Spring 2020

Acoustic Analysis of Nomascus Gibbon Songs as a Potential Measure of Current Health Status

Caroline Rowley
Central Washington University, car.rowley@gmail.com

Recommended Citation

Rowley, Caroline, "Acoustic Analysis of Nomascus Gibbon Songs as a Potential Measure of Current Health Status" (2020). *All Master's Theses*. 1377.
https://digitalcommons.cwu.edu/etd/1377

ACOUSTIC ANALYSIS OF *NOMASCUS* GIBBON SONGS AS A POTENTIAL MEASURE OF CURRENT HEALTH STATUS

A Thesis

Presented to

The Graduate Faculty

Central Washington University

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

Primate Behavior and Ecology

by

Caroline Audrey Rowley

March 2020

CENTRAL WASHINGTON UNIVERSITY

Graduate Studies

We hereby approve the thesis of

Caroline Audrey Rowley

Candidate for the degree of Master of Science

APPROVED FOR THE GRADUATE FACULTY

______________ ______________________________
Dr. Jessica Mayhew, Committee Chair

______________ ______________________________
Dr. Sofia Blue

______________ ______________________________
Dr. Andrew Piacsek

______________ ______________________________
Dean of Graduate Studies

ABSTRACT

ACOUSTIC ANALYSIS OF *NOMASCUS* GIBBON SONGS AS A POTENTIAL MEASURE OF CURRENT HEALTH STATUS

by

Caroline Audrey Rowley

March 2020

Post-release monitoring is vital to the rehabilitation process. Gibbons offer a unique challenge, as they are notoriously difficult to follow through the forest, but their duets offer a non-invasive window into their lives. The aim of this project is to create a method that will evaluate the health of rehabilitated and released gibbons through acoustic analyses. Gibbon duets are in part genetically determined, but learning may play a role in song development. Additionally, songs may indicate resource holding potential, and are vital to acquiring mates and producing offspring. Captive-raised gibbons are often denied the experience of co-singing with their parents, and are generally less fit than their wild counterparts due to living in confined spaces. The female great call is a primary holder of information during a song bout, and will be the focus of this study. To explore how captivity could impact singing, we recorded the great calls of six individuals from three *Nomascus* species of rehabilitated gibbons at the Endangered Primate Rescue Center (EPRC) in Cuc Phuong National Park, Vietnam. The first song bout from each day was used for analysis. We extracted 23 parameters from 102 great call recordings (n = 10-25/gibbon). A Principal Component Analysis revealed that the first three components accounted for 71.81% of the variance in the data. PCI focused on the bark phrase, PCII focused on the Oo phrase, and PCIII focused mainly on temporal parameters. We then ran correlations to explore how these principal components related to age and weight. This study provides preliminary evidence to support a non-invasive way to monitor behavior and rehabilitation using acoustic markers. Our results suggest that genetics, age, and weight impact the production of female *Nomascus spp.* great calls. The significance of acoustic markers in rehabilitation practices is generally overlooked in the literature and merits further investigation. Future studies should implement acoustic markers to monitor individuals in captivity to better inform rehabilitation and release practices.

ACKNOWLEDGEMENTS

I would like to thank Dr. Sofia Blue for her endless hours of mentorship, support and encouragement for studying bioacoustics. I feel beyond grateful to have her as a teacher and a friend. I would like thank Dr. Jessica Mayhew for her guidance, patience, incredible dedication to all her students and sense of humor during my time at CWU. I would like to thank Dr. Andrew Piacsek for participating on my committee as well as offering his expertise in physical acoustics. I want to thank several years of Primate Behavior and Ecology cohorts for their friendship and encouragement. I want to thank my family for supporting me to pursue primatology, even if they weren't quite sure what it meant or where I might go. I want to thank my partner, Jessica Jimerson, for listening, supporting, distracting and encouraging me throughout collecting data and writing this thesis. I want to thank the staff of the Endangered Primate Rescue Center for welcoming me into their lives and making me feel at home in Cuc Phuong. I would like to acknowledge the Pete and Sandra Barlow Award, the Arlen and Debra Prentice Scholarship for Primate Research, and Central Washington University's Graduate Student Research Support award for funding my research. I also want to thank April and Richer of Ape & Bird for constructing and selling hats to help fund this project. Finally, I would like to thank the 27 gibbons who live at the EPRC for waking me every morning, humbling me and reminding me that it's time to get to work.

TABLE OF CONTENTS

LIST OF TABLES

Journal Article

LIST OF FIGURES

Journal Article

CHAPTER I
INTRODUCTION

a. Hylobatidae Natural History

Gibbons, family Hylobatidae, are small arboreal apes that inhabit the rainforests of eastern and southeastern Asia (Bartlett, 2006). The Hylobatidae, along with the large-bodied apes, make up the superfamily Hominoidea (Simpson, 1945; Bartlett 2006). The Hylobatidae diverged from Pongidae (orangutans) and Hominidae (gorillas, chimpanzees, bonobos, and humans) approximately 17 mya (Cunningham & Mootnick, 2009). Gibbons are monomorphic and far smaller than other hominoids, weighing 5-15 kg (Bartlett, 2006). They are almost exclusively arboreal. They move through the canopy via a mixture of brachiation, bipedal running, and leaping (Fleagle, 1976). Gibbons are brachiation specialists with their elongated, muscular arms, flexible shoulder joints, hooked hands, and divergent thumbs (Bartlett, 2006). There are four genera of gibbons (*Hylobates, Hoolock*, *Symphalangus*, and *Nomascus*) containing 14-19 species (Chatterjee, 2009; Roos & Geissman, 2001; Zihlman, Mootnick, & Underwood, 2011). Gibbon genera are defined by the number of chromosomes in their diploid cells: *Hoolock*, 38; *Hylobates*, 44; *Nomascus*, 52; *Symphalangus*, 50 (Chatterjee, 2006; Zihlman, Mootnick, & Underwood, 2011).

Gibbons are generally thought to be socially monogamous, although recent studies show significant variability in social structure (Palombit, 1994; Lappan, 2007; Reichard & Barelli, 2008; Fan et al., 2006). Family units consist of two to six individuals, generally a breeding pair and their offspring (Lappan & Whittaker, 2009). Gibbons are territorial, and groupings of family units are sometimes referred to as neighborhoods (Lappan & Whittaker, 2009). They are sometimes referred to as the “songbirds of the primate order" as most species sing pair-bonded duets (Geissmann, 2002). Gibbons rely heavily on ripe fruit pulp as a substantial part of the diet (Chivers, 1984; 59% of a gibbon's annual diet, Barlett, 2006). Gibbons' ability to exploit the terminal branch niche has long been cited as an essential component of their adaptive complex (Ellefson 1974).

There are currently seven species of crested gibbon (*Nomascus*) recognized (Konrad & Geissmann, 2006; Roos, Thanh, Walter, & Nadler, 2007; Thinh et al., 2010a; Thinh et al., 2010b**;** Thinh, Mootnick, Thanh, Nadler, & Roos, 2010c). These include the Hainan gibbon (*N. hainanus*), the eastern black gibbon (*N. nasutus*), the western black gibbon (*N. concolor*), the northern white-cheeked gibbon (*N. leucogenys*), the southern white-cheeked gibbon (*N. siki*), the northern buff-cheeked gibbon (*N. annamensis*) and the southern buff-cheeked gibbon (*N. gabriellae*) (Thinh, Hallam, Roos, & Hammerschmidt, 2011). The *Nomascus* genus is the rarest and least studied of the Hylobatids (Mootnick & Fan, 2011). *Nomascus concolor, N. hainanus, N, leucogenys,* and *N. nasutus* are all listed as critically endangered by the International Union for Conservation of Nature (IUCN) Red List; *N. siki* and *N. gabriellae* are listed as endangered, and *N. annamensis* is not listed by the IUCN. Research on this genus is a high priority for conservationists and primatologists given their endangered status and decreasing population trends.

b. Gibbon Rehabilitation and Release

As deforestation and the pet trade continue, the number of gibbons being kept in captivity will only increase. Rehabilitation and reintroduction is quickly becoming one of the only options to save hundreds, if not thousands of pet gibbons (Cheyne, 2004). Additionally, rehabilitation and reintroduction can contribute to community and international education, and plays a valuable role in increased awareness (Chivers, 1991; Cheyne & Brulé, 2004). This is especially important for gibbons, whose conservation issues and even existence is not as recognized or well-known across the globe as other primates. The IUCN has recognized the importance of post-release monitoring and lists it as an essential step in the rehabilitation process (Campbell, Cheyne, & Rawson, 2015). Studies on captive-raised gibbons should involve comparisons with wild individuals from the same species to help quantify the success of their reintroduction (Cheyne, 2009).

Determining the success of gibbon reintroduction should be measured by their survival post-release (i.e., finding suitable food), and the maintenance of the pair bond measured through duetting, copulation, and the reproduction and survival of offspring (Cheyne, 2009). The main threats to rehabilitated and released gibbons' success in the wild are starvation, hunting, disease, and aggressive territorial disputes (Bennett, 1992). If a rehabilitated and released gibbon is unable to access the food required to adequately thrive, or is suffering from disease or injury from a territorial dispute, it is possible that their current lack of energy or health would be apparent in their songs.

Gibbon duets are in part genetically determined (Brockelman & Schilling, 1984; Tenaza 1985; Geissmann 1984), but given the wide song repertoire in every gibbon species (Geissmann, 2000) and the individuality that exists among wild populations, learning must play a role in song development (Goustard, 1979, 1983; Brockelman and Schilling, 1984; Geissmann, 1984; Tenaza, 1985). In the wild, gibbons learn to sing by copying their parents (Goustard 1979, 1983), an experience captive-raised gibbons are denied (Cheyne, Chivers, & Sugardjito 2007; Cheyne, 2004). Older, captive-raised gibbons (*Hylobates albibarbis*) produce louder, longer, and more complex songs (Cheyne et al., 2007). This finding suggests that even though captive-raised gibbons do not have the same opportunity to learn their song from a same-sexed parent, they still retain the ability to develop complex songs (Cheyne, 2004). Comparing the great calls of rehabilitated and released gibbons with those of their wild counterparts could provide important insights to how they are adjusting to the wild, and how we could incorporate a non-invasive passive acoustic monitoring method to evaluate their reintroduction.

