al. 2013; Askew and Morrogh-Bernard 2016). Information about a male’s direction of travel may allow other individuals to space themselves around the calling individual based on an acoustic assessment (Mitani 1985a; Delgado 2006; van Schaik et al. 2013; Askew and Morrogh-Bernard 2016). Less dominant males may travel away from the sender, more dominant males may travel towards the sender to engage in conflict and drive the sender away, and females may travel towards the calling male for mating opportunities (Buckley 2014). Multiple social and ecological differences have been observed between Sumatran and Bornean orangutans (e.g., Wich et al. 2009; Delgado & Van Schaik 2000; Dunkel et al. 2013; Fox et al. 2004). Sumatran forests experience fewer food droughts and generally higher food availability, and Sumatran orangutans are more social and live at a higher density (Singleton and Schaik 2001; Husson et al. 2009; Marshall et al. 2009). Given these differences, the influences driving vocal behavior of male orangutans on the two islands may also be different.

Among the great apes, orangutans are particularly interesting for examining how social and environmental influences affect calling behavior for three reasons. First, orangutans are the least social great ape (e.g., Marchant and Nishida 1996), which should facilitate dissection of different social factors and their influence on calling behavior. Second, orangutans appear to experience longer periods of food droughts than the other great apes (Harrison et al. 2010). Interspecies and island comparisons have shown how different environmental conditions and food availability affect orangutan behavior (Knott 1998; Wich et al. 2006; Marshall et al. 2009). Lastly and presumably as a result of the typically large spatial separation between individuals within a population, male orangutans produce a potentially risky long-distance vocalization that reveals the current location of the sender and occasionally results in a chase or a fight (Setia and van Schaik 2007; Spillmann et al. 2017). Here we use a long-term database to investigate the environmental and social influences on long-calling behavior of male orangutans in Southern Borneo and assess our findings in the context of what is known about other populations in different social and environmental conditions (e.g., Mitani 1985a; Setia and van Schaik 2007; Vogel et al. 2015).

3.1 Methods

3.1.1 Research location

The study was conducted in the Natural Laboratory of Peat-swamp in the Sabangau forest in collaboration with the Center for International Cooperation in Sustainable Management of Tropical Peatlands (LLG-CIMTROP) at the University of

Palangka Raya. The Sabangau Forest lies 20 km southwest of Palangka Raya in southern Borneo, Central Kalimantan, Indonesia. Concession logging in the Sabangau forest ended in 1997, illegal logging continued until 2004 and periodic fire has occurred in some areas outside of the research grid. The habitat is a mixed-peat swamp and is home to the orangutan subspecies *Pongo pygmaeus wurmbii*. Orangutans have been studied in this area since 1995, with behavioral studies beginning in 2003.

3.1.2 Data collection

3.1.2.1 Social

A behavioral database was collected from September 2003-December 2012 from focal follows of flanged male orangutans for the extent of their activity period (encompassing all observed activities from night-nest to night-nest). Spontaneous 5-minute data sampling was used following recommendations of the Leakey Foundation Orang-utan Compared Workshop (Morrogh-Bernard et al. 2003; Morrogh-Bernard 2009). Because our study involved focal animals in the field, it was not possible to record blind data. To obtain a representative depiction of daily calling behavior, only follows of 5 hours and longer were used, which is about half of the average activity period of male orangutans. When the focal animal produced a long call, the time, direction of the LC, and the sender’s location were noted. When a long call was heard from another flanged male, the direction and estimated distance were noted. To account for different observation times and activity periods, calling behavior was normalized by dividing the number of long calls by follow hours to produce a rate at which the focal animal produced or heard long calls.

We analyzed calling behavior of flanged male orangutans during associations with other individuals; associations with another individual were noted every 5 minutes along with the rest of the behavioral data. An association was defined as another orangutan being within 50 meters of the focal male (as is standard, Morrogh-Bernard 2009). The other individual was categorized by sex as female, male, or unknown individual (juveniles were not considered in this analysis and a distinction between flanged and unflanged males was not made). For days the focal male was associated with a female, the LC rate was separated into the calling rate before, during, and after association. The few instances in which the focal male was shortly separated from the female, i.e., would fall into both before and after category, were omitted. The calling rates on days associated with a female were compared with days when the focal male was not associated with a female or any other individual, i.e., solitary days.

To examine the calling behavior of focal males involved in a male-male interaction (defined as either a fight or a chase), we classified each individual in an interaction as a “winner” or a “loser”. Because both the winning and losing males are not typically followed on the days immediately preceding and following the interaction, we initially grouped the average LC rate of all winners and compared it to the average LC rate of all losers, if they were followed around the time of the interaction (±15 days), for a general calling behavior of the individual at that time. To further examine if the interaction influenced call behavior or if individuals who call more won more interactions, we generated three separate averages: 10 days preceding the interaction, the day of the interaction, and 10 days following the interaction, and compared the calling rate between winners and losers.

3.1.2.1 Environmental

Plant fruiting and flowering phenology is often used as a proxy for food availability (e.g., Chapman et al. 1994; Wich et al. 2006). These data were collected once a month from 2003-2012, following established protocols by Morrogh-Bernard (2009), and described previously (e.g., Harrison et al. 2016; Harrison et al. 2010). Roughly 2,400 individual trees were surveyed in six permanent phenology plots (total area 2.4 ha) and one phenology circuit, each month. The results were then separated into three categories, fruiting only, flowering only, and total (the combination of fruiting and flowering). Data were expressed as a percentage of the number of trees fruiting or flowering divided by the total number of trees surveyed. In addition, we assessed the phenology of orangutan-specific food resources compared to entire forest phenology (including the orangutan-specific phenology) based upon orangutan diet lists derived from previous research (Morrogh-Bernard 2009; Harrison et al. 2010).

Litter fall data are frequently used as an approximation for forest productivity. Litter fall data in Sabangau were collected every month from December 2005 to December 2012, following methods described previously (Harrison 2009). In total the contents of 16 x 1 m^2 litter fall traps were collected, dried, and separated into their constituent parts (leaves, reproductive parts, branches, bark, and miscellaneous debris) (Harrison 2009). To estimate forest productivity, the litter fall data were examined in total ($kg \cdot ha^{-1}$) as well as the dry mass consisting of merely leaf litter fall to help disentangle the relationship of calling behavior with different aspects of forest productivity. Because litter fall and phenology data are collected monthly, the daily LC rate of individuals was compared to the closest collection time for both measures.

In addition, temperature and rainfall data was collected daily as an indication of the current ambient condition, following methods outlined by Harrison et al. (2016). Rainfall (mm) data were collected every 12 hours at 0700 and 1900h using a rain gauge in an open area located at the research camp. Temperature (°C) was examined by the daily maximum and minimum values. The temperature data were collected in a shaded area inside the forest near the research camp.

3.1.3 Statistics

To examine environmental and social influences on the long call behavior of male orangutans, a Spearman's rank correlation (temperature and rainfall), linear regression (litter fall), or an ANOVA (social associations and male/male interactions) was used to examine the relationship with long calling rate. To reduce the influence of individual variation, only males with over 30 follows were used in environmental comparisons (8 out of 24 individuals, a reduction of 20% of follow hours to 3265 hours). However, when examining social factors, all individuals were used to maximize sample size. To examine which social and environmental factors have the greatest influence on male long call rate, a multivariate generalized linear model (GLM) was used in R (v. 3.2.3; R core team (2015)). The best model was identified through a backwards elimination stepwise approach, where initially every social (association with another individual) and environmental (temperature, rainfall, litter fall, and phenology) variable was included. Each variable was then systematically eliminated to examine its effect on LC rate until all variables with no significant effect were removed and the model with the lowest Akaike information criterion (AIC) value was discovered. To reduce the individual biases in sample size for the model, only the eight individuals with over 30 follows were used; individual variation was still added into the model as a random effect using lme in the nlme package (Pinheiro et al. 2017). Because environmental influences are likely to impact the LC behavior of other individuals in addition to the focal male, an interaction was used in the model between LCs heard and phenology. The interaction term between LCs heard and phenology was testing using bootstraps, which gave consistent results.

3.2 Results

3.2.1 Social influences

Overall, the LC rate of a focal male was higher for days on which he was associated with another individual compared to solitary days (ANOVA; $p<0.0001$, $F=6.58$, $n=353$; Figure 3.1). This relationship was significant for days associated with unknown individuals (compared to solitary days; Tukey post hoc; $p=0.001$, $n=31$), or both male and female ($p=0.04$, $n=7$). However, no significant difference was found for days with an association with another male ($p=78$, $n=15$) or female ($p=0.08$, $n=39$). The LC rate was significantly higher before (compared to solitary days; Tukey post hoc; $p<0.001$, $n= 34$) and during ($p<0.01$, $n=68$) association with a female than after ($p=0.99$, $n=33$) or no association (ANOVA; $p<0.0001$, $n=508$; Figure 3.2). The length of time spent with the female was not correlated to the LC rate (lm; $p=0.28$, $R^2=0.02$).

The mean LC rate of the winners (0.43 ± 0.06) around the time of the interaction (±15 days) was significantly greater than of males who lost (0.28 ± 0.08) an interaction that month (- ANOVA; $p=0.02$, $F=4.64$, $n=59$). Further, males who won an interaction had a significantly higher LC rate than the mean LC rate of individuals not seen to be involved in an interaction (ANOVA; p=0.01, F=4.64, mean LC rate of individuals not in an interaction=0.29 ± 0.02), whereas males who lost an interaction did not differ from the mean (ANOVA; p=0.72, F=4.64). On the day of the interaction, there was no significant difference in the LC rate between winners and losers (Welch two-sample t-test; p=0.41, t=0.83, n=24), nor was there a difference 10 days following the interaction (t-test; p=0.26, t=1.13, n=58). However, winners had a higher LC rate 10 days preceding the date of the interaction (t-test; p=0.002, t=3.13, n=89; Figure 3.3). Thus, it appears that the interaction is not causing winners to have a higher LC rate, but rather individuals who have a higher LC rate are more likely to win interactions.

3.2.2 Environmental influences

In the absence of annual variation, no relationship was found between the daily minimum or maximum temperature and calling rate (Spearman; min p=0.41, rho=0.044; max p=0.88, rho=0.008). In contrast, daily rainfall had a negative relationship with calling behavior (Spearman; p=0.01, rho=-0.138).

Litter fall data had to be analyzed as a subset of the database due to the differences in the collection length from the rest of the database (Dec. 2005-Dec. 2012). The monthly total and leaf litter fall data were positively correlated with monthly LC behavior of the eight males (lm; total p=0.032, R^2=0.01; leaf p=0.047, R^2=0.01).

3.2.3 GLM: Phenology and long calls heard

The GLM with the lowest AIC consisted solely of phenology based food availability and the rate of LCs (produced by other males) heard, suggesting that these two variables are the most prominent determinants of LC rate. The phenology results were separated into the entire forest phenology and phenology of orangutan food trees. Within these two categories, fruiting and flowering phenology was examined separately. Each phenology category was run in the model separately from the other phenology data to prevent multicollinearity. The entire forest phenology (fruiting and flowering combined) was the best model (GLM; forest fruiting and flowering AIC=160, forest fruiting AIC=165, forest flowering AIC=166, orangutan fruit and flowering food AIC=169, orangutan fruit food AIC=171, orangutan flower food AIC=163).

For the eight males with the most follows, calling behavior was positively correlated with both LC heard rate (GLM; $p=0.041$) and entire forest phenology ($p<0.0001$; Figure 3.4). However, the interaction of the two resulted in a negative relationship with call rate of the focal male ($p=0.023$). If the LCs heard rate is high, there is no relationship between food availability and LC rate. If there are no LCs heard or if the heard rate is low, there is a strong correlation between food availability and LC rate (Figure 3.4). When we examined this model on the individual level for each of the eight males, these relationships remained mostly consistent, except for two individuals, “Peter Pan” and “Wallace”, which had the opposite relationship with LC heard rate, forest phenology, and the interaction (Table 3.1).

3.3 Discussion

The calling rate of flanged male orangutans was related to both social and environmental factors. This is the first study to reveal a positive correlation between food availability and flanged male orangutans LC rates, and, more importantly, variation in food availability was the major determinant of call rate variation. The use of a long-term database enabled us to reveal the effects of potential influences on vocal behavior that may be seasonal and may vary from year to year (such as food availability). Despite a complex set of variables, the long-term database enabled us to disentangle the different influences of these factors. Furthermore, our analysis shows substantial interindividual variation and, without observing multiple males over the years, the general trend may therefore be misinterpreted. Individual variation may be a result of multiple social factors that arise from the fact that orangutans have a long lifespan, during which, for example, their dominance status, home ranges, body condition, and other factors may fluctuate (Buckley 2014; Askew and Morrogh-Bernard 2016).

3.3.1 Social influences

Overall, flanged male orangutans have a higher LC rate on days during which they are associated with another individual compared to solitary days. On days focal males are associated with a female, they have a high LC rate before and during association. The higher LC rate of males with an association with another individual is attributable to the higher LC rate they have before and during the association. Although not fully tested due to limited sample size, there was a trend of a higher LC rate before and during association with a female, before and during association with a male or an unknown individual. There was no correlation between the time spent with the other individual and calling rate, although the duration of the association with another individual varied greatly. Associations between two males were always short and typically under 15 minutes, whereas associations with females were on average over 3

1/2 hours long. Before associating with either sex, the LC rate of the focal male orangutan was more than two-fold higher than after association. Potentially, males may not be aware of the nearby orangutan’s identity or sex before encounters and may increase their call rate to ward off males or to attract females and, during the association with a female, may maintain a high LC rate in courtship (Askew and Morrogh-Bernard 2016; Spillmann et al. 2017). Immediately following an interaction with a female, there is less obvious benefit to a male continuing to call at a higher rate: if the male wishes to interact with that female again in future, he can presumably attract her back by simply calling again.

Setia and van Schaik (2007) found that Sumatran female orangutans approached long calling males, but males did not call during association with the female. However, at our site on Borneo, males maintained a high LC rate both before and during association with a female. This could be attributed to differences in the social behavior of the two orangutan species, arising from ecological differences (e.g., Knott 1998; Wich et al. 2006; Marshall et al. 2009). Female Sumatran orangutans are typically associated with a male for days at a time (Delgado and Van Schaik 2000; Setia and van Schaik 2007), whereas Sabangau females are associated with a male for as little as 5 minutes and courtships that last for an entire day are rare. In addition, higher population density on Sumatra could explain why male LC behavior is reduced during association with a female. The likelihood of another male approaching a calling male may be higher in Sumatra (Vogel et al. 2015), and thus males may reduce calling once they are associated with a female to prevent interference from another male (Setia and van Schaik 2007). However, the ratio of flanged males to unflanged males is lower in Sumatra compared to

Borneo (Delgado and Van Schaik 2000). It is possible that Sumatran flanged males do not need to ward off other flanged males. In contrast, Bornean male orangutans may still use LCs during associations to court the female during the short duration of the interaction and will suffer fewer costs from doing this owing to the reduced risk of interference by another male. Alternatively, since males have to compete for access to females (Mitani 1985b), maintaining a high LC rate may act to ward off other males from approaching the area and ruining their chances of mating (Spillmann et al. 2017). These social differences could give rise to contextual differences in the use of the LC between the species or perhaps even orangutan populations (Spillmann et al. 2010; Askew and Morrogh-Bernard 2016).

A recent study using an acoustic location system on Bornean orangutans discovered that the LC rate of male orangutans increased with the number of cycling females in the area (Spillmann et al. 2017). In addition, the number of flanged males in the area was also positively correlated with LC rates of individuals, and the presence of cycling females increased a male's reaction to LCs heard. These results are consistent with our findings, even though we examined male association with females and Spillmann et al. (2017) examined overall LC behavior in the vicinity of cycling females and not specifically direct interactions. If males are in the vicinity of cycling females, they may maintain a high LC rate to attract the female as well as deter other flanged males from approaching the area (as previously discussed).

The outcome of an antagonistic interaction with another male did not affect LC rate. Even before the interaction, individuals seen to win an interaction had nearly double the LC rate of individuals who lost an interaction. Further, individuals who had recently lost an interaction were calling at the same rate as males not seen to be recently in an interaction. Thus, individuals who lost an interaction are not calling less; rather individuals who recently won an interaction are calling at a higher rate. However, these results should be interpreted carefully, because the sample size of males observed prior to, during, and after the interaction is small. Nevertheless, these findings are consistent with data from other studies on orangutans and other primates in that loud calling at high rates is related to dominance (orangutans, Mitani 1985a; baboons, Kitchen et al. 2003; rhesus macaques, Manson 1996).