Although strip and line transect census methods are the most commonly used methods for estimating primate density, they are not very reliable for Hylobatids because of their low visibility and unpredictable behavior (e.g.fleeing) upon detecting humans (Brockelman & Srikosamatara, 1993). Gibbons have relatively stable social groups in permanent territories, and mated pairs regularly sing (Brockelman & Srikosamatara, 1993). Monitoring gibbons through acoustic surveys offers a more accurate and less invasive way of conducting research (Brockelman & Ali, 1987; Brockelman & Srikosamatara, 1993; Cheyne, Thompson, Phillips, Hill, & Limin, 2008; Buckley, Nekaris, Husson; 2006; Gilhooly, Rayadin, & Cheyne, 2015; Kidney et al., 2016).

Post-release monitoring is vital to ensure that gibbons are adequately adapting, and allows conservationist to counter any problems that may arise. Important consideration must be given to the development of an individual gibbon’s song. The majority of rehabilitant gibbons will not have learned their song by copying their same-sex parent (Cheyne et al., 2007). Demonstrating sufficient individuality and complete song bouts will be important to a rehabilitant’s capability to hold a territory and thrive in the wild. Collecting vocal samples in released gibbon pairs could offer insight into their overall health, and thus prove to be crucial information for conservation programs.

CHAPTER II
LITERATURE REVIEW

a. The Loud Calls of Hylobatidae

In most species of gibbon, both males and females sing loud, complex song bouts that are often combined to produce coordinated duets (Cowlishaw, 1992). Females follow a pattern of repetitive great calls in their solo bouts, whereas males contribute notes and songs to the introductory and interlude sequences (Cowlishaw, 1992). Typically, males become silent at the beginning of a female's great call and will begin their coda during or following it (Haimoff, 1984a; Marshall & Sugardjito, 1986). Gibbon song bouts convey information about the species, sex, identity, and location of the signaler (Cowlishaw, 1992).

Duets are usually female-dominated, notably by the presence of the females' *great call*, which is comprised of 6-80 notes and lasts between 7-30 seconds in a species-dependent pattern (Cowlishaw, 1992; Haimoff, 1984a; Marshall & Sugardjito, 1986; Geissmann, 2002). Great calls vary consistently between individuals (Haimoff & Tilson, 1985; Terleph, Malaivijitnond, & Reichard, 2015; Oyakawa, Koda, & Sugiura, 2007; Dallmann & Geissmann, 2001), which may facilitate individual recognition of conspecifics (Raemaekers & Raemaekers, 1985**;** but see Mitani, 1985). Due to its stereotypy and individuality, it is believed that the great call is the primary carrier of information in the bout (Cowlishaw, 1992).

The great call's function is best explained by the territory defense hypothesis (Ellefson, 1974; Tenaza, 1976) because it is believed that the great call mediates intergroup spacing. Loud calls commonly carry for 2 km (Brockelman & Ali, 1987), which is loud enough to be heard by both neighboring groups and some non-neighboring groups (Raemaekers et al., 1985)**.** Protecting a territory allows the female exclusive access to ecological resources, which is an important determinant in reproductive success (Trivers, 1972). During intergroup encounters, females are more likely to sing if there is another female present (Cowlishaw, 1992; Brockelman & Srikosmatara, 1984; Mitani 1984, 1987). If songs advertise territory ownership, singing during these encounters would enable individuals to identify territorial owners through song matching (Gosling, 1982), which contributes to resolving conflicts between owners and non-owners (Grafen, 1987).

The territory defense hypothesis is further strengthened by the results of playback experiments. During Mitani's (1985) experiment, playbacks of female solo and duet song bouts elicited both sexes of the targeted group to orient towards the playback location. Approaches toward the sound source were typically female led. The strength of the response depended on the location of the playback, with songs located in the center of the residents' range evoking a stronger response than those heard near the boundaries (Mitani, 1984, 1987; Raemaekers, Raemaekers & Haimoff, 1984), emphasizing the spacing function of the female song (Cowlishaw, 1992). Additionally, when pairs responded to playbacks with duets, great calls were sung more frequently than usual (Raemaekers et al., 1984), and longer duets were sung more frequently on the day of and the day following the playback (Mitani, 1985). This provides strong evidence for advertisement of the territory, rather than songs being used to indicate intruders (Cowlishaw, 1992).

Male motivation to call is thought to be driven largely by mate defense. Calling functions to repel other males, and therefore avoid cuckoldry, mate harassment, and infanticide (Van Schaik & Dunbar, 1990). There is a positive correlation between song bout duration of mated males and th**e** floater density of bachelor males in the area (Cowlishaw, 1992). This evidence supports the hypothesis that male calling is driven by mate defense, rather than territorial defense.

The Pairbond Advertisement Hypothesis suggests that duetting advertises the mated status of a gibbon pair and can be interpreted similarly to the mate defense hypothesis (Gittins 1979). By singing with her mate, the female can defend her territory and also advertise that her mate is paired, reducing the likelihood that another female will approach him (Cowlishaw, 1992). Similarly, the male might duet with the female to prevent other males from approaching and copulating with his mate or possibly killing his infant (Van Schaik & Dunbar, 1990). Furthermore, duetting may advertise their paired status to neighbors, which could reduce the aggression of territorial encounters through the threat of coalitionary support (Cowlishaw, 1992). This is supported by the increased coordination of the great call sequence of the female and the coda of the male the longer the pair is bonded (Maples, Haraway, & Hutto, 1989; Haimoff, 1984a). Using Srikosmatara’s (1980) data, in 1992 Cowlishaw found that encounters between gibbons are more likely to escalate into prolonged intrasexual chases when encounters are a result of a visual, rather than vocal, cue. Intrasexual chases are considered to be the most extreme form of escalation during a territorial dispute (Gittins, 1980). Duets are costly to perform, but territorial aggression is costlier (Cowlishaw, 1992). The duets of bonded gibbons are central to their sociality, and offer important insight into their lives.

b. The Loud Calls of *Nomascus spp.*

The song structure of *Nomascus* spp. differs from the rest of the Hylobatidae family in several aspects (Geissmann, 2000; Haimoff, 1984b; Konrad & Geissmann 2006). Unlike other gibbon species, there is no overlap between the sexes in note or phrase repertoire. Crested gibbons show the highest degree of sex-specificity in their note type repertoire. In most species of other gibbon genera, females produce short phrases in addition to their great call. Female *Nomascus* gibbons contribute only great-calls and great-call fragments to their duet songs. Male and female crested gibbons exhibit no overlap in their note and phrase repertoire (Geissmann, 2002).

Acoustic terminology for my study is adapted from Haimoff (1984a), which has been frequently used in gibbon vocal literature. This terminology was adapted by Konrad and Geissmann (2006) and Ruppell (2010) to better describe *Nomascus* vocals (see table 1).

Adult female *Nomascus* great call phrases consist of three phrases: *oo* phrase, bark phrase (accelerando-part), and the twitter phrase (Konrad and Geissman 2006; see fig. 1). The *oo* phrase consists of long notes of slowly increasing frequency, while the bark phrase is made up of short notes with a steep frequency increase. The great call then ends in the twitter phrase, which occurs after the climax of acceleration for the bark phrase. Bark notes tail off into the twitter phrase (*fc* notes-fig. 1), which do not travel far (Konrad and Geissmann, 2006; Ruppell 2010).

Table 1

List of Acoustic Terms

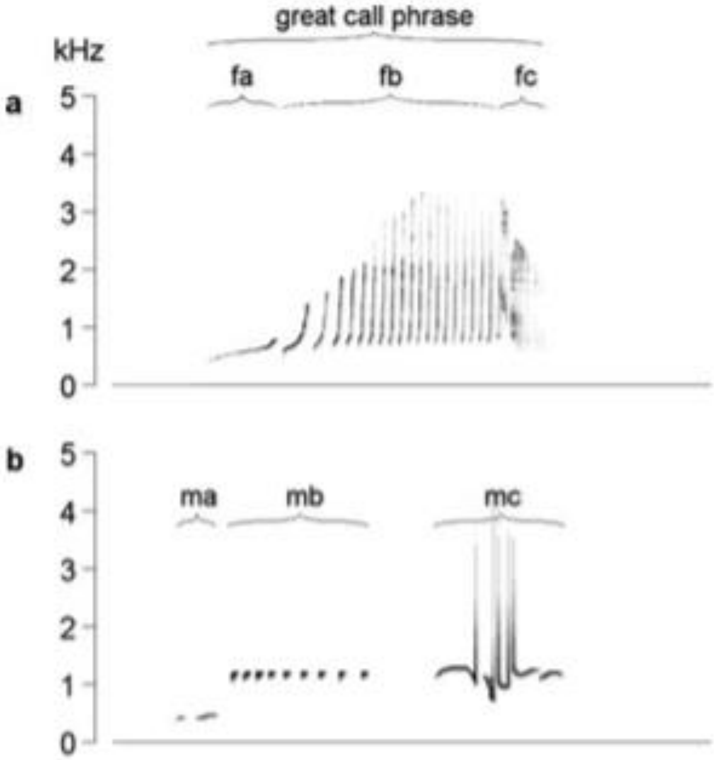
Term	**Definition**
Note	Any single continuous song of any distinct frequency or frequency modulations that may be produced during inhalation of exhalation
Element	A basic recognizable vocal unit of a single individual and composed of a single note or a short series of notes
Phrase	A single vocal activity consisting of a larger or looser collection of notes and elements. These parts may be produced together or separately.
Coda	A phrase produced by the male wherein each roll includes a steep decrease in frequency followed by a steep increase
Roll	A characteristic of notes produced by the male wherein each roll includes a steep decrease in frequency followed by a steep increase
Great Call	The most stereotyped and most easily identifiable phrase of the gibbon song and produced by adult females
Great Call Sequence	Combination of the female great call and the corresponding successive coda of the male
Song	After Thorpe (1961, p. 151) A series of notes, generally of >1 type, uttered in succession and so related as to form a recognizable sequence or pattern in time
Song bout	Includes the first to last loud note produced with no period of silence of >10 min between notes
Solo song bout	Song bout produced by a single individual (male or female) alone
Duet song bout	Song bout in which both sexes produce their loud sounds and exhibit vigorous movements in an interactive manner (i.e., performing a mutually cooperative and coordinated display)

Note From Ruppell (2010); adapted from Konrad and Geissmann (2006)

Fully developed song phrases of adult male *Nomascus* consist of three different note types: boom notes, *aa* notes, and a multimodulated phrase (see fig. 1). Boom notes (sometimes referred to as *ma* notes) are very deep notes of constant frequency and are produced during the inflation of the throat sac. Boom notes are usually produced as single notes rather than a short series or in phrases. The *aa* notes (also referred to as staccato notes) are short, relatively monotone repeated sounds. The multimodulated phrase, or coda, consists of several notes that exhibit rapid and steep frequency modulations. Adult males typically perform their multimodulated phrase during or shortly after the climax of the female's great call (Konrad & Geissmann, 2006; Ruppell 2010; see figure 1).

Figure 1

Sample Sonogram of Nomascus Song



Note Figure from Konrad and Geissmann, 2006, showing sexual dimorphism in typical song phrases of the northern white-cheeked crested gibbon (*Nomascus leucogenys leucogenys*). (a) Great call phrase of an adult female. The great call begins with *oo* notes (fa), followed by barks (fb), and ends with twitter notes (fc). (b) Phrase of an adult male. The sequence begins with booms (ma), followed by staccato notes (mb), and ends with a multimodulated phrase (mc).

In a fully developed duet song bout, the male continuously cycles through his three types of phrases. When the female begins her great call phrase, the male will interrupt his song and sing his multimodulated phrase at the end of the female's great call phrase. He then resumes cycling through the three phrases (Konrad & Geissmann, 2006).

Vocal data is considered to be largely genetically determined and species-specific (Brockelman & Schilling, 1984; Tenaza 1985; Geissmann 1984). Thinh et al (2011) examined whether the song structure of six crested gibbon species, especially in the four most closely related species (and my target species) *N. leucogenys, N. siki, N. annamensis,* and *N. gabriellae,* is persistently distinct enough to be regarded as a phylogenetic trait. They found only minor differences in song structure among these four species (Thinh et al., 2011).

Males of *N. leucogenys* gave regular, loud *aa* (staccato) notes which were rare in *N. siki* and *N. annamensis* and nearly absent in *N. gabriellae*. *N. leucogenys* also produced great calls that were longer duration and a faster frequency modulation than the three other species. *N. siki* calls were more similar in their song structure to *N. leucogenys* than to *N. annamensis*. The main criteria to tell the difference between *N. siki* and *N. annamensis* were criteria 2 and 4- duration of the first note (2) and duration of the horizontal part (4) (see table 2). *N. annamensis* and *N. gabriellae* were highly similar; the main criteria to distinguish them were 3 and 5- relative duration of the first notes (3) and relative duration of the horizontal part (5) (see table 2). Ultimately, the researchers were able to find significant differences between the songs of the four southern species through detailed acoustic analyses. These differences correlated with the genetic relatedness found in recent studies (Konrad & Geissmann, 2006; Roos, Thanh, Walter, & Nadler, 2007; Thinh et al., 2010a; Thinh et al., 2010b, Thinh et al., 2010c). They also found a highly significant correlation between similarity in song structure and geographic distance (Thinh et al., 2011). This finding emphasizes the importance of studying captive-raised gibbons to determine whether they are singing species-specific songs. As both learning and genetics play a role in song development (Goustard, 1979, 1983; Brockelman and Schilling, 1984; Geissmann, 1984; Tenaza, 1985), it is necessary to study the songs of captive-raised gibbons before they are released (Cheyne et al., 2007). Singing their sex and species-specific songs is vital to attracting same species mates.

Table 2

List of Acoustic Parameters and Their Descriptions

No.	Code	Acoustic parameter	Description
1	DGC	Duration of entire great call [s]	Time at (p-A)
2	NN	Number of notes	Total number of elements
3	RF	Range of start frequencies [Hz]	Frequency at (P-A)
4	NO	Number of Oo notes	Notes with frequency increase of <=1kHz/s
5	DO	Duration of Oo phrase [s]	Time at (F-A)
6	RDO	Relative duration of Oo phrase [%]	No. 5 in % of No. 1
7	NB	Number of bark notes	Notes with a frequency increase of >1kHz/s
8	DB	Duration of bark phrase [s]	Time at (p-G)
9	RDB	Relative duration of bark phrase [%]	No. 8 in % of No. 1
10	DNO1	Duration of the first note of Oo phrase [s]	Time at (B-A)
11	DNO2	Duration of the second note of Oo phrase [s]	Time at (D-C)
12	DNB1	Duration of first note of bark phrase [s]	Time at (F-E)
13	DNBL	Duration of last note of bark phrase [s]	Time at (p-P)
14	RFO1	Frequency range of first note of Oo phrase [Hz]	Frequency at (B-A)
15	RFO2	Frequency range of second note of the Oo phrase [Hz]	Frequency at (D-C)
16	RFO3	Frequency range of third note Oo phrase [Hz]	Frequency at (F-E)
17	RFB1	Frequency range of the first note of the bark phrase [Hz]	Frequency at (H-G)

Table 2 continued

No.	Code	Acoustic Parameter	Description
18	NIO1	First inter-note interval of Oo phrase [s]	Time at (C-B)
19	NIO2	Second inter-note interval of Oo phrase [s]	Time at (E-D)
20	NIBL	Last inter-note interval of bark phrase [s]	Time at (P-o)
21	RFO12	First start frequency range between second and first note of Oo phrase [Hz]	Frequency at (C-A)
22	RFO	Second start frequency range between first note of bark and last note of Oo [Hz]	Frequency at (G-E)
23	RFBL	First start frequency range between last and previous note of bark phrase [Hz]	Frequency at (G-H)

Note adapted from Thinh et al., 2011.

c. Loud Calls as a Measure of Current Health Status

Terleph et al. (2016) found age related decline in female lar gibbons (*Hylobates lar*) great call performance, which suggests that call features are correlated with an individual's physical condition. Territorial vocalizations may serve to honestly indicate an individual's resource holding potential (RHP) if calling is affected by physiological constraints (Vehrencamp, 2000; Smith & Harper, 2003). The characteristics of vocalizations, both their spectral and temporal parameters, are influenced by an individual's body size, age, rank, hormonal state and fatigue level (Terleph et al., 2016; Davies & Halliday, 1978; Clutton-Brock & Albon, 1979; Ryan & Brenowitz, 1985; Inoue, 1988; Bee, Perrill, & Owen, 1999; Sanvito, Galimberti, & Miller, 2007; Reby &

McComb, 2003; Fischer, Kitchen, Seyfarth, & Cheney, 2007; Vannoni & McElligott, 2008; Erb, Hodges, & Hammerschmidt, 2013). All of these are measures of physical condition, and thus are assumed to be correlated with RHP (Terleph et al., 2016). RHP is difficult to measure directly under wild conditions (Ulijaszek, 1992), therefore, field researchers often rely on the aforementioned correlates as indirect measures to evaluate physical condition (Inoue, 1988; Hammerschmidt, Freudstein, & Jurgens, 2001). For example, a reduction in abdominal muscle mass (body size) can indicate a decrease in respiratory function, which declines with age due to a loss of elasticity and dispensability in the lungs (Wahba, 1983; Awan, 2006; Quanjer et al., 2012; Herring et al., 2013; Sataloff et al., 1997). The decrease in muscle mass, which implies a decrease in physical fitness, can be measured through vocalizations.

The fundamental frequency (F0) and degree of change in fundamental frequency (ΔF0) associated with an individual's loud call may also indicate RHP (Titze & Riede, 2010; Titze, 1989). A high F0 can signal an individual's hormonal condition: male lar gibbons with higher androgen levels produce calls with a higher F0 (Barelli, Mundry, Heistermann, & Hammerschmidt, 2013)**.** Calling with a high F0 also requires extreme muscular strength to stiffen the vocal cords, indicating an individual's larynx strength, which is likely to correspond with overall body strength; however, this hypothesis has not been tested in Hylobatidae or any non-human primate (Titze & Riede, 2010). Additionally, the temporal aspects of a call can be correlated with a caller's energy levels, providing potential cues to an animal's immediate physical condition (Clutton-Brock & Albon, 1979; Fitch & Hauser, 1995). This hypothesis has been tested using age as a proxy (Terleph et al., 2016), and results indicated that young female *H. lar* gibbons produce climaxes in their great call at a higher frequency range (Δ F0), maximum F0 frequency, and duty cycle compared to older female lar gibbons. My study aims to further our understanding of how Hylobatidae call performances correlates with physical condition by analyzing the songs of captive-raised *Nomascus* with known health histories and ages.

Unlike other notes in the lar gibbon repertoire, the great call often contains multiple harmonics and rapid jumps in pitch, creating unstable and noisy qualities that are associated with the chaotic vocal-fold vibrations that occur when a mammal's vocal folds have reached their amplitude and/or frequency limit (Wilden, Herzel, Peters, & Tembrock, 1998; Fitch, Neubaeuer, & Herzel, 2002). Due to the high intensity of great call climaxes, Terleph et al. (2016) hypothesize that the production of a great call climax pushes females to their physical limit, therefore making them a valid indicator of RHP.

Furthermore, if a gibbon ceases singing, it is typically just before climax, suggesting that the climax is the most difficult part of the song to produce and therefore energetically costly (Terleph et al., 2016). Because of singing's function as an honest signal of RHP, it can be used as an indicator of health for released gibbons. Examining the calls of gibbons allows us to non-invasively examine multiple parts of their life. The vocal performances of gibbons are used to attract and defend mates, defend their territory, and advertise the pair bond (Cowlishaw, 1992; Gittins, 1979; Van Schaik & Dunbar, 1990; Ellefson, 1974; Tenaza, 1976; Trivers, 1972). By analyzing characteristics of their songs, we can infer how the gibbons have adjusted to the wild. The importance of the duets in their day-to-day lives, as well as its role as an honest signaler of RHP

(Terleph et al., 2016) allows researchers to infer multiple things from the calling behavior of a gibbon, including their current health status or the state of their pair bond.