By not making assumptions about dominance, we can examine multiple social influences on male LC rates. Because winners of male antagonistic interactions call at twice the rate of males who lost and the mean call rate of males not seen in an interaction, the hypothesis that more dominant males call more often is supported. This finding is consistent with a more direct investigation of dominance where more dominant male orangutans also called at higher rates (Galdikas 1983; Mitani 1985a; Buckley 2014). However, since Bornean males may have a less stable dominance structure, males may need to more continuously advertise their dominance status with high turnover rates of males in the area (Spillmann et al. 2017). This effect may explain why less dominant males may continue calling even after losing an antagonistic interaction. By examining the relationship between LCs produced and the number of LCs heard, or if the focal male approached other long calling males, as previous studies have done (Setia and van Schaik 2007; Buckley 2014), one could better speculate about the dominance of an individual. Dominant males may call more often in response to LCs they hear and approach the other long calling males (Setia and van Schaik 2007), whereas less dominant males may not risk calling in response to LCs to avoid confrontation.

3.3.2 Environmental influences

Weather, such as wind and rain, produces ambient noise in addition to affecting sound attenuation (Wiley and Richards 1978; Lengagne and Slater 2002). Reduced signal transmission and ambient noise may affect the timing and rate of vocal production to reduce interference with signal transmission by background noise (Dominoni et al. 2016; Stanley et al. 2016). Thus, it is no surprise that orangutans also call at a reduced rate during times of heavy rain. In a previous study, hourly LC rate was significantly lower when it was raining, but rain was not found to be a major determinant of daily call rate (Spillmann et al. 2017). Rainfall did not emerge as a significant factor in our GLM model although a significant correlation was still discovered when examined separately. The difference in study period may explain the discrepancies in the results. Reduced calling in the rain has also been observed in other primate species (e.g., gibbons, Cheyne et al. 2007). Furthermore, it may also be more difficult to hear other orangutans approaching during rain (from our experience, it is much more difficult for human observers to hear and follow orangutans during heavy rain). Decreased call production in orangutans may therefore also function to not reveal their location if they are uncertain of the proximity of other males.

Litter fall data were analyzed separately from the model and phenology data, because they were collected over a shorter time frame. Forest productivity, measured as litter fall, was positively correlated with long call behavior. Further investigation is needed to illuminate which specific aspect of forest productivity influences LC behavior of flanged male orangutans. Litter fall predominantly measures leaf production and turnover, as indicated by the strong correlation between leaf litter fall and total litter fall (lm; $p<0.001$, $R^2=0.92$). Leaves are a fallback food for Bornean orangutans (Knott 1998; Harrison and Marshall 2011), and orangutans only eat or prefer to eat young leaves of some species. Thus, to meet their daily caloric intake, orangutans may depend on leaf turnover in times of low food availability. This could be the driving factor for the positive correlation between litter fall and LC behavior. Such an interpretation should be treated with caution, however, as leaf fall will be comprised primarily of older dying leaves, rather than the young leaves/shoots that orangutans typically prefer.

3.3.3 Phenology and long calls heard

This interactive model highlights the importance of both social and environmental influences on vocal behavior. High food availability was positively correlated with increased LC rates, as has also been observed in gibbon singing behavior (Cowlishaw 1996). In addition, the more LCs an individual heard, the more they produced. This is consistent with a recent finding that male presence increased with increased food availability, and more males in the area resulted in higher calling activity (Spillmann et al. 2017). However, if the LCs heard rate was high, the relationship between food availability and LC rate no longer persisted. Therefore, food availability is an important factor influencing LC rate. However, social factors can override the environmental influence. The interaction of LCs heard and food availability has a negative effect on the LC rate of the focal male. Potentially, the focal male may not call or may call at a low rate to not get chased away and lose access to food during periods of high food availability and when individuals hear many LCs (from competing males). Furthermore, males may tolerate each other more in areas with high food availability, because there is less need to fight for it. This would reduce energy expenditure for fights and chases and reduce the risk of losing access to the food, as well as losing time for feeding. However, Spillmann et al. (2017) did not find a relationship between food availability and LC rates. Two possible differences between our studies may explain the discrepancy in these results. First, the studies were conducted over very different time periods. Our long-term data set offers more power for detecting such a relationship. Second, the two forests differ markedly in food availability and quality (Vogel et al. 2015; see below).

Two individuals had the opposite relationship to the overall trend in the model. Even though the linear regression was not significant for these individuals, both sustained either a high (Peter Pan) or low LC rate (Wallace). The interaction of LCs heard and food availability in the model for Peter Pan has a high slope, implying that he called at a higher rate during times of high food availability and when he was hearing more long calls. Peter Pan has typically been followed during times of high food availability (0.10-0.13%), which could explain this different relationship and why he upheld a high LC rate. In contrast, Wallace was an older individual who maintained a low LC rate irrespective of food availability. Further exploration is needed to understand the variation between individuals. Individual variation could be attributed to many different factors, including the internal state of the individual, daily activity, dominance, cycling female orangutans, and the individual’s travel patterns (van Schaik et al. 2013; Askew and Morrogh-Bernard 2016; Spillmann et al. 2017). For example, LCs are thought to indicate direction of travel, which might lead dominant males to call more frequently on days when they move greater distances (van Schaik et al. 2013; Buckley 2014; Askew and Morrogh-Bernard 2016). Interindividual differences in responses to the same influences highlight the complex interrelations of multiple factors that affect motivation for call production.

Fruiting phenology was the main factor driving the relationship between food availability and calling behavior. Fruit is the main food source in Bornean orangutans when it is available, and changes in fruit availability drastically affect the caloric intake of orangutans (Knott 1998; Harrison et al. 2010; Vogel et al. 2015). Nonetheless, flowering phenology is also important in the diet of orangutans, especially when fruit availability is low, and the addition of flowering phenology in the analysis always provided a better model (Knott 1998; Wich et al. 2006). This is especially true for Sabangau orangutans whose diet consists of a higher percentage of flowers compared to orangutans at other sites (Harrison 2009; Morrogh-Bernard et al. 2009). The entire forest phenology, rather than just orangutan specific food phenology, produced the best model in the GLM. Entire forest phenology and orangutan food phenology are significantly correlated (Pearson; $p<0.001$, $R=0.70$), but the correlation is not as high as in a previous study of a Sumatran forest (Pearson; $p<0.001$, $R=0.99$; Wich et al. 2006). It is unclear whether this difference is related to less fluctuation in food availability in Sumatra (Wich et al. 2006). Because the relationship with orangutan specific food (fruiting and flowering) phenology did not result in the best model, we either do not have the full scope of what orangutans are eating, or the fruiting phenology of other trees also plays a nonspecific role in affecting calling behavior of orangutans. The lower correlation between the two phenology measurements in Sabangau suggesting that Bornean orangutans are directly or indirectly relying on more tree species than included in the orangutan specific food phenology surveys.

Primary social differences between the two orangutan species residing on Sumatra and Borneo have been largely attributed to differences in forest composition (e.g., Knott 1998; Wich et al. 2006; Marshall et al. 2009). Sumatran forests have a more continuous supply of figs and, in general, more fertile volcanic soil gives rise to higher quality and quantity of fruit (e.g., MacKinnon 1974; Marshall et al. 2009; Harrison and Marshall 2011). Thus, Sumatran orangutans studied to date do not experience the same troughs in food availability as those in Borneo, and thus typically do not need to rely on fallback foods, or have seasonal signs of fat metabolism as is experienced by Bornean orangutans (Knott 1998; Wich et al. 2006; Harrison and Marshall 2011). This allows Sumatran orangutans to live at higher densities (Chapman and Chapman 1999; Chapman et al. 2010; Vogel et al. 2015), leading to more social interactions (Delgado and Van Schaik 2000; Vogel et al. 2015). Therefore, certain influences on vocal behavior in one species may not be the main influencing factor in the other. For example, LC behavior in Sumatran orangutans is not correlated with food availability (Setia and van Schaik 2007), which is consistent with their relatively constant year-round food supply. Furthermore, because Sumatran orangutans are more social (Delgado and Van Schaik 2000), their vocal behavior may be more and differently influenced by social influences. Thus, observed differences between the two island species seem to arise from ecological differences.

If environmental differences are the primary driving force for social differences, we can expect to see different patterns in calling behavior even between populations that experience different habitat quality within an island (personal correspondence with Matt

Nowak). The Sabangau and Tuanan field sites are only 63 km apart and are classified as the same forest type (mixed peat-swamp forest) with the same orangutan subspecies residing in it (*P. pygmaeus wurmbii*). However, multiple ecological and social differences have been observed between the two sites. Although orangutans share many of the same fruits in their diet at the two sites, the Tuanan forest has better quality food, and thus orangutan energy intake is higher compared to the Sabangau forest (Vogel et al. 2015). Furthermore, Tuanan orangutans live at nearly double the density of the nearby Sabangau orangutans (Husson et al. 2009). This results in higher LC rates in Tuanan than we have observed in Sabangau (Spillmann et al. 2017). Therefore, we can reasonably predict that the factors with strong influence on Tuanan male orangutan LC behavior may differ from those influencing orangutans in Sabangau. Because the ecological factors differ between these sites, they may exert different pressures at these sites. This may also explain why Spillmann et al. (2017) did not find a correlation between food availability and LC rate. For example, if fruit is consistently high at site A but at site B fruit availability varies from moderate to low, we may expect to see no correlation between fruit and calling behavior at site A but a strong correlation at site B. This does not mean fruit is less important at site A, only that other factors, such as social factors, might be a stronger influence on call behavior than fruit. However, if fruit were to decrease at site A, it would become a stronger influence in calling behavior. This highlights the importance of examining social and environmental influences on behavior simultaneously, because ecological differences between populations may influence the behavior of orangutans to different extents.

With our large orangutan database that spans nearly a decade, it is possible to address questions about complex influences on production of a long-distance vocalization. Furthermore, observations over multiple years may reveal even weak influences that may be seasonal or acting infrequently. Many different factors affect vocal behavior and the respective contributions of abiotic, biotic, and social influences depend on orangutan population density and the permissive ecological situation. These factors can either act directly or indirectly, as for example through influences on individual body condition. Because of differences in food availability, males from even geographically close populations may show substantial differences in how specific factors affect calling rate.

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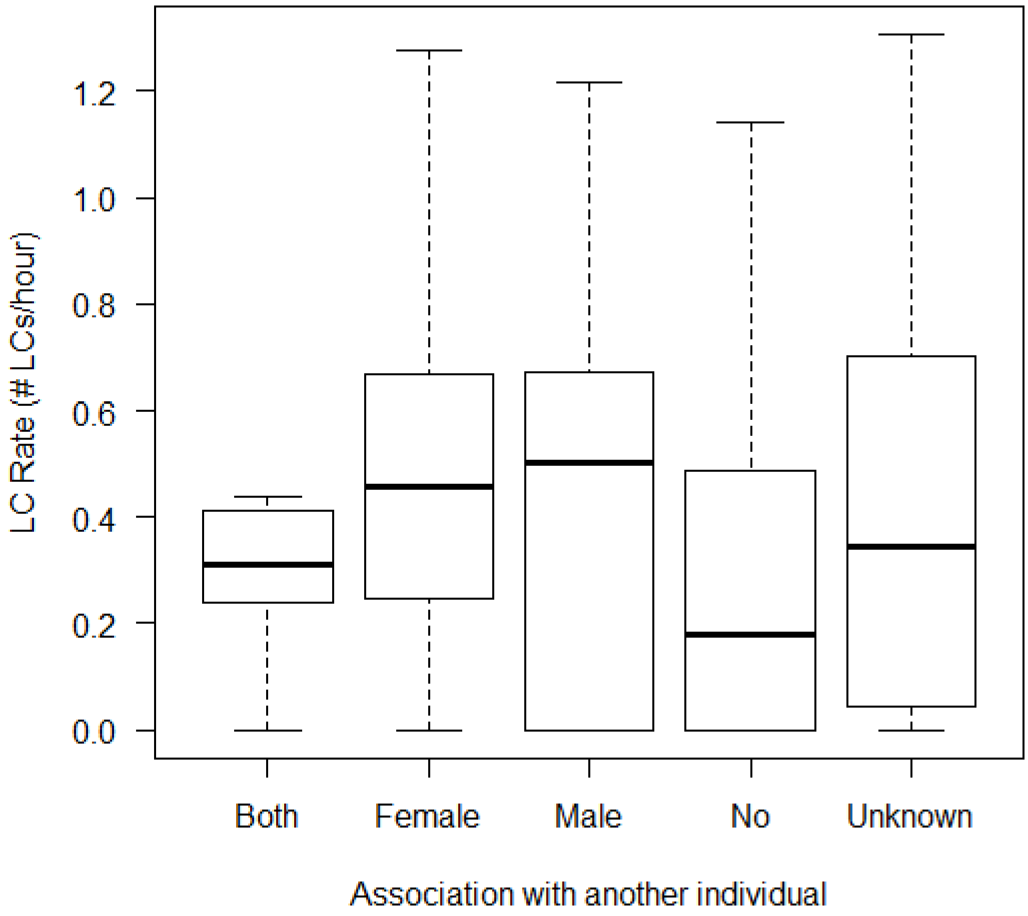

Figure 3.1 Long call rate on days associated with another individual.
Boxplot of the LC rate on days the focal male associated with another individual (ANOVA, $p<0.0001$, n=353(Both=7, Female=39, Male=15, No=261, Unknown=31); $p<0.05$*, $p<0.001$***). The boxes represent the upper and lower quartile, with the thick line in the middle referring to the mean; the dotted lines represent the range of the data.

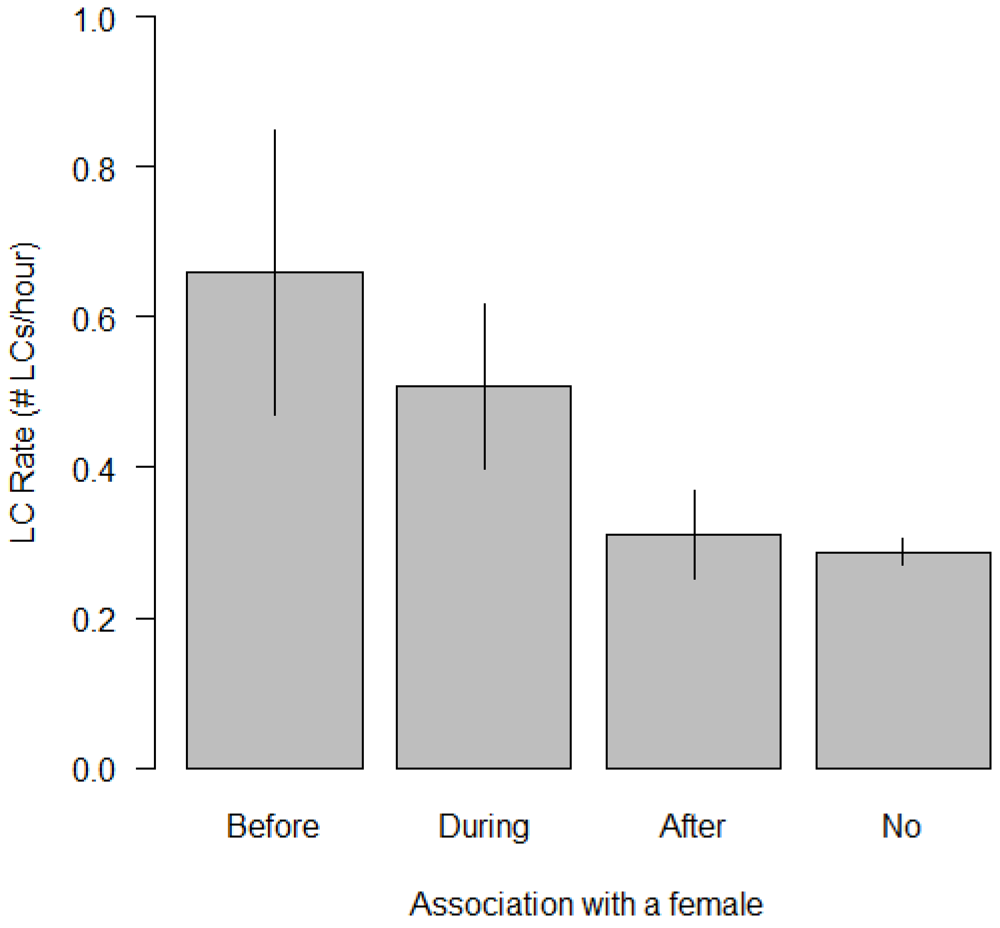

Figure 3.2 Long call rate on days associated with a female.
The mean (± se) LC rate before, during, and after association with a female compared to days without associations with a female or another individual (ANOVA, $p<0.0001$, $n=508$ (Before=34, During=68, After=33, No=373); $p<0.05$*, $p<0.01$**, $p<0.001$***).