CHAPTER III

GREAT CALL QUALITY OF FEMALE *NOMASCUS* SPP. IS ASSOCIATED WITH PHYSICAL CONDITION IN CAPTIVE GIBBONS HOUSED AT THE ENDANGERED PRIMATE RESCUE CENTER

Abstract

Gibbon duets are in part genetically determined, but learning may also play a role in song development. In addition, songs may indicate resource holding potential, and are vital to acquiring mates and producing offspring. Captive-raised gibbons are often denied the experience of co-singing with their parents, and are generally less fit than their wild counterparts due to living in confined spaces. To explore how captivity and fitness could impact singing, we recorded the great calls of six individuals from three *Nomascus* species of rehabilitated gibbons at the Endangered Primate Rescue Center (EPRC) in Cuc Phuong National Park, Vietnam. The first song bout from each day was used for analysis. We extracted 23 parameters from 102 great call recordings (n=10-25/gibbon). A Principal Component Analysis revealed that the first three components accounted for 71.81% of the variance in the data. PCI focused on the bark phrase, PCII focused on the Oo phrase, and PCIII focused mainly on temporal parameters. We then ran correlations to explore how these principal components related to age and weight. These variables were chosen as proxies for health. This study provides preliminary evidence to support a non-invasive method to monitor behavior and rehabilitation using acoustic markers. Our results suggest that age and weight impact the production of female *Nomascus spp.* great calls. The significance of acoustic markers in rehabilitation practices is generally overlooked in the literature and merits further investigation. Future studies should implement acoustic markers to monitor individuals in captivity to better inform rehabilitation and release practices.

Keywords

Hylobatidae, bioacoustics, rehabilitation, gibbons, post-release assessment, health status

Introduction

Gibbons, family *Hylobatidae*, are small arboreal apes that inhabit the rainforests of eastern and southeastern Asia (Bartlett, 2006). There are four genera of gibbons (*Hylobates, Hoolock*, *Symphalangus*, and *Nomascus*) containing up to 20 species (Fan et al., 2017). Gibbon genera are defined by the number of chromosomes in their diploid cells: *Hoolock*, 38; *Hylobates*, 44; *Nomascus,* 52; *Symphalangus,* 50 (Chatterjee, 2006; Zihlman, Mootnick, & Underwood, 2011). There are currently seven species of crested gibbon (*Nomascus*) recognized (Konrad & Geissmann, 2006; Roos, Thanh, Walter, & Nadler, 2007; Thinh et al., 2010a; Thinh et al., 2010b**;** Thinh, Mootnick, Thanh, Nadler, & Roos, 2010c). These include the Hainan gibbon (*N. hainanus*), the eastern black gibbon (*N. nasutus*), the western black gibbon (*N. concolor*), the northern white-cheeked gibbon (*N. leucogenys*), the southern white-cheeked gibbon (*N. siki*), the northern yellow-cheeked gibbon (*N. annamensis*) and the southern yellow-cheeked gibbon (*N. gabriellae*) (Thinh, Hallam, Roos, & Hammerschmidt, 2011). The *Nomascus* genus is the rarest and least studied of the *Hylobatids* (Mootnick & Fan, 2011). *N. concolor, N. hainanus, N, leucogenys,* and *N. nasutus* are all listed as critically endangered by the International Union for Conservation of Nature (IUCN) Red List; *N. siki* and *N. gabriellae* are listed as endangered, and *N. annamensis* is not listed by the IUCN. Research on this genus is a high priority for conservationists and primatologists given their endangered status and decreasing population trends.

As deforestation and the pet trade continue, the number of gibbons being kept in captivity will only increase. Rehabilitation and reintroduction are quickly becoming the only options to save hundreds, if not thousands of gibbons rescued from these threats

(Cheyne, 2004). Additionally, rehabilitation and reintroduction can contribute to community and international education and play a valuable role in increased awareness (Chivers, 1991; Cheyne & Brulé, 2004). This is especially important for gibbons, whose conservation issues are under-researched and public awareness of the challenges they face is far less when compared to other apes. As we gain knowledge about gibbons' behavior in captivity and release more individuals, it is important to compare our understanding of captive raised gibbon behavior with wild gibbon behavior. Comparing released, captive raised individuals' behavior to wild individuals' behavior of the same species will help quantify the success of their reintroduction (Cheyne, 2009). Singing is perhaps the most conspicuous gibbon feature, and therefore an ideal target for behavioral comparisons.

Gibbon duets are in part genetically determined (Brockelman & Schilling, 1984; Tenaza 1985; Geissmann 1984), but given the wide song repertoire in every gibbon species (Geissmann, 2000) and the individuality that exists among wild populations, learning must play a role in song development (Koda et al. 2013; Merker and Cox, 1999; Goustard, 1979, 1983; Brockelman and Schilling, 1984; Geissmann, 1984; Tenaza, 1985). In the wild, gibbons learn to sing by co-singing with their parents (Koda et al., 2013; Goustard 1979, 1983), an experience captive-raised gibbons are denied (Cheyne, Chivers, & Sugardjito 2007; Cheyne, 2004). However, older, captive-raised gibbons produce louder, longer, and more complex songs (Cheyne et al., 2007). This finding suggests that even though captive-raised gibbons do not have the same opportunity to learn their song from a same-sexed parent, they still retain the ability to develop complex songs (Cheyne, 2004). Demonstrating sufficient individuality and being able to produce complete song bouts is important to a rehabilitant's capability to hold a territory and thrive in the wild.

Duets are usually female dominated, notably by the presence of the females' *great call*, which is comprised of 6-80 notes, and lasts between 7-30 seconds in a species-dependent pattern (Cowlishaw, 1992; Haimoff, 1984a; Marshall & Sugardjito, 1986; Geissmann, 2002). Great calls vary consistently between individuals (Haimoff & Tilson, 1985; Terleph, Malaivijitnond, & Reichard, 2015; Oyakawa, Koda, & Sugiura, 2007; Dallmann & Geissmann, 2001), which may facilitate individual recognition of conspecifics (Raemaekers & Raemaekers, 1985). Due to its stereotypy and individuality, it is believed that the great call is the primary carrier of information in the bout (Cowlishaw, 1992).

The song structure of *Nomascus* spp. differs from the rest of the *Hylobatidae* family in several aspects (Geissmann, 2000; Haimoff, 1984b; Konrad & Geissmann 2006). Crested gibbons show the highest degree of sex-specificity in their note type repertoire. In most species of other gibbon genera, females produce short phrases in addition to their great call. Female *Nomascus* gibbons contribute only great-calls and great-call fragments to their duet songs. Male and female crested gibbons exhibit no overlap in their note and phrase repertoire (Geissmann, 2002).

Adult female *Nomascus* great calls consist of three phrases: the *oo* phrase, bark phrase (accelerando-part), and twitter phrase (Thinh et al., 2011; see figure 1). The *oo* phrase consists of long notes of slowly increasing frequency, while the bark phrase is made up of short notes with a steep frequency increase. The great call then ends in the twitter phrase, which occurs after the climax of acceleration for the bark phrase. Bark notes tail off into the twitter phrase, which do not travel far (Konrad and Geissmann, 2006; Ruppell 2010). The bark notes are the most physically demanding part of the song, being loud notes that have the largest changes in frequency modulation during the great call. Due to the high intensity of great call climaxes, Terleph et al. (2016) hypothesized that the production of a great call climax pushes females to their physical limit, therefore making them a valid indicator of resource holding potential (RHP).

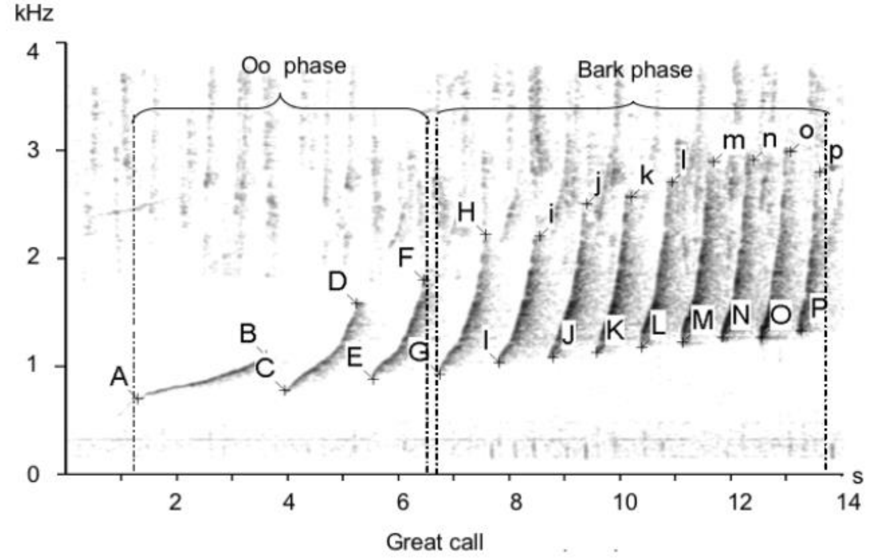


Fig. 1 *Nomascus* great call spectrogram
Note From Thinh et al., 2011. Spectrogram describing acoustic parameter estimation. Letters mark points used to calculate acoustic parameters.

Terleph et al. (2016) found age-related decline in female lar gibbon's (*Hylobates lar*) great call performance, which suggests that call features are correlated with an individual's physical condition. Territorial vocalizations may serve to honestly indicate an individual's RHP if calling is affected by physiological constraints (Vehrencamp, 2000; Smith and Harper, 2003). The characteristics of vocalizations, both their spectral and temporal parameters, are influenced by an individual's body size, age, rank, hormonal state and fatigue level (Terleph et al., 2016; Clutton-Brock & Albon, 1979; Inoue, 1988; Reby & McComb, 2003; Fischer, Kitchen, Seyfarth, & Cheney, 2007; Erb, Hodges, & Hammerschmidt, 2013). These are measures of physical condition, and thus are assumed to be correlated with RHP (Terleph et al., 2016).