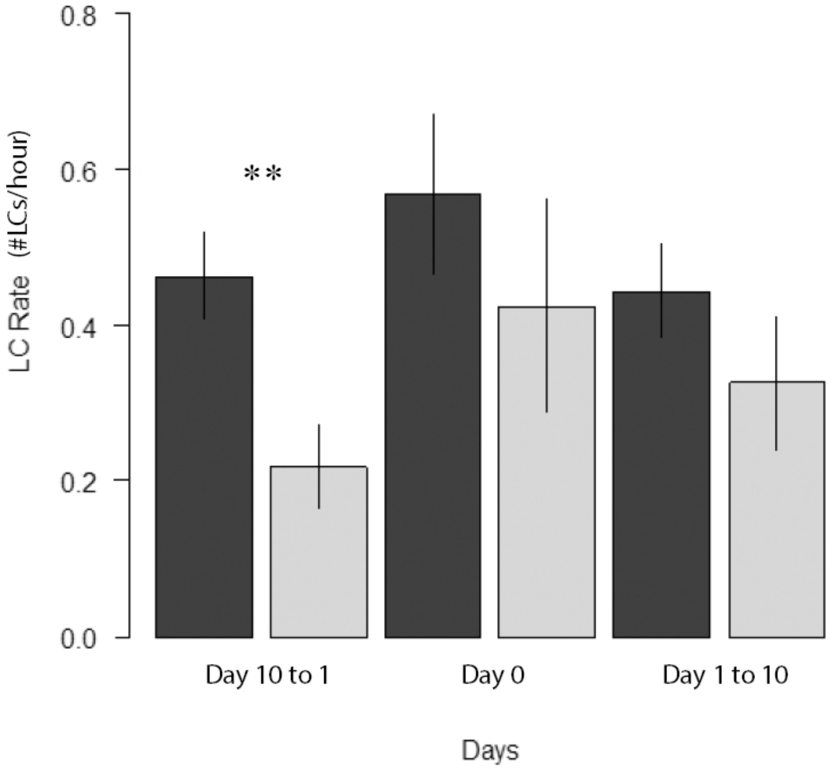

Figure 3.3 Long call rate before, day of, and days following a male/male interaction. The mean (± se) LC rate of winners (black) compared to losers (gray) on the days preceding an interaction (Days 10 to 1), the day of the interaction (Day 0), and the days following the interaction (Days 1 to 10; p<0.01**).

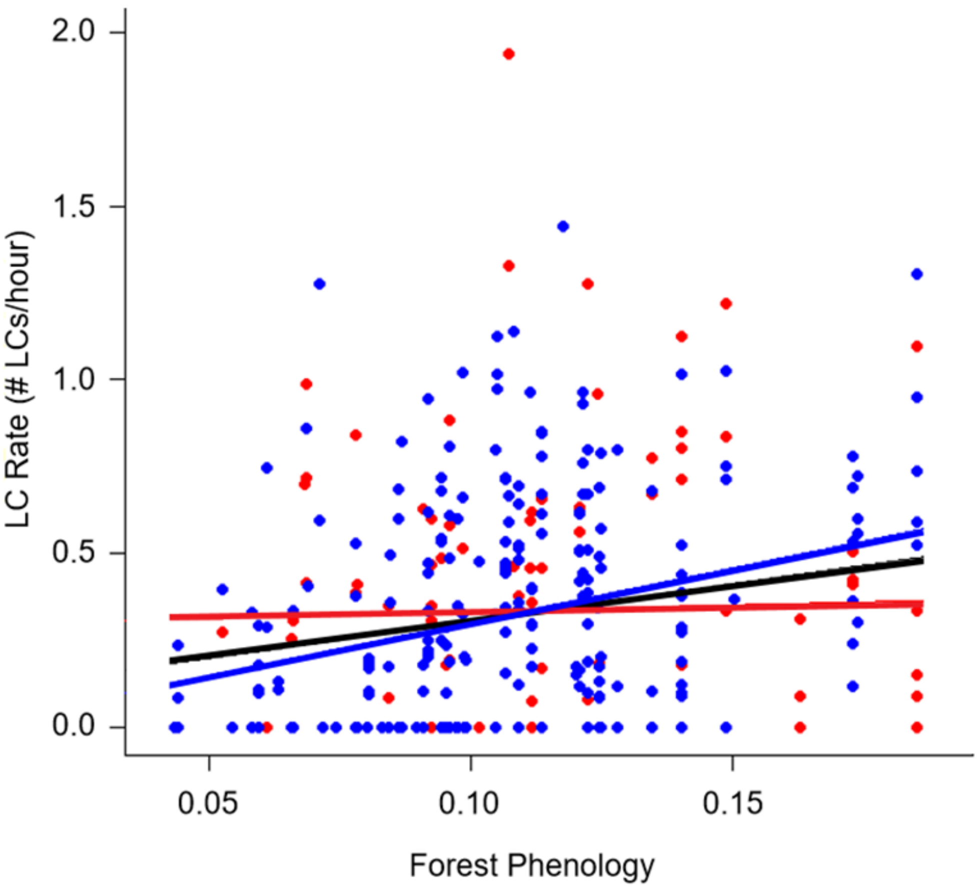

Figure 3.4 Influence of food availability on long call behavior.
Long call rate and entire forest phenology for the eight males with the largest sample size are positively related (glm; $p<0.0001$). The color of the dots corresponds to the number of LCs heard; red dots are LCs heard above the mean LCs heard rate, and blue dots are LCs heard below the mean. The linear regressions are the regression of LC rates compared to phenology when LCs heard are high (red line), LCs heard are low (blue line), and total (black line).

Table 3.1: Individual correlations with food availability and LCs heard

Individual	Sample Size	Heard LC Rate	Forest Food
All	353	0.61*	2.92***
Beethoven	72	1.10	-0.01
Franky	41	0.06	3.46
Hengky	66	0.34	5.51***
Jupiter	36	0.62	2.51*
Mozart	32	3.06***	-0.71
Peter Pan	30	-4.39	-5.66
Salvador	37	2.79	7.11**
Wallace	39	-0.50	-1.7

Results of the GLM model. Individual slope estimates of correlations of LC rates with heard LC rate and entire forest food phenology ($p \sim 0.05$., $p<0.05$*, $p<0.01$**, $p<0.001$***).

CHAPTER 4

VARIABILITY OF THE ORANGUTAN LONG CALL

The ability to identify conspecifics individually through their vocalizations is evolutionarily beneficial, allowing an individual to identify kin, neighbors, new arrivals, and potential competitors (e.g., Galeotti et al. 1997; Ehnes and Foote 2014), and respond accordingly. However, the acoustic features that permit individual recognition are difficult to identify and quantify and often may represent combinations of acoustic features such as complex spectral and temporal aspects. Typically, a multivariate discriminant function analysis is used to test whether individuals can be identified by specific vocalizations. Through these methods, acoustic characteristics have been identified that could permit discrimination of individuals in a wide range of animal taxa (e.g.; birds: Bee et al. 2001; frogs: Ehnes and Foote 2014; mammals: Wich et al. 2003; Townsend et al. 2014). The set of acoustic features that facilitate individual recognition are those that have a distinct individual signature, and, as such, they should remain constant over time (Fox 2008).

Permanent and temporary changes to vocalizations, either acoustic features or repertoire, have been studied in regard to changes in social environment (Elowson and Snowdon 1994), body condition (Galeotti et al. 1997; Martín-Vivaldi et al. 1998; Poulin and Lefebvre 2003), emotional status (e.g., Fischer and Price 2016; Taylor et al. 2016), and territory (Walcott et al. 2006). Relatively few studies have examined the stability of acoustic features with respect to individual recognition over longer time periods (Butynski et al. 1992; Jorgensen and French 1998; Lengagne 2001; Gilbert et al. 2002; Riede et al. 2007; Briefer et al. 2010; Puglisi et al. 2016). A more thorough understanding of acoustic variability over time is required before we can investigate possible links between vocal behavior and age, social status and body condition of the sender.

Understanding the physiology and morphology of vocal production can help pinpoint which acoustic features vary over time, and which remain stable (Taylor et al. 2016). The mammalian vocal apparatus consists of two basic components: the sound source (the larynx) and the upper vocal tract (Fant 1960), both of which must function in tight coordination with the respiratory system (Riede and Goller 2010). Sound in mammals is primarily produced by tissue oscillations of the sound source, and is filtered by the upper vocal tract (source-filter theory, Fant 1960). Source-filter theory predicts that, because acoustic features are constrained by the morphology and physiology of the individual caller (e.g., Taylor et al. 2016), vocalization itself should be an honest signal (Schmidt-Nielsen 1975; Reby and McComb 2003). Indeed, the dominant resonance frequencies of the upper vocal tract, formants, are inversely related to vocal tract length (Fitch 1997; Riede and Fitch 1999; Plotsky et al. 2013). Formant frequencies and spacing have been closely linked to both vocal tract length and body size (Fitch 1997; Reby and McComb 2003). Resonance frequencies might therefore provide information about identity (since the upper vocal tract is constrained by body size), or about the body condition of the caller. Specializations in the upper vocal tract, such as laryngeal air sacs, appear to change with age and body condition (MacKinnon 1974; Delgado and Van

Schaik 2000; Banes et al. 2015), and could alter the resonance of the upper vocal tract. If resonance frequencies remain constant over time, they may indicate individual identity; if resonance frequencies vary over time, they may reliably indicate body condition.

If conspecifics can reliably recognize individuals over multiple years, acoustic features that encode individual recognition need to show greater variation between individuals than within an individual, and remain stable over time (Fox 2008). In this chapter, we address three main questions pertaining to acoustic features of the orangutan long call. First, we tested whether individuals could be correctly identified by various acoustic features given a limited sample size. Previous studies have been able to identify individuals via the long call (Lameira and Wich 2008; Spillmann et al. 2010; Askew and Morrogh-Bernard 2016; Spillmann et al. 2016). However, these studies have had a limited sample size that was collected over a short time period. With this limitation in mind, we used measurements on long calls from one day and asked whether calls recorded days, months, and years from the reference day could still be correctly assigned to the calling individual.

Secondly, to examine an acoustic feature that may encode individual identity, we investigated variation of the fundamental frequency. The fundamental frequency is primarily determined by the viscoelastic composition of the vocal folds, and secondly, by the length of the vocal folds (e.g., Titze 1988; Zhang et al. 2009). We hypothesize that there is selective pressure on male orangutans to communicate individual identity through acoustic features of the long call. Therefore, once fully developed, the composition and length of the vocal folds of male orangutans may remain constant. To address this, we examined the rate and the frequency of two similar pulse types that are produced by airflow over the vocal folds in different directions. The ‘bubble pulse’ is produced with expiratory airflow and the ‘inhale pulse’ is produced with inspiratory airflow. Both pulses, and potentially the difference between the pulses, may indicate the individuality of the vocal folds. These variables could therefore provide distinguishing characteristics for individuals.

Lastly, we examined the resonance frequency of the upper vocal tract as a potential individual-specific feature or as a possible indicator of current body condition. Male orangutans have vocal sacs and secondary sexual characteristics that have been observed to change with age and body condition (MacKinnon 1974; Delgado and Van Schaik 2000; Banes et al. 2015). If these morphological structures affect acoustic features such as spectral content of the long call, condition-dependent acoustic signatures may result. Alternatively, if interindividual variation exists and the resonance frequencies do not vary over time, the resonance frequencies could be used to distinguish individuals. To test the variability of the upper vocal tract, the dominant frequencies and fundamental frequency were examined over time.

4.1 Methods

The research was conducted in the Natural Laboratory of Peat-swamp in the Sabangau forest, in southern Borneo, Central Kalimantan, Indonesia. This research was in collaboration with the Borneo Nature Foundation and the local counterpart, the Center for International Cooperation in Sustainable Management of Tropical Peatland (CIMTROP). Approximately 6,900 individuals of the Bornean orangutan subspecies *Pongo pygmaeus wurmbii* are thought to reside in the Sabangau forest (Morrogh-Bernard et al. 2003; Husson et al. 2009). Some of these orangutans were followed using a grid trail system covering about 8 km^2.

High quality recordings were collected by following flanged male Bornean orangutans from September of 2012 to December of 2015. Long call recordings were collected from follows of flanged male orangutans for the extent of their activity period, from exiting their night nest in the morning to building and entering their night nest at night. All long calls recorded from known individuals were used, regardless of the length of the follow. Long calls were recorded with a Sony PCM-M10 portable linear PCM recorder with a sampling frequency of 44.1 kHz at 24 bit using a directional Sennheiser shotgun microphone ME 66 (frequency response between 40 to 20,000 Hz, ±2.5 dB) with a K6 power module.

To study the variability of the long call, only individuals with the most long call recordings, around 40 per individual, were used: Casanova=37, Henry=42, Napoleon=38, and Vulkan=53 for a total of 170 long calls. The long calls for two individuals were collected over the short time period of only a couple of months, Napoleon (August – September 2014) and Henry (January – April 2014). These two individuals produced multiple long calls a day, which allowed us to examine the variability of the long call from day to day. The long calls from the other two individuals were collected over several years, Casanova (September 2012 – September 2015) and Vulkan (August 2012 – December 2014), which allowed us to examine whether the long call changes from year to year.

Long call analysis was completed in Praat (ver. 6.0.21) software. To better distinguish acoustic details and more accurately measure frequency bands, all long calls were first scaled by a quarter time, which quadruples the frequencies. The spectrogram was viewed using standard settings in Praat (Fourier methods, Gaussian window shape) with a viewing range of 0 to 10,000 Hz (window length of 0.05, dynamic range of 80 dB). Frequency and temporal data were converted back to the original values after they were extracted from the long call, amplitude data were not changed by this conversion.

Initially, each expiratory pulse in the long call was classified according to the description by Ross and Geissmann (2007) and Spillmann et al. (2010). The seven pulse types are: huitus, volcano, high roar, low roar, intermediaries, sighs, and bubbles. The huitus was defined as a high-energy pulse that ascends and descends with either a silent period or a section of deterministic chaos in the middle. The volcano is aptly named for the shape of the pulse; it is a high-energy pulse that ascends and sharply descends, creating a point at the max frequency in the middle. The high roar is a high-energy pulse that ascends and descends like the volcano but does not come to a point at the top. The low roar is a low-energy pulse with a fundamental frequency around 100 Hz and weak frequency modulation. The intermediary pulse can take multiple forms; it can either start high, descend, with another short ascending and descending section in the middle, or it is a flat pulse that has a small ascending and descending section towards the end. The sigh pulse is a low-energy pulse that can have a few “bubbles” leading up to a descending pulse. Finally, bubbles are a series of short harmonic pulses. Furthermore, we also measured and classified a bubble-like pulse that is likely produced during inhalations between the expiratory pulses, called inhale pulses.

Multiple measurements of the entire long call and each pulse type were taken. For the entire long call, the duration of the long call, the number of pulses, and the pulse repetition rate within the call (number of pulses per second) were measured. We split pulses in three sections (beginning, mid-point and end) and took multiple measurements on each third to account for changes in acoustic features throughout a pulse. Duration of each pulse and interpulse interval was measured from the time wave form by identifying amplitude patterns characteristic of pulse on- and offset, instead of a computerized threshold analysis, because these were field recordings, and the wave events of each pulse were easier to standardize. The fundamental frequency ($F0$) and the relative amplitude of harmonics were extracted at the onset, maximum frequency point, and the end of each pulse using a power spectrum. Because the huitus pulse had a break in sound in the middle, i.e., at the maximum frequency point, the frequency was taken before and after the break. For the bubble and inhale pulse, pulse rate (pulses per second) and the fundamental frequency or dominant frequency were measured.

To test variation in the long call between calls over multiple time intervals, one day with 10 or more long calls from each male was used as a reference for subsequent comparison, hereafter referred to as the reference day. The various possible behavioral contexts during call production were not taken into consideration. Calls were pooled irrespective of whether they were produced after a snag crash, a long call heard, or without obvious provocation. Most calls were produced spontaneously (155 out of the 170 long calls analyzed), although the context of 12 calls was unknown. We pooled all calls for this analysis, because the sample size did not allow us to establish correlations with call context. Furthermore, if calls are recorded with a passive acoustic monitoring system, the behavioral context is not known.

A principle component analysis (PCA) was run in R (v. 3.2.3; R core team

(2015)) using the prcomp function. The PCA was run on frequency and temporal variables from three pulse types, volcano, high roar, and low roar. The measured and derived variables used were: duration, interval duration, duration to peak frequency, duration from peak frequency to the end of the pulse, the slope of the rising frequency, the slope of the falling frequency, the change in frequency from the onset to the max frequency, the change in frequency from the max frequency to the end of the pulse, fundamental frequency and difference in amplitude between the first harmonic and the fundamental frequency at the onset, maximum and end.

Two discriminant functions (DF) were run in R using the lda function in the MASS package to test whether individuals can be recognized based on the measured acoustic features and a limited sample (reference day). The first DF was based on acoustic characteristics (duration, interval duration, fundamental frequency and difference in amplitude between the first harmonic and the fundamental frequency at the onset, max and end) of each pulse in the long call. Three pulse types were used in this DF, the volcano, high roar, and low roar. The second was based on the pulse composition of the entire long call, the number of each pulse type as well as duration and rate (number of pulses per second). Initially, the DFs were run on the long calls produced from the reference day (about 40% of the entire database) and then the entire database. Estimating and testing the model based on partial data sets of the reference day was not possible because of the limited sample size. These DF values were then used to make predictions about individual identity, first for the reference day and then for the entire database to test whether identity of each individual can be accurately predicted over time from a limited sample.

To test, if the bubble and inhale pulses were an indication of vocal fold length, the fundamental frequencies were compared. On a few occasions where the fundamental frequency of the inhale pulse could not be clearly measured due to a broad chaotic noise band, the peak amplitude extracted from a power spectrum was used as the fundamental frequency. Furthermore, repetition rate of voiced elements (vER) within each pulse of the two types, may also be limited by physiological constraints. Since these pulses are produced with airflow in different directions across the vocal folds, the different rate and frequency between the inhale and exhale (bubbles) pulse was first examined within an individual, using a Welch two-sample t-test. Next, to test whether these measurements differ between individuals, a one-way ANOVA was used (aov). Lastly, a one-way nested (long calls produced nested within the day they were produced) ANOVA was used to test if there are significant changes in the vER and frequency of the bubble and inhale pulse from day to day and year to year for each individual.

To examine the resonance frequencies of the upper vocal tract, one high energy pulse (the high roar) was used, because its frequency modulation covers most of the frequency encountered in a long call. A power spectrum of the entire pulse was created, and the frequencies and corresponding power (dB/frequency) were extracted. For the long calls from the reference day, the power spectrum of each note was normalized from a scale of 0 to 1, to account for the different recording qualities. Next, the pulses from the reference day were binned into 10 Hz increments and the mean was taken to be used as comparison to the pulse taken at other times. The dominant frequency of each high roar note was extracted, after it was normalized on a scale from 0 to 1, and changes over time were assessed using an ANOVA. In addition, we assessed variability of $F0$ over time in the four individuals.

Because dominant frequency for the entire pulse is a product of amplitude and upper vocal tract resonance, we measured relative amplitudes of $F0$ and $F1$ at 3 points during the pulse, onset, maximum frequency and end.

4.2 Results

4.2.1 Identifying individuals by vocal characteristics over time

A PCA was run on three pulse types, the volcano, high roar, and low roar. Even though 80% of the variance was explained by the first 3 PCs (PCI, 53%, PCII 18%, PCIII 9%), it did not yield a clear separation of individuals (mean PC ± standard deviation; PCI Casanova= -1.106±2.233, Henry=0.004±2.328, Napoleon=0.199±2.463, Vulkan=0.528±2.376; PCII Casanova=0.231±1.281, Henry=0.837±1.225, Napoleon=-0.286±1.606, Vulkan=-0.454±1.111; PCIII Casanova=-0.517±1.082, Henry=-0.400±0.826, Napoleon=0.448±0.999, Vulkan=0.159±0.785). The main variables loading on PCI were frequency variables, maximum $F0$, rising slope, and falling slope. PCII loadings consisted of temporal variables, including duration to the peak, pulse duration, and interpulse interval. Because the PCA did not separate individuals, it was not used for variable selection in the DF. Instead, derived variables, such as slope, had the highest correlations (≥ 0.90) with other variables and were therefore left out of the DF analysis.

Initially, a discriminant function analysis using the entire data set on acoustic variables was run on each of the three pulse types to establish if certain pulse types reveal individual identity more strongly than others. Individual assignments were most often correct for the volcano pulse (90%) compared to the high (68%) and low (75%) roar

(Table 4.1a). The measurements on low roar pulses were less consistent in recognizing individuals. For Casanova and Henry, the correct assignment percentage was high (83 and 100%), whereas for Napoleon and Vulkan it was below 60%.

For the second discriminant analysis based on acoustic characteristics, we trained the model on 10 or more long calls produced on 1 day (reference day) and first tested individual recognition on each of these. Then this model was used to test recognition for call features from all other recording dates. The discriminant function model based on the reference day of each individual gave a prediction accuracy of 76%. Maximal fundamental frequency contributed most strongly to the loading of the first factor of the reference day model, and duration of the pulse to the second factor.

Next, the DF model using the entire dataset correctly assigned the individual 63% of the time across all individuals. In this model, the difference in relative amplitude between $F1$ and $F0$ loaded predominantly on factor one, and the duration of the pulse on factor two. The model from the reference day was then used on the total dataset, minus the overlapped dates, to test if using a limited sample can accurately predict individuals from calls recorded on different days, months, and years. Overall this model performed poorly and assigned the individual correctly only 42% of the time. The two individuals, Henry and Napoleon, for which we had collected data over a few months had mixed results. Sixty-nine percent of Napoleon's calls were identified correctly, whereas Henry's calls were identified correctly only 44% of the time. The calls from the two individuals with data sets spanning multiple years, Casanova and Vulkan, were identified least reliably, 25% and 30%. For these two males, the model correctly assigned pulses within a few days of the reference day 71 and 80% of the time (Figure 4.1a). However, for recordings several months prior to the reference day, correct identification of Vulkan's calls was drastically reduced and remained near 30% for up to 2 years. The model only correctly identified Casanova's calls less than 0.08% of the time in calls recorded 2-3 years prior to the reference day. Surprisingly, Henry's calls were infrequently identified on recording days close to the reference day, but were more accurately identified months later. In contrast, the prediction accuracy of Napoleon remained fairly constant (61-77%).

Next, the same discriminant function analysis was applied to the composition of the long call. Calls from the reference day were most accurately identified. One individual was predicted correctly 100% of the time, two individuals over 90% of the time, and one was only predicted correctly 60% of the time (Table 4.1b). The most important factor in the discriminant analysis was the pulse rate (the number of pulses per second) of the long call. The discriminant function trained on the entire database and used to predict individual calls did so correctly 69% of the time. The loading of the first factor was the number of intermediate and huitus pulses, and pulse rate determined the second factor. The long call composition model performed poorly in predicting caller identity from the DF model trained on the reference day data. On average, 46% of the individuals were assigned correctly (Table 4.1).

Similar to the acoustic features model, caller identification varied greatly for the four individuals. Casanova was accurately predicted around the days of the reference day (88%), but the model was not able to predict long calls produced during prior years (Figure 4.1b). In contrast, for Vulkan's calls a low prediction accuracy was found for calls recorded only days or months prior to the reference day (17-33%), whereas 86% of calls recorded a year earlier were identified correctly. However, calls recorded 2 years prior to the reference day were not identified correctly. Call identification for Napoleon remained consistent for days and months, whereas Henry had a low prediction accuracy of long calls only days from the reference day and 100% accuracy 2 months after the reference day.

4.2.2 Bubbles vs. inhale

The bubble and inhale pulses are composed of multiple short bursts of harmonic stacks. Although they are similar in acoustic composition, they appear to be produced during opposite phases of the respiratory cycle (bubble pulses during exhalation and inhale pulses during inspiration). The fundamental frequency of these short bursts of harmonic pulses may be limited by vocal fold size. It is unknown how the different direction of airflow during production of these two pulses may impose limitations on acoustic characteristics.

The repetition rate of voiced elements (vER) within each pulse of the two types showed high variation across and within individuals. In all males, the vER of the inhale pulse was 2-3 times greater than that of the bubble pulse (Figure 4.2a). The vER of the bubble pulse was significantly different between all males (Figure 4.2a; ANOVA, $p<0.0001$, $F=71.08$; Tukey post hoc, $p<0.0001$ between all male pairs, except for $p=0.012$ between Henry and Casanova). The vER of the inhale pulse was also significantly different between males, with one exception (ANOVA, $p<0.0001$, $F=72.42$; Tukey post hoc, $p<0.0001$ between all males except Vulkan and Napoleon, $p=0.14$). Variation in absolute vER of the two pulse types was not consistent. The males with lower vER in the bubble did not necessarily also produce a low vER in the inhale pulse.

The *F*0 of the inhale pulse was significantly higher than that of the bubble pulse in all males (Figure 4.2b). Fundamental frequency of the bubble was significantly different in 3 out of 6 paired comparisons (ANOVA, p=0.0005, F=5.957; Tukey post hoc, Vulkan-Casanova, p=0.049, Vulkan-Henry, p=0.023, Vulkan-Napoleon, p=0.0002, Henry-Casanova, p=0.98, Napoleon-Casanova, p=0.35, Napoleon-Henry, p=0.66), whereas *F*0 of the inhale differed in 5 out of 6 (ANOVA, p<0.0001, F=40.83; Tukey post hoc, Napoleon-Casanova, p=0.77, Vulkan-Casanova, p<0.0001, Vulkan-Henry, p<0.0001, Vulkan-Napoleon, p<0.0001, Henry-Casanova, p=0.027, Napoleon-Henry, p<0.0001).

Frequency and vER of pulses varied to differing degrees within individuals across time. For Henry, whose long calls were collected over a couple of months, the vER and *F*0 of the bubble pulse did not significantly differ from day to day (ANOVA; vER, p=0.069, Tukey post hoc, 1 out of 6 comparisons between days significantly differed; *F*0, p=0.194, 0 out of 6). For Henry's inhale pulses, *F*0 did not differ between days, but vER did (ANOVA; vER, p<0.0001, 4 out of 6; *F*0, p=0.211, 0 out of 6). In Napoleon, whose long calls were also collected over a period of months, vER of the bubble pulse and *F*0 of the inhale pulse differed significantly between days (ANOVA; bubble vER, p<0.0001, 2 out of 10; bubble *F*0, p=0.284, 0 out of 10; inhale vER, p=0.179, 0 out of 10; *F*0, p<0.0001, 4 out of 10).

For the two males, whose long calls were collected over a few years, an ANOVA was run with the days nested within the year (the long calls were still nested within the day). Casanova had significant differences in the vER and *F*0 for both the bubble and inhale pulse for 2015 (ANOVA; bubble vER, p<0.0001; Tukey, 12-15, p<0.0001, 14-15,

$p<0.0001$; *F*0, $p<0.0001$; all years $p<0.0001$; except 13-15, p=0.001; 12-14, p=0.77; inhale vER, p=0.0002; 12-15, p=0.0009, 13-15, p=0.018, 14-15, p=0.031; *F*0, $p<0.0001$; 12-15, $p<0.0001$, 13-15, p=0.003, 14-15, p=0.051), whereas Vulkan only significantly differed in 2014 in the vER of the bubble pulse (ANOVA; bubble vER, $p<0.0001$; Tukey, 12-13, p=0.61, 12-14, p=0.002, 13-14, $p<0.0001$; *F*0, p=0.136; inhale vER, p=0.064; *F*0, p=0.46). However, day to day variance was high in Vulkan in each measurement except for vER of the inhale pulse (ANOVA; bubble vER, $p<0.0001$; *F*0, p=0.003; inhale vER, p=0.11; *F*0, p=0.0009). Casanova also had significant variance day to day in all measurements (ANOVA; bubble vER, p=0.009; *F*0, $p<0.0001$; inhale vER, p=0.009; *F*0, p=0.0002).

4.2.3 Resonance frequencies compared to fundamental frequencies

Upper vocal tract filter properties of male orangutans were examined by comparing energy distribution across the harmonic spectrum using power spectra of one high energy pulse with the broadest frequency modulation (high roar). Comparisons within individuals across time and between individuals were made to assess to what degree filter characteristics vary. The other high energy pulse types (volcano and huitus) from the long calls produced on the reference day were also viewed to compare the peak resonance frequencies between pulses that have similar frequency ranges. Because the results for all high-energy pulse types were similar, only data from the high roar will be shown below.

For the high roar pulse, all males had the highest energy (peak frequency) around 600 Hz. The mean peaks of the long calls from the reference day were as follows:

Casanova: mean±1std=670 ±160 Hz; Henry: 580±70 Hz; Napoleon: 600 ±380 Hz; Vulkan: 550 ±160 Hz. Energy distribution around this first major resonance peak displayed two patterns (Figure 4.4), which likely indicate a combination of different emphases of the frequency modulated segments (not integer multiples of $F0$) and different resonance properties.

Combining the high roars from all recording days, the dominant frequency was marginally not significantly different between individuals (ANOVA, p=0.051, F=2.616). The dominant frequency peak ranged from 250-1200 Hz, which reflects different emphasis across the frequency modulated pulse and the best resonance frequency.

The $F0$s between individuals were taken at three positions of the pulse, the onset, maximum, and end. Between individuals, only the $F0$ at the onset of the pulse of Casanova significantly differed from the other males (ANOVA, p=0.005, F=4.445; Tukey, Casanova-Henry, p=0.017, Casanova-Napoleon, p=0.019, Casanova-Vulkan, p=0.011). The $F0$ of the end of the pulse showed no significant differences between individuals (ANOVA, p=0.50, F=0.80). However, the $F0$max at the middle portion of the pulse gave varying results (ANVOA, p=0.0001, F=7.378); Casanova was only significantly different compared to Henry (Tukey, p=0.003), and Napoleon was significantly different from Henry (p=0.0003) and Vulkan (p=0.02).

The dominant peak frequency did not shift within individuals where long calls were recorded over a few years (ANOVA; Vulkan p=0.8, F=0.229; Casanova, p=0.17, F=1.892; Figure 4.5). From day to day, the dominant frequency did not vary substantially, except in Henry (ANOVA; Casanova, p=0.29, F=1.268; Henry, p=0.008, F=4.256; Napoleon, p=0.79, F=0.239; Vulkan, p=0.825, F=0.3; Figure 4.5, 4.6).

The fundamental frequency over the 2 years for Casanova and Vulkan remained fairly constant, with two exceptions. The *F*0 of the onset of the high roar was significantly higher in Casanova in 2015 (ANOVA; *F*0 onset, p<0.0001, F=30.31, Tukey, 2015-2014, p=0.014, 2015-2013, p=0.038, 2015-2012, p<0.0001; *F*0 max, p=0.39, F=1.04; *F*0 end, p=0.80, F=0.332), and max *F*0 of the high roar of Vulkan was significantly higher in 2013 from that in 2012 and 2014 (ANOVA, p=0.009, f=5.149; Tukey, 2013-2012, p=0.021, 2013-2014, p=0.011, 2012-2014, p=0.66). The *F*0 of the onset and the end of the high roar for Vulkan did not significantly change (ANOVA; *F*0 onset, p=0.56, F=0.587; *F*0 end, p=0.338, F=1.104).