Gibbon calls carry an incredible amount of information. In addition to indicating RHP and being individually specific, vocal data is considered to be largely genetically determined and species-specific (Brockelman & Schilling, 1984; Tenaza 1985; Geissmann 1984). Thinh et al. (2011) examined whether the song structure of six crested gibbon species, especially in the four most closely related species (three of which are target species in this study) *N. leucogenys*, *N. siki*, *N. annamensis,* and *N. gabriellae*, is persistently distinct enough to be regarded as a phylogenetic trait. The findings suggest only minor differences in song structure among these four species, but distinct enough differences to consider singing a phylogenetic trait (Thinh et al., 2011).

In addition, Thinh et al. (2011) found eight parameters necessary to classify great calls to the species level. These parameters were duration of the entire great call, range of start frequencies [kHz], number of Oo notes, duration of the first note of the Oo phrase, duration of the second note of the Oo phrase, duration of the last note of the bark phrase, frequency range of the first note of the bark phrase, and the last inter-note interval of the bark phrase (DGC, RF, NO, DNO1, DNO2, DNBL, RFB1, and NIBL (see table 1)). Thinh et al.'s findings compliment previous research on *Nomascus* vocals which support that similar parameters distinguish these species' great calls (Konrad & Geissmann, 2006; Ruppel 2010). They also found a highly significant correlation between similarity in song structure and geographic distance (Thinh et al., 2011). This finding emphasizes the importance of studying captive-raised gibbons to determine whether they are singing species-specific songs. As both learning and genetics play a role in song development (Goustard, 1979, 1983; Brockelman and Schilling, 1984; Geissmann, 1984; Tenaza, 1985), it is necessary to study the songs of captive-raised gibbons before they are released (Cheyne et al., 2007). Singing appropriate sex and species-specific song bouts is vital to attracting same species mates and defending territory.

Table 1

List of Acoustic Parameters and Their Descriptions

Code	**Acoustic parameter**	**Description**
DGC	Duration of entire great call [s]	Time at (p-A)
NN	Number of notes	Total number of elements
RF	Range of start frequencies [Hz]	Frequency at (P-A)
NO	Number of Oo notes	Notes with frequency increase of <=1kHz/s
DO	Duration of Oo phrase [s]	Time at (F-A)
RDO	Relative duration of Oo phrase [%]	No. 5 in % of No. 1
NB	Number of bark notes	Notes with a frequency increase of >1kHz/s
DB	Duration of bark phrase [s]	Time at (p-G)
RDB	Relative duration of bark phrase [%]	No. 8 in % of No. 1
DNO1	Duration of the first note of Oo phrase [s]	Time at (B-A)
DNO2	Duration of the second note of Oo phrase [s]	Time at (D-C)
DNB1	Duration of first note of bark phrase [s]	Time at (F-E)
DNBL	Duration of last note of bark phrase [s]	Time at (p-P)
RFO1	Frequency range of first note of Oo phrase [Hz]	Frequency at (B-A)
RFO2	Frequency range of second note of the Oo phrase [Hz]	Frequency at (D-C)
RFO3	Frequency range of third note Oo phrase [Hz]	Frequency at (F-E)
RFB1	Frequency range of the first note of the bark phrase [Hz]	Frequency at (H-G)
NIO1	First inter-note interval of Oo phrase [s]	Time at (C-B)
NIO2	Second inter-note interval of Oo phrase [s]	Time at (E-D)
NIBL	Last inter-note interval of bark phrase [s]	Time at (P-o)
RFO12	First start frequency range between second and first note of Oo phrase [Hz]	Frequency at (C-A)

Table 1 continued

Code	Acoustic Parameter	Description
RFO	Second start frequency range between first note of bark and last note of Oo [Hz]	Frequency at (G-E)
RFBL	First start frequency range between last and previous note of bark phrase [Hz]	Frequency at (G-H)

Note adapted from Thinh et al., 2011.

Since vocalizations can reflect both physiological and psychological aspects of welfare and are encoded with physiological, emotional, and individual information, there is an incredible amount of untapped potential. Especially since the application of bioacoustics for assessing animal welfare is not widespread in the literature, and is restricted to studies in livestock, marine mammals, and birds (Mcloughlin et al. 2019). In addition, bioacoustic monitoring in ecology and conservation is limited to a few approaches (i.e., detection of animal presence in habitat that is disturbed or has low visibility, quantifying the number of individuals in a population through passive acoustic monitoring, identifying individuals through acoustic fingerprinting, using vocalizations to infer emotional state; automated detection of stress-related calls; Mcloughlin et al. 2019; Whitham and Miller, 2016). These studies emphasize the rate and frequency at which vocalizations are used across contexts, and do not account for the discrete acoustic properties of the calls and how they are related to the health status of the individual. This is a significant gap in the literature, therefore there is an urgent need to create methods for assessing health through an in depth analysis of acoustic parameters and their relationship with the animal's physiology. In effect, this will help us to listen in on how these acoustic markers can also provide physiological markers for health.

Ultimately, the goal of rehabilitation is to ensure that individuals post-release will produce offspring that survive to adulthood. Therefore, focusing on the calls within the mating context may be the most salient method for assessing health and welfare through acoustic markers. Calls within this context may serve as honest signals reflective of the individual's fitness, and are therefore encoded with vital information about the caller (e.g., dominance status, physical condition, etc.) that can then be used by the audience (i.e., potential mates) to select a mate (Hauser, 1993). Honest signals must be associated with costs, and vocalizations emitted in the mating context have been cited as indicators of quality or physical condition because they are costly to produce (Hauser, 1993). Therefore, female great calls are ideal for assessing *Nomascus* welfare since they are essential for the propagation of a species, and they are encoded with vital information concerning an individual's quality and fitness.

We believe in the need to develop non-invasive, ecologically valid approaches, and focusing on calls within the mating context provides us with that unique opportunity. These calls are not only indicators of physical condition, but they are also vital to an individual's ability to attract mates and produce viable offspring. In some species, especially for Critically Endangered gibbons, calls within the mating context determine the survival of a species. If individuals are unable to call and attract mates, they will not produce offspring in the wild, and therefore the goals of population reinforcement via rehabilitation and release are not fulfilled. In order to protect biodiversity and enhance the survival of a species, it is essential that we pay close attention to calls within the mating context, as they are a gold mine of information on health and welfare, and essential in the propagation of a species.

The goal of this study is to examine how age and weight impact female *Nomascus* gibbons' great call production. The gibbons at the Endangered Primate Rescue Center (EPRC) are rescued from the wildlife trade and more specifically, the pet trade. *Nomascus leucogenys, Nomascus siki*, *Nomascus annamensis* and *Nomascus gabriellae* are kept at the center. This creates an environment where all four species can hear one another, a circumstance that does not occur in the wild. Due to their social nature, individuals are ideally paired with a member of the same species but this is not always possible. Young, rescued gibbons are often paired with an adult of a different species and are able to hear all four species as they learn to sing. As a result, individuals could be learning to sing from a different species. Furthermore, captivity limits their fitness level due to enclosure confinement, which could be evident in their singing.

To explore the link between welfare, health, and mating calls we recorded the great calls of six gibbons at the Endangered Primate Rescue Center.

We predict that:

1. Since three previous studies (Ruppell, 2010; Thinh et al., 2011; Konrad & Geissmann, 2006) all found range in start frequencies (RF) to be a defining parameter in *Nomascus* species singing differences, RF will maintain its importance as a distinguishing factor among the species in this study.
2. Age will influence singing behaviors based on Terleph et al.'s (2016) findings that age can be used as a proxy for resource holding potential (RHP). We predict that older individuals at the EPRC will perform lower quality songs than younger adults.
3. Weight can also be used as a proxy of health or RHP. We predict that gibbons that weigh more have a greater body mass and are in better physical health, and therefore will

be able to produce higher quality songs than individuals who weigh less. This prediction assumes that none of the gibbons at the EPRC are obese.

Methods

Study Site and Subjects

This study was conducted from July 5th to October 5th, 2018, at the Endangered Primate Rescue Center (EPRC) in Cuc Phuong National Park (CPNP), Ninh Binh Province, Vietnam. The EPRC was established in 1993 through a collaboration between Frankfurt Zoological Society and CPNP. Currently, the center is managed under the umbrella of the Vietnam Primate Conservation Program, and is jointly operated by Zoo Leipzig and CPNP. The center houses lorises, langurs, and gibbons. It is home to approximately 180 primates from 15 species. Three species of female gibbons were the focus of our study: *Nomascus siki*, *N. leucogenys,* and *N. annamensis.* CR collected data from six adult female gibbons. Vocal samples were taken from two *N. siki* individuals, two *N. leucogenys* individuals, and two *N. annamensis* individuals (see table 2). All of the gibbons in this study were rescued from the pet trade in Vietnam. The gibbon's ages range between 9-24 years. Three of the gibbons (Polly, Daisy, Simba) were rescued when they were 1 year old or less and hand-reared by EPRC keepers. Two of the gibbons were rescued when they were 7-8 years old (Hu and Lo Lem), and have been at the EPRC for less than 2 years. The final gibbon (Gabi) came to the EPRC when she was 3 years old, and has been at the EPRC for 21 years (see table 2).

Each of these gibbons lived in a same species pair, except for Hu who lived alone for the first half of the study, and with an immature female of the same species during the second half of the study. Daisy was the only gibbon living with a family group, and shared her enclosure with her partner and their two sons. Lo Lem gave birth half way through the study.

Table 2

Gibbon	Species	Age	Weight (kg)	Songs recorded	Great Calls analyzed
Polly	*leucogenys*	24	8.5	5	21
Lo Lem	*leucogenys*	9	7.6	5	16
Simba	*siki*	20	7.8	5	17
Daisy	*siki*	25	7.1	5	25
Hu	*annamensis*	9	6.3	3	10
Gabi	*annamensis*	24	7.5	5	13

List of Gibbons in the Study With Category Values Used to Run Correlation Test

The gibbons all lived in large wire mesh enclosures. The cages have bamboo grid structures that allow for brachiation. Most of these enclosures were free standing and offer varying amounts of visual barriers from the other gibbons. The gibbons were able to hear every other gibbon in the center sing. One gibbon in the study, Simba, shared fencing with two neighboring gibbons. Most of the gibbons lived in one section of the EPRC and were easily able to see and hear one another. The gibbons were provided nesting boxes and access to water at all times. The gibbons were fed five times a day. Their diet included vegetables, fruit, leaves, flowers, nuts, seeds, eggs, and rice porridge.