The daily variation in the fundamental frequency was constant within all individuals, with one exception (the two individuals with recordings over multiple years had daily variation nested within the year). There was no daily variation in the *F*0 at the onset, max or end, for three males (ANOVA; Casanova, onset, p=0.619, F=0.666; max, p=0.906, F=0.253; end, p=0.515, F=0.829; Henry, onset, p=0.781, F=0.362; max, p=0.231, F=1.482; end, p=0.87, F=0.235; Napoleon, onset, p=0.437, F=0.972; max, p=0.137, F=1.884; end, p=0.2, F=1.598). Vulkan did have daily changes in *F*0 at the onset and end of the pulse (ANOVA; onset, p=0.0432, F=2.266; max, p=0.162, F=1.579; end, p<0.0001, F=9.920).

The difference in relative amplitude between *F*0 and *F*1 at all three points of the high roar, the onset, maximum, and end, was examined to test whether resonance frequencies of the upper vocal tract of each individual change over the course of the pulse. It appears that the resonance frequency of the upper vocal tract is not static and has some dynamic modification. This is clearly seen in the relative amplitude difference at each frequency, which can have a change in relative amplitude from the *F*1 up to 30 dB (Figure 4.7). The difference in relative amplitude was substantially altered for the *F*0 at the onset of the pulse compared to that at the end for most individuals (difference between blue and red lines), indicating changing upper vocal tract resonance. Because frequency differences at the end of the pulse frequently matched those at *F*0max (where *F*0 overlaps), it appears that some modification of the upper vocal tract occurred from onset to *F*0max and then was maintained to the end of the pulse.

The relative amplitude between *F*0 and *F*1 at all three points in the high roar remained fairly constant over time. Henry did not have daily changes in relative amplitude (ANOVA; onset: p=0.16, F=1.99; max: p=0.27, F=1.23; end: p=0.92, F=0.008). However Napoleon did have significant daily variation at the onset of the pulse (ANOVA; onset: p=0.0009, F=13.27; max: p=0.82, F=0.05; end: p=0.90, F=0.02). Casanova did not have significant changes in his relative amplitude daily or yearly, with the exception of daily variation at the end of the pulse (ANOVA; onset: daily, p=0.36, F=1.36, yearly, p=0.27, F=1.12; max: daily, p=0.94, F=0.195, yearly, p=0.21, F=1.57; end: daily, p=0.009, F=3.91, yearly, p=0.61, F=0.62). However, at the end of the pulse, Vulkan had significant daily and yearly changes, as well as daily variation at the max (ANOVA; onset: daily, p=0.14, F=1.67, yearly, p=0.87, F=0.14; max: daily, p=0.03, F=2.68, yearly, p=0.07, F=2.9; end: daily, p=0.006, F=3.35, yearly, p=0.003, F=6.46). Between males, the relative amplitude between *F*0 and *F*1 did not significantly differ between males at the onset (ANOVA; onset, p=0.08, F=2.30), but did significantly differ in 3 out of 6 paired comparisons at the max, and Vulkan was significantly different at the end of the pulse (ANOVA; max: p<0.0001, F=13.26, Tukey post hoc, Henry-Casanova

$p<0.001$, Henry-Napoleon $p<0.0001$, Napoleon-Vulkan $p<0.0001$; end: $p<0.0001$, $F=10.19$, Vullkan-Casanova $p=0.005$, Vulkan-Henry $P<0.0001$, Vulkan-Napoleon $p=0.002$).

4.3 Discussion

4.3.1 Discriminant function – Individual identity over time

To test whether representative orangutan long calls collected over a short time period, over the course of 1 day in this study, could accurately predict the caller identity on different days, months and years, we trained a discriminant function model using the reference day calls. Because the PCA eliminates covariation, and the variance from the PCA did not appear to be contributed to individual differences, the covariance of the variables used in the DF is not a strong influencing factor. The reference day DF model correctly assigned individual identity in 76 and 86% of the cases within the reference day, which falls within the range of accuracy achieved in previous studies on individual discrimination based on the long call (Spillmann et al. 2010; Askew and Morrogh-Bernard 2016; Spillmann et al. 2016). However, the reference day model identified calls recorded on other days only slightly better than the 25% expected from chance. The acoustic characteristic model had a satisfactory accuracy rate identifying long calls within days of the reference day, whereas the call composition did not have a high accuracy rate within days of the reference day. Males in the Sabangau forest typically do not call more than once or twice a day. Therefore, on days where there are 10 calls, the calls may be produced under different contexts. The rate of the call, which is included in the call composition analysis, is the strongest identifying factor for call context (Spillmann et al.

2010; Askew and Morrogh-Bernard 2016). This could explain why we found low day to day prediction rates for call composition measurements compared to the acoustic features. However, Spillmann et al. (2016) also did not make a distinction in call context and their DF did not appear to suffer as a result. In addition, call context should not affect the DF based on acoustic characteristics, which also performed poorly.

The DF model, trained on the variability of the entire dataset, also had a fairly low prediction accuracy (63-69%). The difference to prediction accuracy from other studies may be attributed to the increased sample size used in this study and the differences in the time periods over which the data were collected. The three previous studies used approximately16 long calls per individual (Spillmann et al. 2010; Askew and Morrogh-Bernard 2016; Spillmann et al. 2016), which comprise half the sample size per individual included in this study. These studies did record long calls in different years; however, for two of the studies, it is unclear whether calls from one individual were collected over the entire time period of the study (Spillmann et al. 2010; Spillmann et al. 2016). Askew and Morrogh-Bernard (2016) did collect long calls from two time periods spaced a year apart for two of their three individuals. They found mixed results with one individual changing call features and one remaining constant. The change was attributed to a change in dominance status. Askew and Morrogh-Bernard (2016) also collected long calls in the Sabangau forest and one individual, Napoleon (named Peter Pan in their study), was recorded and used in both of our studies. Interestingly, Napoleon's calls showed highly consistent features over the year time gap in the Askew and Morrogh-Bernard (2016) study. Napoleon was the most accurately predicted in this study, even when the single day training model was used to identify calls in the entire database. In our data set, the long calls from Napoleon were collected over several months, rather than years. However, the shorter recording period did not necessarily result in better identification of the caller from long call features. Henry’s calls were also collected over a few months, but caller identification for him was as poor as for the two males whose long calls were collected over years. From these two studies, it becomes clear that individual differences exist in how constant call features remain over time.

One potential cause for why certain individuals may have a more stereotyped long call than others is age. Even though the exact age is difficult to determine in orangutans, estimates based on visual inspection are possible. Napoleon is presumably the oldest individual, and has been followed as a fully flanged male since 2009. Vulkan was first followed as an unflanged male starting in 2003, and developed flanges in 2010. When the first long calls were recorded from Vulkan, his flanges were still developing, but by 2013, he was fully flanged. Less information is available for Casanova and Henry. Casanova was fully flanged when he was first followed and recorded in 2012, but based on the conditions of his flanges, he did not appear to be an older flanged male. Henry appeared to have flanges that were still developing. Therefore, we predict Napoleon to be the oldest individual in this study.

Whereas primate vocal development was thought to be completed at an early age (e.g., Seyfarth and Cheney 1986), this may not always be the case. In vervet monkeys (*Chlorocebus aethiops*), juvenile vocal development occurs gradually over 3 years (Seyfarth and Cheney 1986). The production of long calls by male orangutans starts while development of their secondary sexual characteristics is still ongoing. Potentially, it takes time for males to practice their long call, and over time, become more stereotyped.

More data are needed to test whether long call features become more fixed with age or whether large differences in stereotypy exist between individuals irrespective of age.

As found with previous studies (Spillmann et al. 2010; Askew and Morrogh-Bernard 2016; Spillmann et al. 2016), long call features, which are independent of morphology of the vocal apparatus, yielded higher accuracy in identifying individuals when the entire dataset was used to train the model. One could have predicted that the acoustic features of the long call, which may have morphological constraints (e.g., Taylor et al. 2016), may better distinguish individuals than the choice of pulse type used. However, evidence of laryngeal and fine motor control has already been seen in orangutans (Lameira et al. 2015; Lameira et al. 2016). With some level of dynamic control of the vocal apparatus, individual morphological differences may be less pronounced. Therefore, choices about call composition may give rise to individual-specific characteristics more readily than acoustic features.

How individual recognition based on acoustic features can be upheld over time has not been studied extensively. Two studies in birds, on eagle owls (*Bubo bubo*; Lengagne 2001) and great bitterns (*Botaurus stellaris*; Gilbert et al. 2002), found acoustic signatures to be stable over 2 or more years. However, another study on great bitterns found significant variation in males over the course of 3 years (Puglisi et al. 2016). In fallow deer (*Dama dama*), Briefer et al. (2010) found a trade-off between acoustic features to encode individuality and quality, because the same features that encode individuality also encode quality, and ultimately, they are more reliable ques for quality than individuality. Two studies in primates, on chimpanzees (*Pan troglodytes*; Riede et al. 2007) and blue monkeys (*Cercopithecus mitis stuhlmanni*; Butynski et al. 1992), both found that vocalizations remained relatively constant over the course of 8 to 10 years. In contrast, Jorgensen and French (1998) found in tuffed-ear marmosets (*Callithrix kuhli*) over the course of 3 years high correct classification of calls within a year, but only 50% accuracy between years. They suggest that for long-term monitoring, recognition mechanisms must be modified over time. Overall, studies on long-term recognition of individuals by their vocalizations have given mixed results. Individual recognition using recordings from passive acoustic monitoring systems (PAM) is possible (Spillmann et al. 2016). However, before these systems can be fully utilized, more research is required. If acoustic features are not stable within an individual over time, potentially, calls recorded with PAM systems may have to be supplemented with occasional observer-based resampling of individuals over time. With long-lived animals, more long-term data are required to fully understand the stability and variability of different acoustic features over time and changes with age, body condition, or dominance status.

4.3.2 Bubbles vs. inhale

We hypothesized that the fundamental frequencies of the bubble or inhale pulse may reflect individuality of the vocal folds. Significant differences were found between the inhale pulse and the bubble pulse, which are produced by inspiratory and expiratory airflow, respectively. The differences in the vER of the bubble and inhale pulse were more distinct between individuals than the fundamental frequencies. Daily variation was not significant for one of the two individuals whose long calls were recorded in a short time frame. However, for the two males with long calls recorded over a couple of years, the day to day variation was significant. The individuals with long-term datasets showed mixed results with respect to changes. Vulkan's *F*0 and vER remained relatively constant for all measurements, except the vER of the bubble pulse. In Casanova, significant variation was found across years. Even though significant differences between individuals existed, the high daily variation may make features of the bubble and inhale pulses unreliable individual signatures.

The mean *F*0 of the bubble and inhale pulse may be indicative of vocal fold length, but substantial variation in *F*0 may be caused by different subglottal pressure conditions. The *F*0 range of the inhale and bubble pulses might constitute a more reliable individual signature. The minimum and maximum frequencies in fallow deer and Iberian wolves (*Canis lupus signatus*) have been found to distinguish individuals (max, Palacios et al. 2007; min, Vannoni and McElligott 2007). In hyenas, individuals could be identified based on the pitch. However, this parameter was also an indication of age and was likely to change (Mathevon et al. 2010). The difference in the vER between the bubble and inhale varies substantially between individuals. Because it is not known how this feature varies over the life of an orangutan, its potential for establishing caller identity is unclear.

Alternatively, the viscoelastic properties of the vocal folds, which largely determine *F*0 (e.g., Titze 1988; Zhang et al. 2009), may fluctuate and therefore make it difficult to use *F*0 to distinguish between individuals. Differences in viscoelastic properties of the vocal folds have been seen between species (mammals, Alipour et al. 2011; birds, Goller and Riede 2012) and between sexes (humans, Chan et al. 2006; rocky mountain elk, Riede and Titze 2008; rhesus monkeys, Riede 2010). Collagen and elastin composition is sensitive to sex steroid levels; for example, an increase in testosterone increases the collagen/elastin ratio in rats (Fischer and Swain 1980). The presence of hormone receptors, and therefore the sensitivity of vocal fold composition to hormone fluctuations have been seen to vary across sex and age in humans (Newman et al. 2000; although another study contradicts these results, Schneider et al. 2007). Therefore, the viscoelastic properties of the vocal folds may fluctuate from 1 year to the next or even over a shorter time course. However, detailed information on the relationship between hormonal fluctuation and vocal fold composition and its effects on $F0$ are lacking, which leaves its relevance for maintenance of acoustic features for individual recognition unclear. We hypothesized that because of the limited interaction between individuals in orangutans, there may be increased selective pressure to encode and maintain individual identification over time. But if the composition of the vocal folds can fluctuate with changes in hormones, then it may make individual identification by $F0$ and related frequency parameters difficult. One study examined how $F0$ of the pant hoot changed over time and with age in chimpanzees (Riede et al. 2007). The researchers did not find a significant correlation between $F0$ and age, but they did observe that the max $F0$ was the highest in the dominant male. The high max $F0$ of dominant males decreased when the male lost dominance status. Changes in dominance status can lead to drops and changes in testosterone levels (e.g., Muller and Wrangham 2004; Muehlenbein and Watts 2010), which may change the viscoelastic properties of the vocal folds and explain the decrease in max $F0$ of the previously dominant males. Potentially, such an effect could have contributed to the significant changes in the $F0$ of the bubble and inhale pulse in our study. The large fluctuations in $F0$ could render this acoustic parameter a very unreliable cue for individual identity.

Significant differences between the inhale pulse and the bubble pulse were observed. In all individuals, the inhale pulse had a higher *F*0 and had a faster vER than the bubble. While phonation during inhalation may be a feature of orangutan vocal behavior (Lameira et al. 2016) its relevance for long-range communication may be limited. Most likely, sounds produced during inhalation, like the inhale pulse, attenuate more quickly than louder components of the long call. In the Southern-Bornean gibbons, who also reside in the Sabangau forest, entire notes of their duet song are almost completely attenuated at distances over 350 m (O'Hagan 2013). Gibbon song is used in territory defense but also for pair bonding. The authors attributed those sections in the song that were highly compromised over distance to intragroup communication. The bubble pulse of the long call can be heard 200 m from the calling male and may only be intended for close range listeners. The inhale pulse is even softer and therefore cannot be heard over distance and may simply be a byproduct of the quick inspiratory breaths between the expiratory pulses.

4.3.3 Are resonance frequencies static or dynamically adjusted?

The frequency peak with the most energy of the high roar pulse in the long call occurs around 600 Hz. The energy peak was constant from day to day (Henry being an exception) and over multiple years. However, males were marginally not distinguishable. During this study, Vulkan increased in size and underwent substantial growth in his secondary sexual characteristics (flanges). Nevertheless, his peak energy frequency did not change significantly. We predicted that changes in the vocal sac may cause shifts in the peak energy frequency, but did not observe this effect. The relative amplitude of the

*F*0 compared to the amplitude of *F*1 did have significant variation in only one of the three positions measured for Vulkan. However, this also varied daily for Vulkan and another individual. This is consistent with a model-based finding that vocal sacs may not cause major shifts in resonance frequency as has been previously predicted (Riede et al. 2008). Formants have been used to recognize individuals of several diverse species (Townsend et al. 2014), and have been linked to both vocal tract length and body size (Fitch 1997; Reby and McComb 2003). Because we did not see a clear change of resonance features in Vulkan, morphological changes may not play a major role; instead, dynamic changes may determine filter properties. Whether or not spectral features of the long call provide reliable information about the sender or his body condition is therefore questionable.

The *F*0 of the high roar is also not a reliable indicator of individual identity. The *F*0 has long been studied as an indication of body size and individual identifications, because the length of the vocal fold is expected to scale with body size (e.g., Taylor et al. 2016). However, findings have been inconsistent, and even though size inversely scales with sound frequency in large interspecific comparisons, intraspecific comparisons yielded mixed results (e.g., Ey et al. 2007; Taylor et al. 2016). In the orangutan long call, differences in the onset and end *F*0 did not allow identification of individuals (Casanova’s onset *F*0 being an exception), whereas the max *F*0 was significantly different for half of the paired comparisons. Over time, more variation was seen in the *F*0 than the dominant frequency, making it a poor acoustic feature for identifying individuals.

Potentially, it may be more important to advertise the current condition of the male with the long call than revealing individual identity. This may be especially important if the same acoustic features that identify individual males also encode quality, as seen in fallow deer (Briefer et al. 2010). Because male orangutans have a large, dynamic home range, they might not encounter the same males often. It may be more important to know the current condition of the vocalizing male, rather than his identity.

In gibbons, experiments have demonstrated active coordination of upper vocal tract filtering and the vocal folds, causing a nonlinear interaction between the two to enhance $F0$ during their iconic loud song (Koda et al. 2012). Similarly, indications for neural control of the larynx were identified in orangutans (Lameira et al. 2015; Lameira et al. 2016) as well as for fine motor control of the upper vocal tract (Lameira et al. 2013; Lameira et al. 2015). However, it is largely unknown to what extent dynamic control of laryngeal and upper vocal tract properties is employed during long call production. Over the course of the frequency-modulated high roar pulse, we found the difference in relative amplitude between $F0$ and $F1$ to change nearly 30 dB at the same $F0$. This change suggests that male orangutans display some articulation with their upper vocal tract in that they change the resonance frequency of their upper vocal tract actively during the pulse (best seen in Vulkan, Figure 4.7d).

For $F0 < 200$ Hz, relative energy content for upper harmonics is greater than that of $F0$, which is consistent with the 600 Hz dominant frequency throughout the pulse in all individuals. These findings suggest that the resonance frequency of the vocal tract of males promotes the highest frequency components of the long call. This is surprising, given that the long call is a long-distance signal and lower frequencies are less attenuated over distance. Perhaps the emphasis of higher frequencies constitutes a handicap and therefore indicates strong sexual selection on this feature of the orangutan long call.

In conclusion, the measured long call features did not permit reliable identification of individual males over the time span of 1 to several years. However, males varied substantially in how stereotyped call features remained over time. More research is needed to ascertain whether stereotypy emerges with increasing age of male orangutans.

4.4 References

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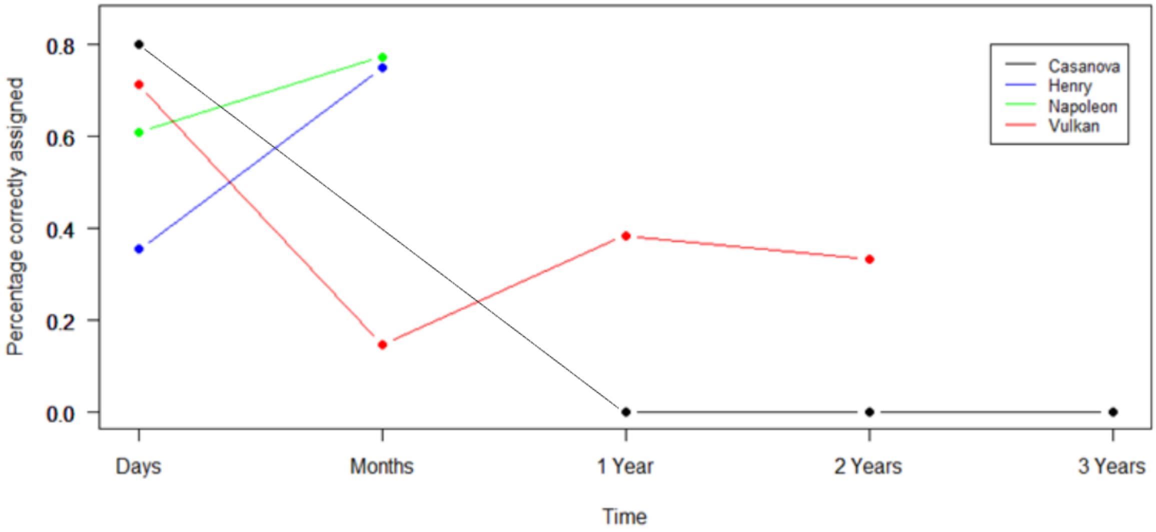
a. Acoustic characteristics model



b. Call composition model

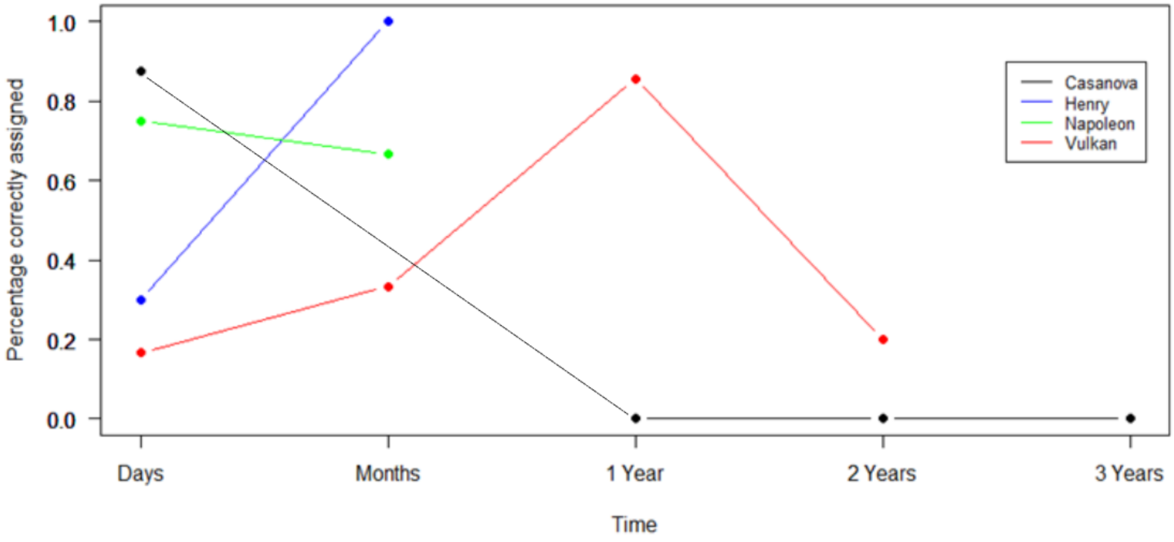
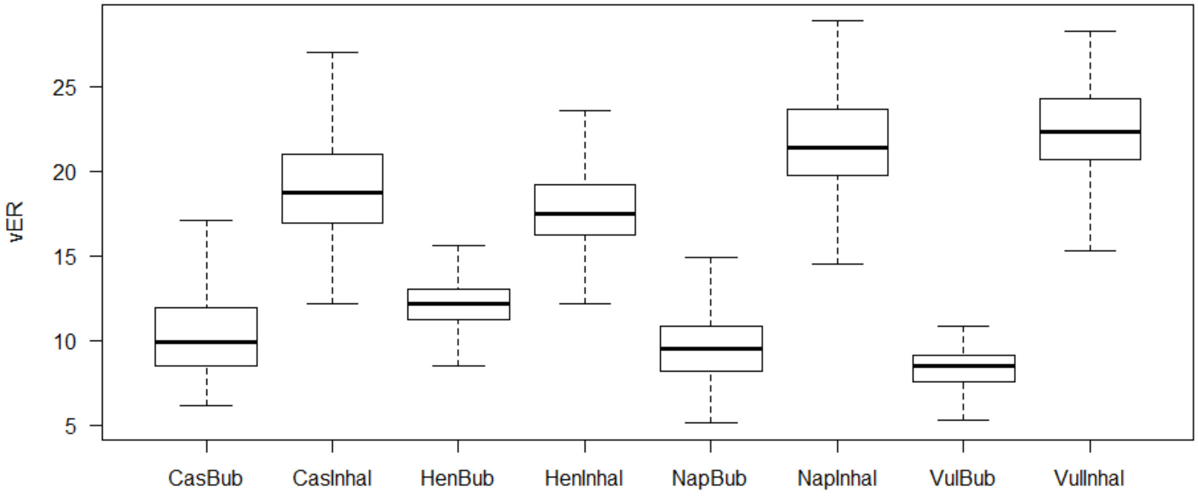


Figure 4.1 Percentage of correctly assigned individuals according to DF model.
The percentage of correctly assigned identities based on the reference day DF model predicting the total data per individual. The accuracy of the model predicting the long call identity within days, months, and years away from reference day.

a. vER



b. Fundamental frequency

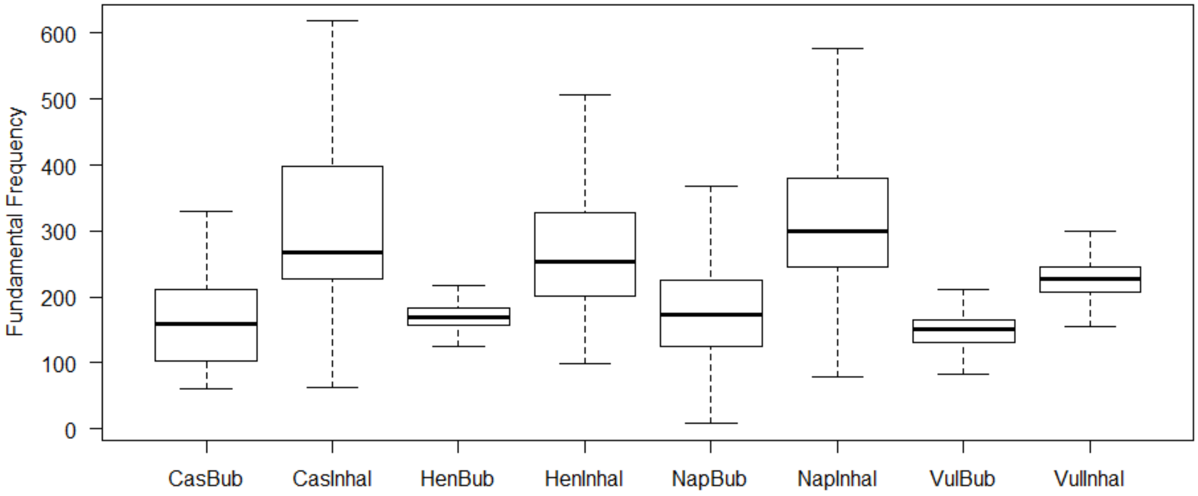
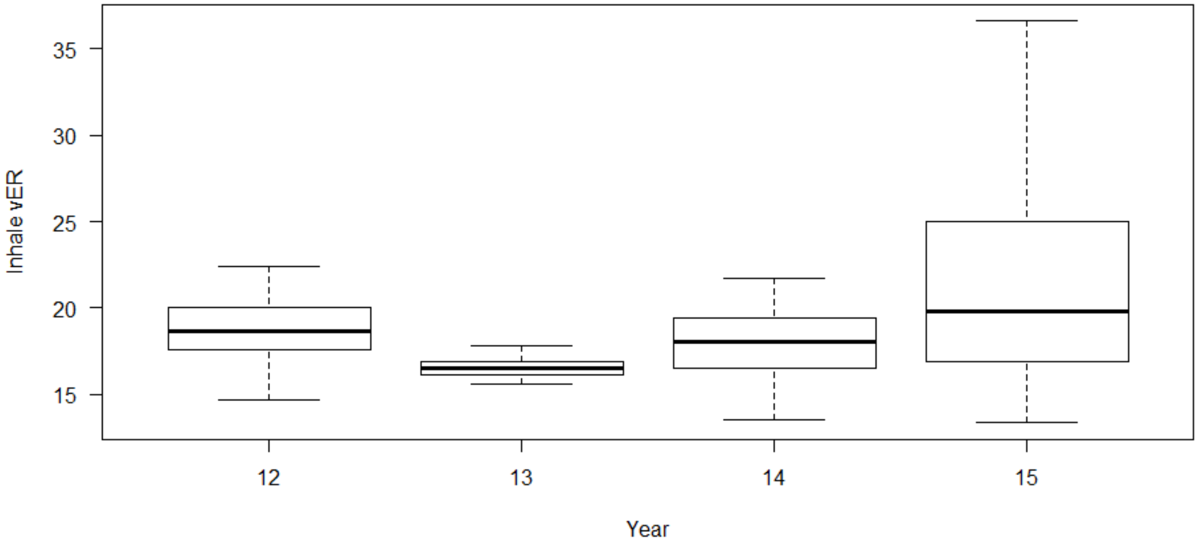


Figure 4.2 vER and fundamental frequency of inhale pulse.
The bubble and inhale vER (a) and fundamental frequency (b) of each male. Using a Welch two-sample t-test, both the vER and the *F*0 of bubble and inhale pulse were significantly different within all individuals ($p<0.0001$). Sample size of the bubble pulse ranged from 100 to 170 pulses, except for Vulkan (n=46). The sample size of the inhale pulse ranged from 200 to over 300 pulses.

a. Casanova



b. Vulkan

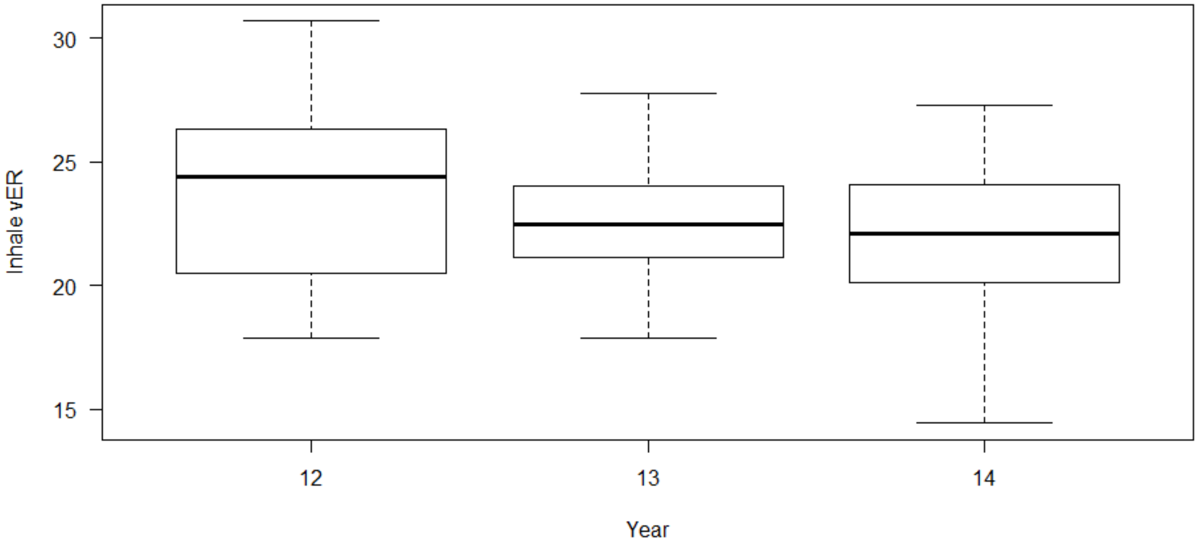
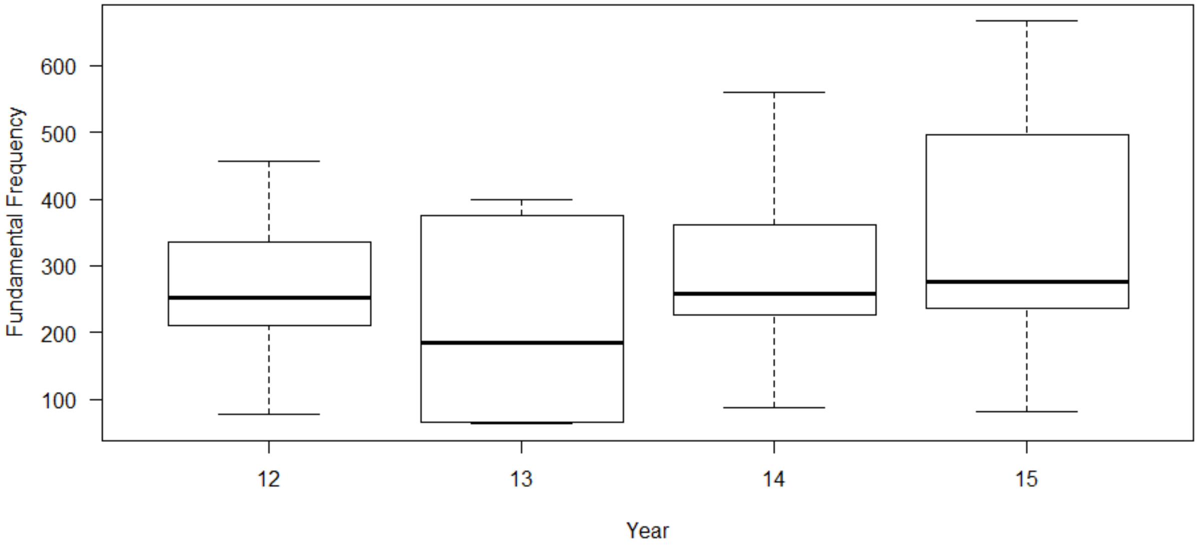