Recording Vocalizations and Acoustic Analyses

CR recorded the first song bout from each day, typically around sunrise (range 0516 am-0601 am) using a Roland R-26 digital recorder at a 48 kHz (16 bits) sampling rate, connected to a Sony ECM-674 directional microphone. Song bouts are defined as including the first to last loud note produced with no period of silence for more than ten minutes between notes (Haimoff, 1984a). Recordings were collected ad libitum from 0440 to 0900 hr, seven days a week. Days with significant rain were not included in the study due to poor recording quality. CR recorded song bouts opportunistically, by walking the paths of the center and recording the closest enclosure whenever any gibbons started their song bout. This allowed CR to record entire song bouts. Any incomplete song recordings were discarded from analyses. To avoid over-/under sampling individuals, CR listened to song bouts for quality control and tallied the songs collected per individual each day. CR focused on recording under-sampled individuals to evenly distribute song recordings throughout the study period.

CR analyzed vocal samples using Avisoft-SASLab Pro 5.2.09 (R. Sprecht, Berlin, Germany) to generate spectrograms using a Fast Fourier transform (FFT) size of 1,024 points and an overlap of 50% with the Hamming window function (frequency resolution = 47 Hz, temporal resolution = 16.4 ms). Great calls were extracted from each song bout. The great call is defined as the most stereotyped and most easily identifiable phrase of the gibbon song produced by adult females (see figure 1)(Haimoff, 1984a). Great calls were considered complete if they contained six or more notes (Thinh et al., 2011). The 23 parameters used in Thinh et al.'s (2011) study were extracted from great calls for analyses (see table 1). If a song bout contained more than five analyzable great calls, we randomly selected 5 great calls from the song bout for analysis.

Statistical Analyses

All statistical analyses were performed in RStudio version 1.1.456 (R Development Core Team, 2019). We conducted a Principal Component Analysis (see table 3) to summarize the 23 acoustic variables extracted from each great call. We used a loading factor of $> |0.22|$ to interpret the principal components and in turn assess which variables had the most significant effect on each component. We then conducted

Spearman's correlations between the parameters highlighted by the PCA with age and weight. Correlations with a p value of < 0.05 were considered significant.

Table 3
Principal Components With Related Acoustic Variables and Factor Loadings

	PCI		PCII		PCIII	
Principal Component Interpretation	NB. Number of Bark Notes		NO. Number of Oo Notes		DGC. Duration of Entire Great Call (s)	
Percentage of Variance Explained (%)	41.35		16.10		14.36	
Loading Factor	RDB. Relative Duration of Bark Phrase	-0.320	DO. Duration of Oo Phrase	-0.355	NIO1. First Inter-Note Interval of Oo Phrase	-0.395
	NN. Number of Notes	-0.312	RDO. Relative Duration of Oo Phrase	-0.277	DB. Duration of Bark Phrase	-0.392
	DB. Duration of Bark Phrase	-0.262	DGC. Duration of Entire Great Call	-0.260	DNB1. Duration of First Note of Bark Phrase	-0.353
					RF. Range of Start Frequencies	-0.263

Data Availability

The datasets generated and/or analyzed during the current study are available from the corresponding author on reasonable request.

Ethical Note

Our research complied with the protocol approved by Central Washington University's Institutional Animal Care and Use Committee (protocol no. A021803), this research also followed the American Society of Primatologists' Principles for the Ethical Treatment of Primates. The authors declare they have no conflict of interest.

Results

We conducted over 280 hours of direct observation over the course of 70 days during the study. CR recorded 40 song bouts and used 28 song bouts in the analyses after discarding recordings that were poor quality and /or from unidentified callers. The number of songs varied from each individual (n = 3-5), and the number of great calls varied from each individual (n = 10-25) as well. In total, 102 great calls were used for analysis (see table 2), with a mean of 17 analyzable great calls collected per individual. Five of the gibbons had five complete, high quality song bouts recorded. One individual, Hu, was recorded singing at sunrise three times. CR intentionally spent more time near Hu's enclosure in an attempt to evenly distribute recordings. On three mornings, CR recorded Hu's enclosure during the morning song bout, but Hu did not sing with the other gibbons. Hu is the only gibbon in this study that is housed alone.

Acoustic and Statistical Results Summary

Principal Components Analysis

The Principal Component Analysis (PCA) summarized the 23 variables into three Principal Components (PCs) that together accounted for 71.81% of the variance in the data (see table 3). PCs I – III were interpreted from the variables that correlated most strongly with each component: the number of bark notes (NB), the number of Oo notes (NO) and the duration of the entire great call (DGC), respectively. PCI explained 41.35% of the variance in the data and correlated with the relative duration of the bark phrase (RDB), number of notes in the entire great call (NN) and overall duration of the bark phrase (DB). PCII explained 16.10% of the variance in the data, and was driven by the duration of the Oo phrase (DO), relative duration of the Oo phrase (RDO) and duration of the entire great call (DGC). Lastly, PCIII explained 14.36% of the data and was influenced by the first inter-note interval of the Oo phrase (NIO1), the duration of the bark phrase (DB), the duration of the first note of the bark phrase (DNB1) and the range of start frequencies (RF). See table 1 for parameter codes and descriptions.

Correlation Analyses

We ran Spearman's correlations between the 11 parameters highlighted by the PCA with age and weight. A total of 12 of the correlations had significant results (p value < 0.05; see Table 4).

Age and weight had significant correlations with a number of parameters. In PCI, which mainly focused on the bark phrase, duration of the bark phrase (DB) and the number of bark notes (NB) were both positively correlated with weight and negatively correlated with age, while the relative duration of the bark phrase (RDB) and the number of notes in the entire great call (NN) were positively associated with weight. Weight was significantly correlated to all of the parameters in PCI.

Table 4

Correlations Between Principal Component Parameters and an Individual's Age and Weight

PCI	NN	NB	DB	RDB	
Age	0.058	**0.039 (-)**	**0.005 (-)**	0.068	
Weight	**0.003 (+)**	**0.001 (+)**	**<0.001 (+)**	**0.003 (+)**	
PCII	DGC	NO	DO	RDO	NIO1
Age	0.052	0.313	0.534	**0.049 (+)**	**<0.001 (-)**
Weight	0.176	0.115	0.062	**0.003 (-)**	0.476
PCIII	DGC	RF	DB	DNB1	
Age	0.052	**0.034 (-)**	**0.005 (-)**	0.163	
Weight	0.177	**0.046 (-)**	**<0.001 (+)**	**<0.001 (+)**	

Note Correlation scores (positive/negative) shown on significant correlations. Significant results (*p* value < 0.05) are in bold.

In PCII, which was closely associated with the Oo phrase, age and weight also showed significant correlations. Relative duration of the Oo phrase (RDO) was positively correlated with age and negatively correlated with weight, and the first inter-note interval of the Oo phrase (NIO1) was negatively correlated with age. Acoustic parameters highlighted by PCIII were associated with the overall temporal parameters of the great call, and showed significant negative correlations between range of start frequencies (RF) and age and weight. Also, in PCIII, duration of the bark phrase (DB) was negatively correlated with age and positively correlated with weight. Duration of the first note of the bark phrase (DNB1) was positively correlated with weight as well. Weight had significant correlations with three out of four parameters in PCIII (see table 4).

Discussion

The goal of this study was to examine the impact of captivity on the great calls of six female *Nomascus* gibbons at the EPRC. Research on the *Nomascus* genus of gibbons is a priority, given their Endangered and Critically Endangered status in addition to decreasing population trends. This study enabled us to explore how calling might be impacted by health, uses the proxies age and weight. This information is of high importance for gibbon rehabilitation. It is vital that rehabilitated gibbons are singing appropriately before they are released into the wild. Singing bouts are central to a gibbon's life, and play a role in mate attraction, pair bonding, and maintaining a territory.

We predicted that the gibbons at the EPRC would maintain the species-specific calling patterns found by previous researchers. RF was a parameter highlighted by PCA III, but had a lower loading factor than most of the other parameters selected by the PCA (see table 3). RF is the only parameter found to be a distinguishing factor for species calling differences for all three previous papers. Furthermore, RF was the only parameter in our study that had a significant correlation with every variable.

The significance of RF demonstrates that the gibbons at the EPRC are retaining some genetically inherited singing patterns. RF was a significant parameter in our study, and the three previous studies on *Nomascus* vocals (Ruppell, 2010; Thinh et al., 2011; Konrad & Geissmann, 2006) showed that RF varies between *Nomascus* species. *N. leucogenys* and *N. siki* have lower start frequencies that remain constant throughout the great call, while *N. gabriellae's* start frequency is higher, and ascends during the call.

Our second prediction was that age would influence the great calls of the gibbons at the EPRC. Age was found to have a significant correlation with five of the parameters (RF, RDO, NB, DB, NIO1), which is more than most of the other variables. This indicates that age does play an important role in singing performance. All but one of these correlations (RDO) were negative. This indicates that as an individual gets older, they have less of a frequency range (RF), and the number of notes and the duration of the bark phrase decreases (NB, DB). This pattern with these parameters indicates that, as gibbons age, they are less fit and less able to sing the most demanding parts of the song for a long period of time (NB, DB). They have lost some of the elasticity in their lungs and the ability to produce the rapid frequency modulations found in *Nomascus* great calls.

We also predicted that weight would impact singing performance, because it is another proxy for resource holding potential (RHP). Weight correlated with 7 out of 11 parameters. Weight had positive correlations with several temporal parameters and the number of notes in the great call (parameters NN, NB, DB, RDB, DNB1) indicating that heavier individuals had greater lung capacity, and the ability to sing for longer periods of time.

The importance of weight's correlation with temporal features could relate to RHP. Field researchers often rely on the individual's body size, age, rank, hormonal state, and fatigue level as indirect measures to evaluate physical condition and RHP (Fischer, Kitchen, Seyfarth, & Cheney, 2007; Inoue, 1988; Hammerschmidt, Freudstein, & Jurgens, 2001). A reduction in abdominal muscle mass can indicate a decrease in respiratory function, which declines with age due to a loss of elasticity and dispensability in the lungs (Terleph et al., 2016; Wahba, 1983; Awan, 2006; Herring et al., 2013; Sataloff et al., 1997; Quanjer et al., 2012). The decrease in muscle mass, which implies a decrease in physical fitness, can thus be measured through vocalizations. *Nomascus* gibbons in this study were able to sing more notes for a longer period of time as their weight (body mass) increased. These results can be interpreted as relating to physical fitness.