Figure 4.3 vER and fundamental frequency of the inhale pulse by year.
The average inhale vER (a & b) and fundamental frequency (c & d) of Casanova (a &c) and Vulkan (b & d) plotted by year. The number of inhale pulses analyzed for Casanova was 2012=62, 2013=8, 2014=35, 2015=95; and for Vulkan 2012=30, 2013=64, 2014=220.

c. Casanova



d. Vulkan

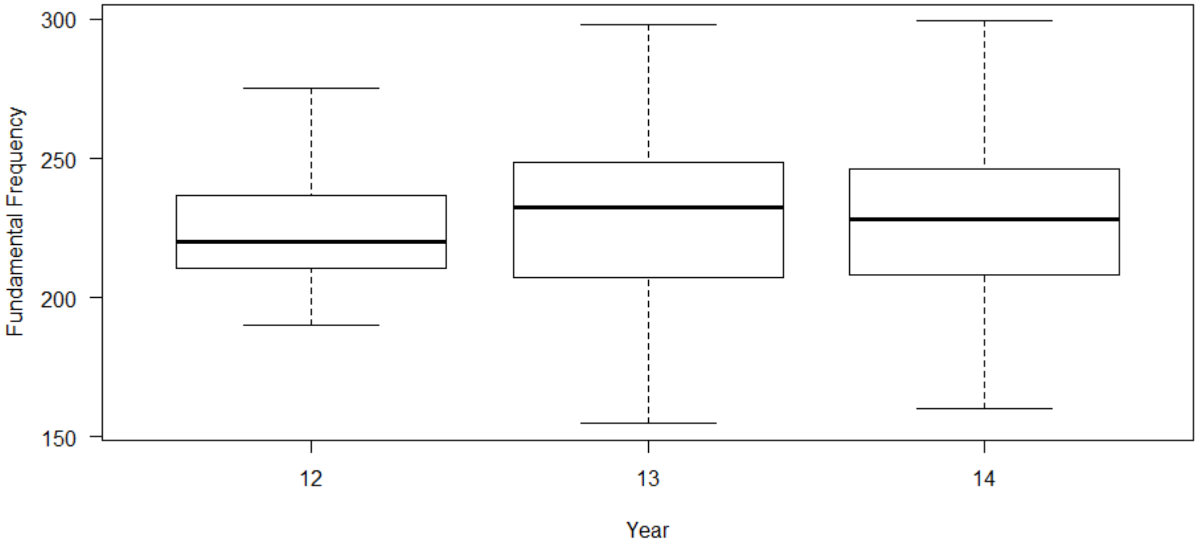
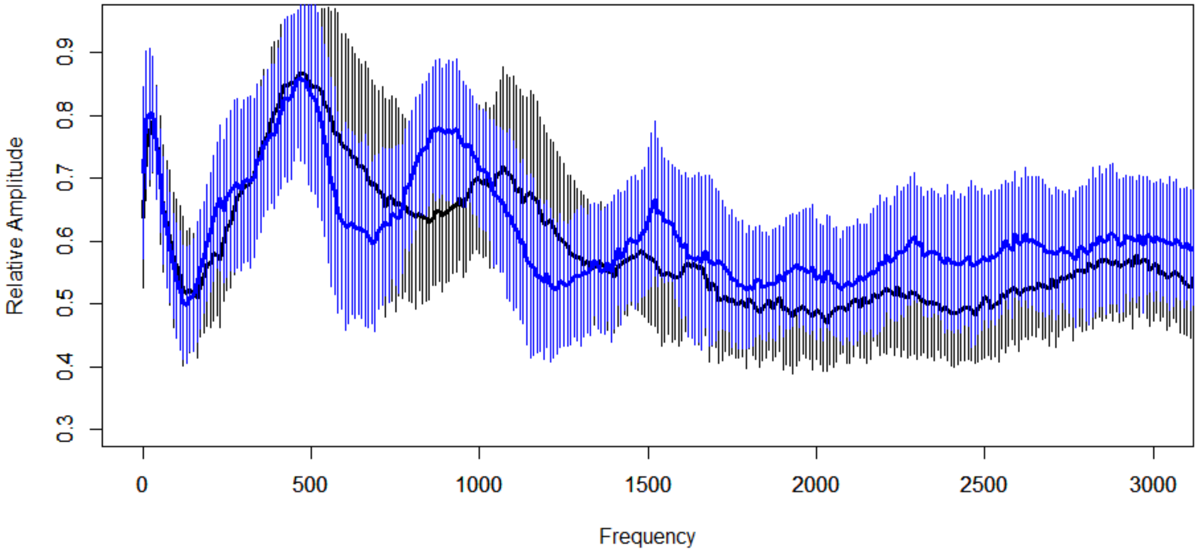


Figure 4.3 continued

a. Vulkan = black, Napoleon = blue



b. Casanova = black, Henry = blue

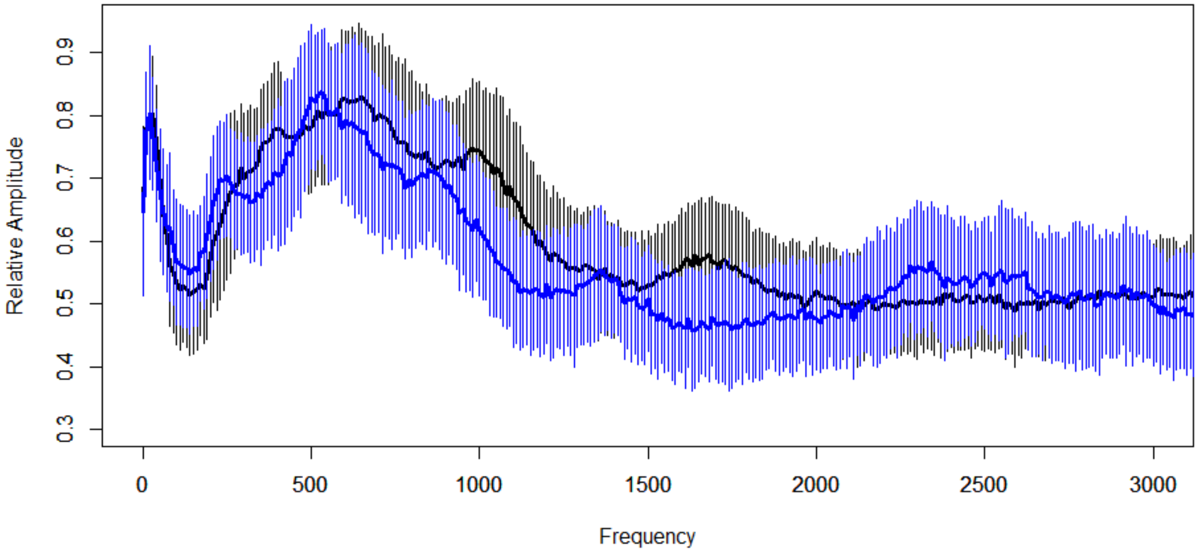
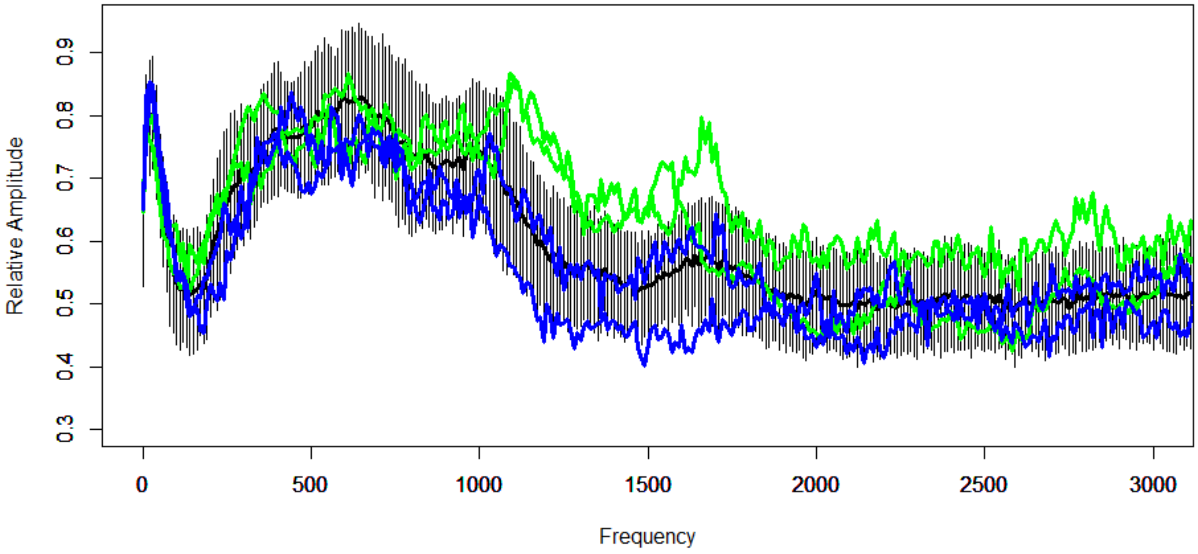


Figure 4.4 Resonance frequency of the high roar pulse.
High roar resonance, mean of the reference day, the vertical lines are the standard deviation.

a.



b.

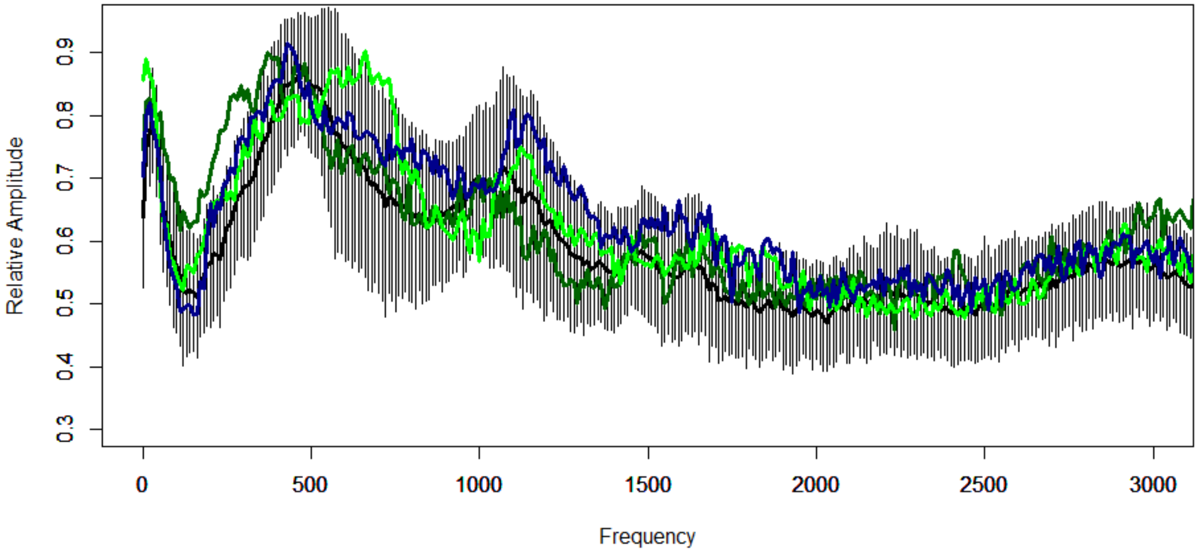
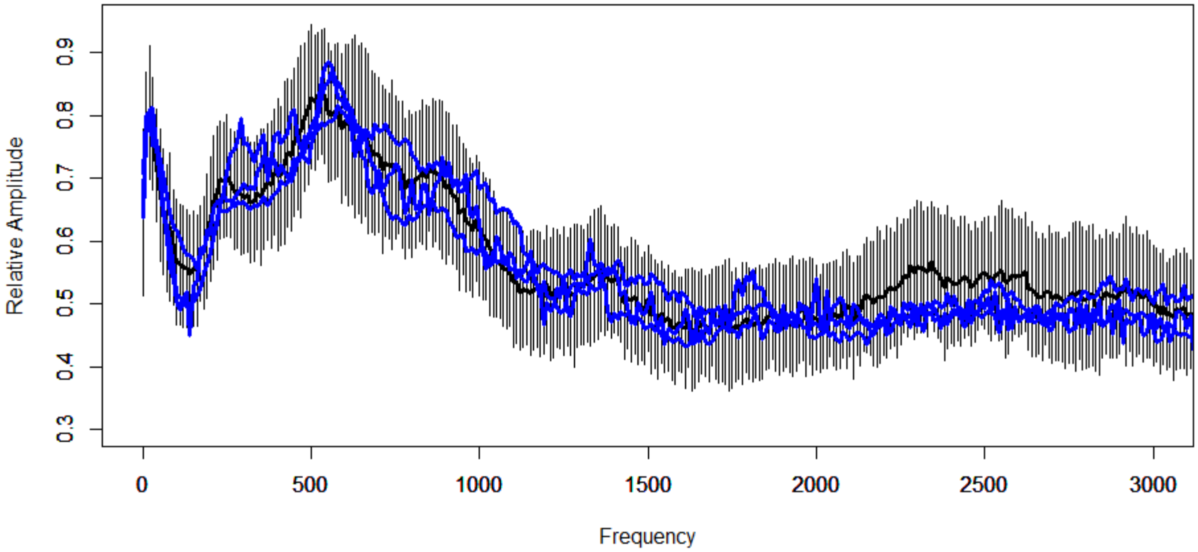


Figure 4.5 Mean resonance frequency by day, month, and year.
Resonance spectrogram for the high roar, the mean resonance from the reference day (black line, black vertical lines are the standard deviation), the other lines are comparison days; blue lines are the mean resonance of the high roars produced from long calls that day that are within a few days of the reference date; green lines are separated by a year, the different shades indicate different years. Further colors, dark blue lines are a couple of months different from comparison.

a. Henry



b. Napoleon

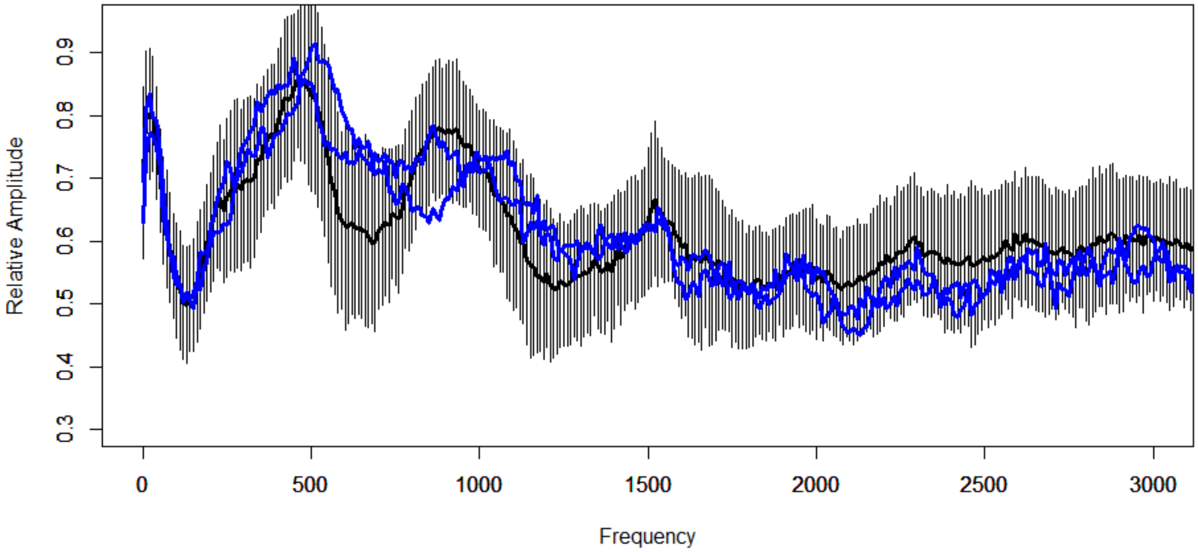
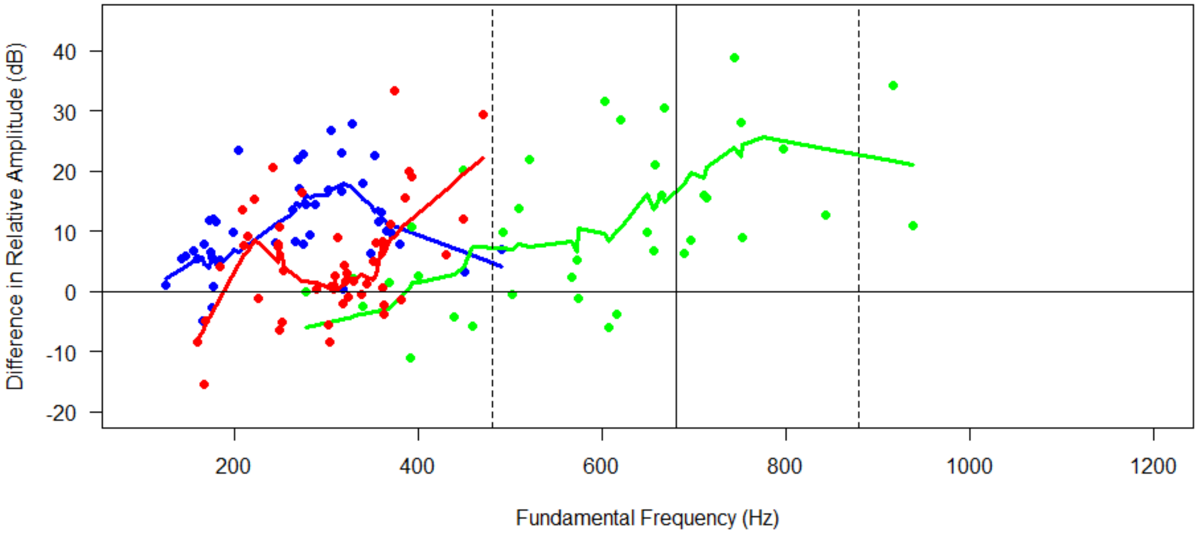


Figure 4.6 Mean resonance frequency within days.
Resonance spectrogram for the high roar, the mean resonance from the reference day (black line, black vertical lines are the standard deviation), the blue lines are the mean resonance of the high roars produced from long calls that day that are within a few days of the reference date.

a. Casanova



b. Henry

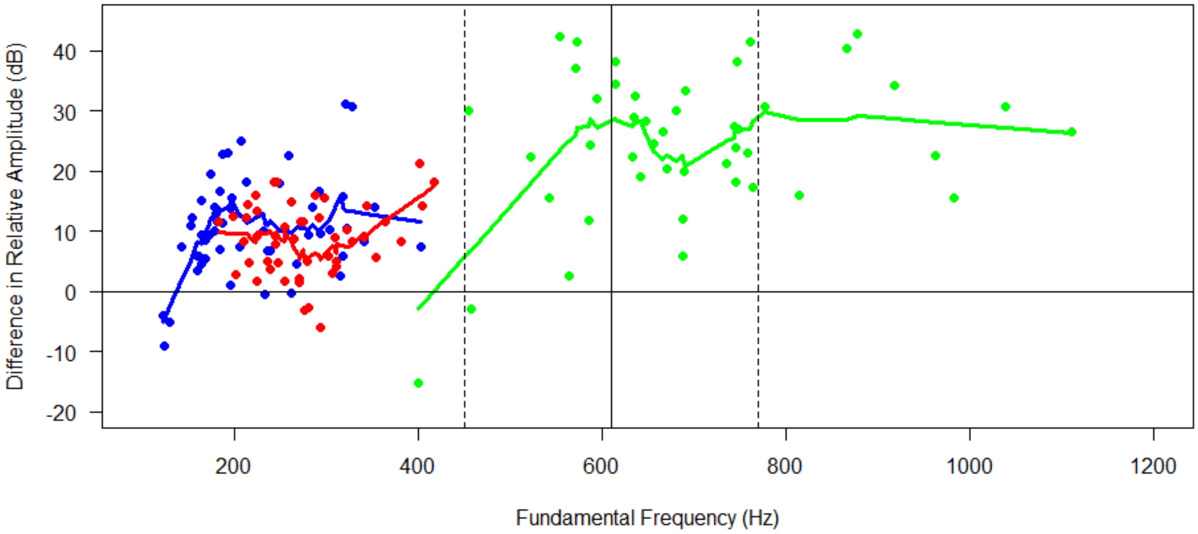
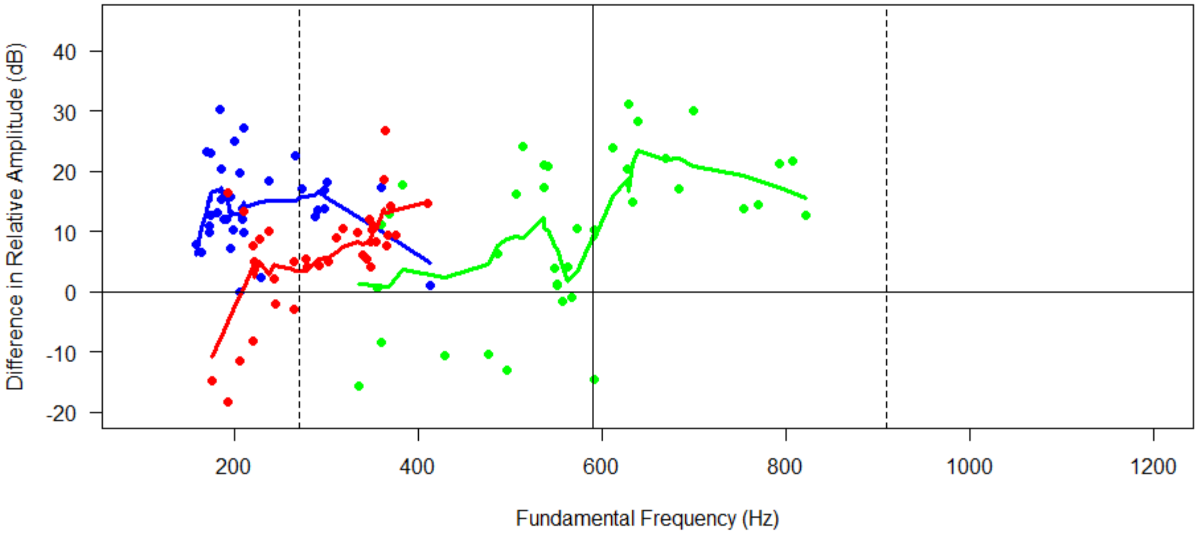


Figure 4.7 Relative amplitude of the fundamental frequency.
The fundamental frequency and its relative amplitude (*F*0 amplitude – *F*1 amplitude) for the high roar pulse. Blue is the *F*0 at the onset of the pulse, green is at the *F*0 at the max, and red is the *F*0 at the end of the pulse. The solid black vertical line is the dominant energy peak frequency, and the black dashed vertical lines are the standard deviation of the dominant energy peak.

c. Napoleon



d. Vulkan

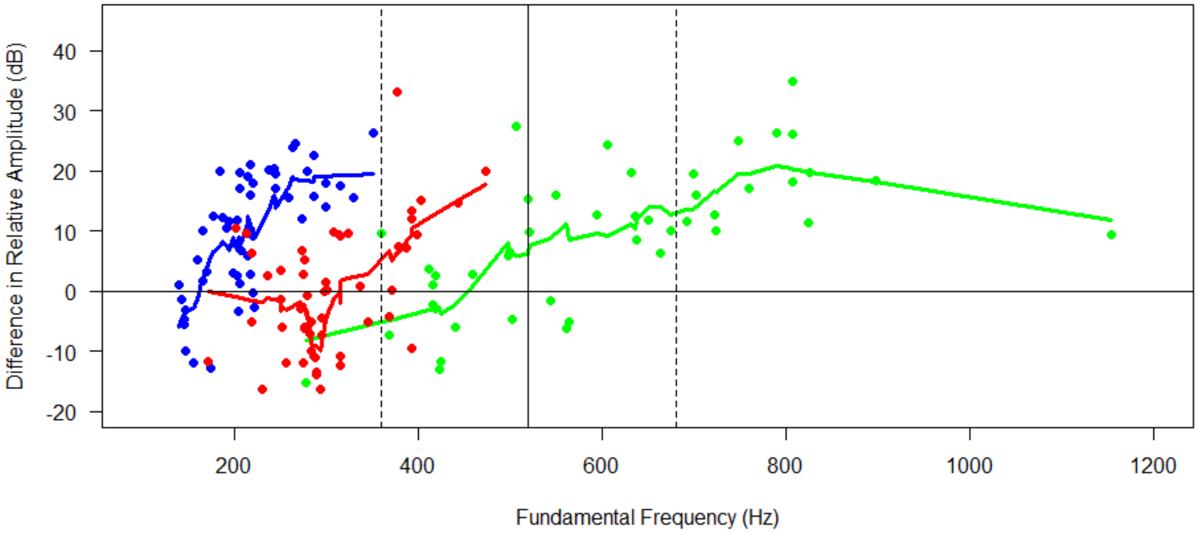


Figure 4.7 continued

Table 4.1 Discriminate function analysis results

a. DF based on acoustic characteristics of the long call

	Casanova	**Henry**	**Napoleon**	**Vulkan**	**Mean**
Volcano	100% (5)	82% (17)	83% (29)	93% (28)	90% (79)
High Roar	55% (31)	73% (33)	76% (34)	68% (25)	68% (123)
Low Roar	83% (24)	100% (14)	58% (26)	59% (22)	75% (86)
Reference Day	80% (20)	80% (25)	84% (44)	60% (20)	76% (109)
Total	63% (60)	63% (64)	66% (89)	60% (77)	63% (290)
Ref pred. tot	25% (40)	44% (39)	69% (45)	30% (57)	42% (181)
Mean	68%	74%	73%	62%	

b. DF based on composition of the total long call: duration, rate, and number of each pulse type

	Casanova	**Henry**	**Napoleon**	**Vulkan**	**Mean**
Reference Day	93% (14)	60% (10)	92% (13)	100% (12)	86% (49)
Total	68% (34)	60% (42)	74% (38)	72% (39)	69% (153)
Ref pred. tot	35% (20)	34% (32)	72% (25)	41% (27)	46% (104)
Mean	65%	51%	79%	71%	

The percentage of correctly assigned identity based on discriminant function analysis for the acoustic characteristics (a) and call composition (b). For the acoustic characteristic DF, initially, a DF was run on each of the three pulse types, volcano, high roar, and low roar. For both tables, the reference day is the DF model trained on the reference day and then predicted itself. The total is DF prediction trained on the entire dataset, then predicted itself. The ref pred. tot (reference day model predicting total) is the DF model trained from the reference day data predicting the individual identity of the total dataset, not including the reference day data.

CHAPTER 5

CONCLUSION

Vocalizations are constrained by physical attributes of an individual, and therefore may be honest signals of identity, age, body condition, dominance status, or reproductive status. Therefore, understanding if and how these attributes are encoded in vocal signals is important for assessing to what degree vocalizations could assist researchers in addressing ecological questions that span from size of home range to body condition of the animal. With the rise and increased use of new technology, namely passive acoustic monitoring systems (PAM), understanding vocal behavior and specific signals encoded in the acoustic features could provide an essential research tool especially for conservation efforts.

Rates of deforestation in tropical forests are increasing around the globe. In Southeast Asia, fewer than 10% of forests are under some form of protection and even these are not relieved from the threat of illegal logging (Sodhi et al. 2009). Borneo has lost tropical forest cover nearly twice as fast as the rest of the world, specifically caused by logging, fires and conversions to plantations (Gaveau et al. 2014). Conservationists are working for more effective protection and to do so seek effective assays of habitat condition and its response to disturbances (e.g., Rolstad et al. 2002). Botanical measurements have been effective, but assays are spatially restricted, subject to potential microhabitat variation and time consuming (Marshall et al. 2009). To circumvent these difficulties, abundance and/or presence of sensitive species (indicator species) has been used to assay habitat quality (e.g., Carignan and Villard 2002). The use of population trends of indicator species has been effective in assessing forest condition (Carignan and Villard 2002). It does, however, not permit early detection of disturbances. Measuring behavior of indicator species, such as vocal behavior, may provide a more sensitive method for evaluating habitat condition. Vocal behavior is easily recorded even in dense forests, and the occurrence and specific acoustic properties of vocalizations may indicate body condition. Because body condition of an individual is habitat dependent (Harrison et al. 2010), certain body-condition dependent features of vocalizations may be useful indicators of forest condition. Because vocalizations can be recorded over long distances, vocal behavior may provide a more rapid and less labor intensive method for assessing forest condition than surveys of population densities of an indicator species. Timely detection may, in turn, facilitate a more rapid response to disturbances in the forest by conservation managers.

Orangutans are an indicator species of Indonesian rain forests, and their vocal behavior can be recorded fairly easily. Before we can assess to what degree vocal behavior can reveal information about habitat quality, three important questions need to be addressed. When do orangutans call? How is calling behavior influenced by the environment? And lastly, how much do call features vary over time?

In Chapter 2, we examined the daily call patterns of orangutans and found that they call frequently at night. Thus, the general assumption that vocal activity coincides with daily activity patterns is not valid. Diurnal and nocturnal vocal behavior were correlated, but occasionally night-time calling occurred during periods where no diurnal vocalizations were recorded. Why male orangutans may call more at night than during the day is unclear. However, we speculate that night-time calling may reduce the risk of antagonistic encounters with other males and may use a temporal window of low background noise.

In Chapter 3, we investigated potential influences on long call behavior with a long-term database which enabled us to detect seasonal variation in behavior and possible correlates in food availability and the social environment. We discovered that food availability had the greatest impact on the call rate of male orangutans. Because differences in orangutan vocal behavior between different forests emerge from different studies, we suggest that environmentally determined behavioral plasticity accounts in part for the observed differences.

In Chapter 4, we examined the variation of acoustic characteristics in relation to time. Based on a limited, but representative sample, individuals were not reliably identified either short-term (only days later) or long-term (years later). However, variability in call features differed substantially between individuals, suggesting the possibility that call features may become more reliable with increasing age. We also provide evidence of dynamic upper vocal tract modification during production of the long call. Dynamic adjustments may allow individual callers to partially mask spectral features that would arise from static upper vocal tract filter properties and would reflect vocal tract length and, thus, body size. In fact, resonances do not emphasize the lowest frequencies of the long call. No clear individual-specific spectral qualities emerged from our analyses and therefore, additional investigation is required.

5.1 Future directions

This study represents a first step toward further close investigation of information content of the long call of male orangutans. We used behavioral data collected over a decade, and acoustic recordings over 4 years. The long-term dataset has enabled us to begin to disentangle social and environmental influences on vocal behavior, and changes in acoustic features over time. However, in long-lived species, even a decade worth of data may not capture changes in life history events. Our understanding of how different factors interact to influence vocal production is still limited, because the network of influences is complex and incorporates a multitude of internal, social, and ecological driving forces. Most studies focus on one or two influencing factors on vocal behavior, but this may cause misinterpretations, leaving an unclear representation of vocal behavior. Furthermore, clear population level differences in acoustic behavior emerged from the different studies (Chapter 2), which cautions against reaching general conclusions from individual investigations.

Whereas rate of call production could be linked to environmental variables, it remains unclear to what extent acoustic features are influenced by them. Four years of vocal recording, although still a small data set over a limited period, showed remarkable variation in most acoustic parameters within individual males. This variation therefore makes it difficult to identify the caller. Regarding other possible information content, such as body condition, longer-term datasets with simultaneous data on environmental condition as well as quantitative measurements of body condition of an individual are required to be able to link acoustic features to condition of the sender. Orangutans can live over 50 years in the wild, thus presenting the opportunity to assess how body condition may influence acoustic features gradually. However, the collection of such long-term data sets requires planning and consistent use of methodology.

More research is required to fully establish which acoustic features, or more likely, what combination of acoustic features of vocalizations, permit individual recognition. Given the variability of even one parameter over even a short time period, it is unlikely that one simple acoustic feature indicates identity. It is more plausible that a multivariate combination of acoustic features permit individual recognition. The prevalence of nonlinear phenomena (NLP) may also play a role, either in individual identity or indication of body condition. In several pulse types of the long call of male orangutans we find segments with sidebands, subharmonics, and deterministic chaos. The presence of NLP is indicative of a destabilization of the laryngeal vibrations. The vocal sac of male orangutans may allow for increased dynamic range of the vocalization, but it could also cause destabilization of the vocal folds (Riede et al. 2008; Boer 2012). In other mammals, NLP has been described to be individualistic and communicate age, sex, or body condition (e.g., Wilden et al. 1998). Future investigation is warranted to explore the potential role of NLP in orangutan and mammalian vocalization.

5.2 References

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