Several of the parameters that significantly accounted for the majority of variation in our study were also important in highlighting species differences in previous papers. DGC, NN, RF, NO were significant parameters for species differences in at least one of the previous studies on *Nomascus* great calls (see table 5). NN was correlated with weight, where an increase in weight yielded an increase in the number of notes in the great call. RF, which was found to be significant in all of the previous studies (see table 5), was significantly correlated with age and weight. In other words, younger and heavier individuals were able to start singing with a greater range of frequencies. Due to of RF's significance in all studies, we can assume that the range of start frequency is impacted by the genetics and the species of an individual. We did not find any significant correlations between NO and age and weight (see table 4).

Table 5
Past Research on Nomascus Vocals and the Parameters Found to be Significant in Species Differences

Parameter	Konrad & Geissmann (year)	Ruppell	Thinh et al.	Rowley & Blue
OGC		X	X	X
NN	X	X		X
RF	X	X	X	X
NO			X	X
DO				X
RDO				X
NB				X
DB				X
RDB		X		X
DNO1		X	X	
DNO2			X	
DNB1				X
DNBL			X	
RFO1				
RFO2				
RFO3				
RFB1			X	

Table 5 continued

Parameter	Konrad & Geissmann	Ruppell	Thinh et al.	Rowley & Blue
NIO1				X
NIO2				
NIBL			X	
RFO12	X			
RFO				
RFBL	X			

We found several parameters that were not significant in previous studies to be central to the variability present in our data. RDO, NB, and DB had significant correlations with both age and weight. DNB1 was correlated with weight and NIO1 has a significant correlation with age (see table 4). These parameters, with the exception of NB, all focused on temporal features that could be related to lung capacity and general fitness. NB can also be associated with health, as the number of bark notes an individual is able to produce during their great call demonstrates their lung elasticity. Additionally, previous papers found some parameters to be significant in their studies that were not found to be significant in ours. Ruppell and Thinh et al. (year) found DGC and DNO1 to be significant in species song differences, and Ruppell and Konrad (year) found NN to be a distinguishing parameter in species differences. It is possible that these parameters are more related to discrete genetic differences in singing rather than health, or that our sample size limited our ability to investigate similar patterns.

This study offers further insight into several areas of *Hylobatidae* research that we hope can benefit these understudied species in practical ways. First, we know that RF maintains its importance as an indicator of species differences in *Nomascus* great calls. Due to the circumstances in which many of these gibbons were raised, they were denied the experience of co-singing with their mother. Maintaining their difference in RF must be a song feature that is in part genetically conserved. Many of our findings also suggest that singing performance is related to health. Age and weight, both of which are used as proxies for health (citation), correlated with acoustic and temporal features of the great call. Our results indicate that indeed physical condition is closely linked to song quality, and may be inferred from acoustic and temporal features of great calls, Future studies should explore additional physiological measures and their relationship with great call production in *Nomascus* gibbons.

Understanding gibbon's singing behavior can benefit their captive welfare, as husbandry keepers can observe how an individual is calling and gauge the animal's current welfare status. While some acoustic analyses require detailed processing on specialized software, some are much easier to observe. For example, if a gibbon is not calling regularly, it would be important to observe that individual and see what changes could be made to their husbandry. Furthermore, for keepers who are familiar with individual animals, it is achievable to measure the time spent in each phrase during the great call. It would be possible to apply some of the temporal patterns found in this paper to captive *Nomascus* gibbons and determine if the gibbon is calling "normally".

The greater implications of this study for conservation will come with future research. If future studies continue to demonstrate that calling behavior correlates with an individual's health status, it would offer a non-invasive way of measuring the health of rehabilitated and released individuals. Tracking collars are expensive, are unsuitable for some species of gibbon due to gular sacs, and are limited in the amount of information they provide conservationists. If a gibbon's song has been recorded before release, and we are able to identify the individual through song and/or tracking, we would be able to determine if the gibbon is remaining healthy and accessing their necessary nutrients by analyzing their calls post-release. Furthermore, acoustic and temporal parameters from released gibbons could then be compared with the results of this study, and the previous literature from their wild counterparts. Future studies should continue to research *Hylobatidae* vocals and increase our understanding of gibbon songs, and their potential for providing non-invasive measures of health and welfare during rehabilitation and post-release assessments.

REFERENCES

Awan, S. N. (2006). The aging female voice: acoustic and respiratory data. *Clinical linguistics & phonetics*, *20*(2-3), 171-180.

Bartlett, T. Q. (2006). The hylobatidae, small apes of Asia. In C.J. Campbell, A. Fuentes, K. C. Mackinnon, M. Panger & S. K. Bearder (Eds.), *Primates in Perspective* (274-289). Oxford: Oxford University Press.

Brockelman, W. Y. and Schilling, D. (1984). Inheritance of stereotyped gibbon calls. *Nature, 312,* 634-636.

Chatterjee, H. J. (2006). Phylogeny and biogeography of gibbons: a dispersal-variance analysis. *International Journal of Primatology*, *27*(3), 699-712.

Cheyne, S. M. (2004). *Assessing rehabilitation and reintroduction of captive-raised gibbons in Indonesia.* (Doctoral dissertation, University of Cambridge).

Cheyne, S. M. (2009). Challenges and opportunities of primate rehabilitation—gibbons as a case study. *Endangered Species Research, 9,* 159-165. Doi: 10.3354/esr00216

Cheyne, S. M. and Brulé, A. (2004). Adaptation of a captive-raised gibbon to the wild. *Folia Primatologica*, *75*(1), 37-39.

Cheyne, S. M., Chivers, D. J., & Sugardjito, J. (2007). Covariation in the great calls of rehabilitant and wild gibbons (Hylobates albibarbis). *The Raffles Bulletin of Zoology*, *55*(1), 201-207.

Chivers, D. J. (1991). Guidelines for reintroductions: procedures and problems. *Symposium of the Zoological Society of London, 62,* 89-99.

Cowlishaw, G. U. Y. (1992). Song function in gibbons. *Behaviour*, *121*(1), 131-153.

Dallmann, R., & Geissmann, T. (2001). Individuality in the female songs of wild silvery gibbons (Hylobates moloch) on Java, Indonesia. *Contributions to Zoology*, *70*(1), 41-50.

Endangered Primate Rescue Center (2016, February 12). *About Us.* Retrieved from www.eprc.asia.

Erb, W. M., Hodges, J. K., & Hammerschmidt, K. (2013). Individual, contextual, and age-related acoustic variation in simakobu (*Simias concolor*) loud calls. *PLoS One, 8*(12), e83131

Fan, P. F., He, K., Chen, X., Ortiz, A., Zhang, B., Zhao, C., Li, Y. Q., Zhang, H. B., Kimock, C., Wang, W. Z., Groves, C., Turvey, S. T., & Roos, C. (2017). Description of a new species of Hoolock gibbon (Primates: Hylobatidae) based on integrative taxonomy. *American Journal of Primatology*, *79*(5), e22631.

Fischer, J., Kitchen, D. M., Seyfarth, R. M., & Cheney, D. L. (2004). Baboon loud calls advertise male quality: acoustic features and their relation to rank, age, and exhaustion. *Behavioral Ecology and Sociobiology, 56,* 140-148.

Geissmann, T. (1984). Inheritance of Song Parameters in the Gibbon Song, Analyzed in 2 Hybrid Gibbons (*Hylobates pileatus* X *Hylobates lar*). *Folia Primatologica, 42*(3-4), 216-235.

Geissmann, T. (2000). *Vietnam Primate Conservation Status Review 2000: Part 1: Gibbons*. Fauna & Flora International, Indochina Programme.

Geissmann, T. (2002). Duet-splitting and the evolution of gibbon songs. *Biological Reviews of the Cambridge Philosophical Society*, *77*(1), 57-76.

Goustard, M. (1979). Stereotype and plasticity of utterances in gibbons (*Hylobates concolor leycogenys*). *C R Seances Acaddemie Sciences D, 288,* 1615-1618.

Goustard, M. (1983). Organization of loud calls (territorial vocalizations) during puberty, in male gibbon (*Hylobates concolor gabriellae*). *C R Seances Acaddemie Sciences D, 296*(15), 743-5.

Haimoff, E. H. (1984a). Acoustic and organizational features of gibbon songs. In H. Preuschoft, D. J. Chivers, W. Y. Brockelman, & N. Creel (Eds.), *The lesser apes* (33-353). Edinburgh: Edinburgh University Press.

Haimoff, E. H. (1984b). The organization of song in the Hainan black gibbon (Hylobates concolor hainanus). *Primates*, *25*(2), 225-235.

Haimoff, E. H., & Tilson, R. L. (1985). Individuality in the female songs of wild kloss' gibbons (*Hylobates klossii*) on Siberut Island, Indonesia. *Folia Primatologica, 44*, 129-137.

Hammerschmidt, K., Freundstein, T., & Jurgens, U. (2001). Vocal development in squirrel monkey. *Behaviour, 138,* 1179-1204.

Hauser, M. D. (1993). The evolution of nonhuman primate vocalizations: effects of phylogeny, body weight, and social context. *The American Naturalist*, *142*(3), 528-542.

Herring, M. J., Avdalovic, M. V., Quesenberry, C. L., Putney, L. F., Tyler, N. K., Ventimiglia, F. F., St. Georrge, J. A., & Hyde, D. M. (2013). Accelerated structural decrements in the aging female rhesus macaque lung compared with males. *American Journal of Physiology-Lung Cellular and Molecular Physiology*, *304*(2), L125-L134.

Inoue, M. (1988). Age gradations in vocalization and body weight in Japanese monkeys (*Macaca fuscata*). *Folia Primatologica, 51*, 76-86.

International Union for the Conservation of Nature. (2018, March 19). *Version 2017-3*. The IUCN Red List of Threatened Species. www.iucnredlist.org.

Koda, H., Lemasson, A., Oyakawa, C., Pamungkas, J., & Masataka, N. (2013). Possible role of mother-daughter vocal interactions on the development of species-specific song in gibbons. *PloS one*, *8*(8), e71432.

Konrad, R., & Geissmann, T. (2006). Vocal diversity and taxonomy of Nomascus in Cambodia. *International Journal of Primatology*, *27*(3), 713.

Marshall, J. T., & Sugardjito, J. (1986). Gibbon Systematics. In D. R. Swindler & J. Erwin (Eds.), *Comparative primate biology, volume 1* (137-185). New York: Smithsonian Institution (USA).

Merker, B., & Cox, C. (1999). Development of the female great call in *Hylobates gabriellae*: a case study. *Folia Primatologica*, *70*(2), 97.

Mootnick, A. R., & Fan, P. F. (2011). A comparative study of crested gibbons (*Nomascus*). *American Journal of Primatology*, *73*(2), 135-154.

Oyakawa, C., Koda, H., & Sugiura, H. (2007). Acoustic features contributing to the individuality of wild agile gibbon (Hylobates agilis agilis) songs. *American Journal of Primatology*, *69*(7), 777-790.

Quanjer, P. H., Stanojevic, S., Cole, T. J., Baur, X., Hall, G. L., Culver, B. H., Enright, P. L., Hankinson, J. L., Ip, M. S. M., Zheng, J., & Stocks, J. (2012). Multi-ethnic reference values for spirometry for the 3–95-yr age range: the global lung function 2012 equations. *European Respiratory Journal*, *40*(6), 1324-1343.

R Development Core Team. 2008. *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Raemaekers, J. J. & Raemaekers, P. W. (1985). Long-range vocal interactions between groups of gibbons (*Hylobates lar*). *Behavior, 95,* 26-44.

Reby, D., & McComb, K. (2003). Anatomical constraints generate honesty: acoustic cues to age and weight in the roars of red deer stags. *Animal Behavior, 65,* 519-530.

Roos, C., Thanh, V. N., Walter, L., & Nadler, T. (2007). Molecular systematics of Indochinese primates. *Vietnamese Journal of Primatology*, *1*(1), 41-53.

Ruppell, J. C. (2010). Vocal diversity and taxonomy of Nomascus in central Vietnam and southern Laos. *International Journal of Primatology*, *31*(1), 73-94.

Sataloff, R. T., Rosen, D. C., Hawkshaw, M., & Spiegel, J. R. (1997). The aging adult voice. *Journal of Voice*, *11*(2), 156-160.

Smith, J. M., & Harper, D. (2003). *Animal signals*. Oxford University Press.

Tenaza, R. R. (1985). Songs of hybrid gibbons (*H. lar* x *H. muelleri*). *American Journal of Primatology, 8*, 249-253.

Terleph, T. A., Malaivjitnond, S., & Reichard, U.H. (2015). Lar Gibbon (*Hylobates lar*) Great Call Reveals Individual Caller Identity. *American Journal of Primatology, 77,* 811-821.

Terleph, T. A., Malaivijitnond, S., & Reichard, U. H. (2016). Age related decline in female lar gibbon great call performance suggests that call features correlate with physical condition. *BMC evolutionary biology*, *16*(1), 4.

Thinh, V. N., Mootnick, A. R., Geissmann, T., Li, M., Ziegler, T., Agil, M., Mooisson, P., Nadler, T., Walter, L., & Roos, C. (2010a). Mitochondrial evidence for multiple radiations in the evolutionary history of small apes. *BMC Evolutionary Biology, 10*(74), 1-9.

Thinh, V. N., Mootnick, A. R., Thanh, V. N., Nadler, T., & Roos, C. (2010b). A new species of crested gibbon from the central Annamite mountain range. *Vietnamese Journal of Primatology, 4,* 1-12.

Thinh, V. N., Rawson, B., Hallam, C., Kenyon, M., Nadler, T., Walter, L., & Roos, C. (2010c). Phylogeny and distribution of crested gibbons (genus Nomascus) based on mitochondrial cytochrome b gene sequence data. *American Journal of Primatology*, *72*(12), 1047-1054.

Thinh, V. N., Hallam, C., Roos, C., & Hammerschmidt, K. (2011). Concordance between vocal and genetic diversity in crested gibbons. *BMC evolutionary biology*, *11*(1), 36.

Vehrencamp, S. L. (2000). Handicap, index, and conventional signal elements of bird song. In G. Rosenqvist, T. Amundsen, & Y. Esprnark (Eds.), *Animal signals: signalling and signal design in animal communication*, 277-300.
song. *Animal signals: signalling and signal design in animal communication*, 277-300.

Wahba, W. M. (1983). Influence of Aging on Lung Function-Clinical Significance of Changes from Age Twenty. *Anesthesia & Analgesia*, *62*(8), 764-776.

Zihlman, A. L., Mootnick, A. R., & Underwood, C. E. (2011). Anatomical contributions to hylobatid taxonomy and adaptation. *International journal of primatology*, *32*(4), 865-877.

CHAPTER IV

CONCLUSION

This study offers further insight into several areas of *Hylobatidae* research that we hope can benefit these understudied species in practical ways. First, we know that RF maintains its importance as an indicator of species differences in *Nomascus* great calls. Due to the circumstances that many of these gibbons were raised, they were denied the experience of co-singing with their mother. Maintaining their difference in RF must be a song feature that is in part genetically conserved. Many of our findings also suggest that singing performance is related to health. Age and weight correlated with singing features, both of which are used as proxies for health. Future studies should explore how health impacts great call production in *Nomascus* gibbons.

Gibbon's songs are incredibly complex. Understanding the impacts of their genetics, learning, current health, motivational state, and any number of other variables on song production creates a complicated research project. In the future, it would be valuable to repeat this research while focusing on a single species. This eliminates one of the largest causes for song differences. Additionally, to evaluate how current health status impacts calling behavior, data should be collected in tandem with scheduled health exams at captive facilities. This allows for the greatest amount of data to be gathered, and hopefully would provide valuable insights into health and great call production.

Weight correlated with 7 out of the 10 acoustic parameters highlighted by the Principal Component Analysis. Weight is often used as a proxy for health, and it is logical that an individual's weight would impact their vocal production. Indeed, heavier individuals were able to perform great calls at a higher quality than lighter individuals.

Heavier individuals in our study were able to sing a greater number of notes in the great call overall, and they were able to sing for longer durations as well.

The greater implications of this study for conservation will come with future research. If we are able to demonstrate that calling behavior correlates with an individual's health status, it would offer a non-invasive way of measuring the health of rehabilitated and released individuals. Tracking collars are expensive, are unsuitable for some species of gibbon due to gular sacs, and are limited in the amount of information they provide conservationists. If a gibbon's song has been recorded before release, and we are able to identify the individual through song and/or tracking, we would be able to determine if the gibbon is remaining healthy and accessing their necessary nutrients by analyzing their calls post-release. Furthermore, acoustic and temporal parameters from released gibbons could then be compared with the results of this study, and the previous literature from their wild counterparts.

Understanding gibbons' singing behavior can benefit their captive welfare, as husbandry keepers can observe how an individual is calling and gauge the animal's current welfare status. While some acoustic analyses require detailed processing on specialized software, some are much easier to observe. For example, if a gibbon is not calling regularly, it would be important to observe that individual and see what changes could be made to their husbandry. Furthermore, for keepers who are familiar with individual animals, it is achievable to measure the time spent in each phrase during the great call. It would be possible to apply some of the temporal patterns found in this paper to captive *Nomascus* gibbons and determine if the gibbon is calling "normally." These kinds of analyses could easily be applied without the need for complex acoustic analyses.

Our study provides preliminary results on the relationship between great call quality (i.e, acoustic and temporal features) and an individual gibbon's physical characteristics (i.e., age and weight). Age and weight were significant factors that affected an individual's singing, where heavier individuals were able to sing higher quality songs, while older individuals suffered costs to their song quality. Through understanding the detail and information carried in great calls, we will be able to extract more information from acoustic studies of wild gibbons. This insight would contribute to our knowledge about gibbon singing behavior and the information encoded, and how that can be applied to various conservation efforts. For example, if we can use a wild gibbon's singing behavior to understand their overall health, we may also gain insight on intergroup movements and transfers. Dispersing males may favor taking over territories with weaker, or older sounding males. Furthermore, this insight on the relationship between acoustic behavior and health status could help facilities during pre-release assessments, by informing decisions on which individuals are best suitable for release. In addition, post-release assessments, which are notoriously difficult to conduct for gibbons, could include analyses of acoustic and temporal parameters of songs. This is an ideal non-invasive alternative to the standard methods of radio collars or trapping to access vital information on the rehabilitated gibbon's status in the wild, especially since many times researchers may only be able to hear the gibbons without being able to sight them. Future studies should continue to research *Hylobatidae* vocals and increase our understanding of gibbon songs, and their potential for providing non-invasive measures of health and welfare during rehabilitation and post-release, as well as in-situ conservation.

COMPREHENSIVE REFERENCES

Awan, S. N. (2006). The aging female voice: acoustic and respiratory data. *Clinical linguistics & phonetics*, *20*(2-3), 171-180.

Barelli, C., Mundry, R., Heistermann, M., & Hammerschmidt, K. (2013). Cues to androgens and quality in male gibbon songs.*PLoS One*, *8*(12), e82748.

Bartlett, T. Q. (2006). The hylobatidae, small apes of Asia. In C.J. Campbell, A. Fuentes, K. C. Mackinnon, M. Panger & S. K. Bearder (Eds.), *Primates in Perspective* (274-289). Oxford: Oxford University Press.

Bee, M. A., Perrill, S. A., & Owen, P. C. (1999). Size assessment in simulated territorial encounters between male green frogs (*Rana clamitans*). *Behavioral Ecology and Sociobiology, 45,* 177-184.

Bennett, J. (1992). A glut of gibbons in Sarawak–is rehabilitation the answer?. *Oryx*, *26*(3), 157-164.

Brockelman, W. Y. and Schilling, D. (1984). Inheritance of stereotyped gibbon calls. *Nature, 312,* 634-636.

Brockelman, W. Y., & Srikosamatara, S. (1984). Maintenance and evolution of social structure in gibbons. In H. Preuschoft, D. J. Chivers, W. Y. Brockeman, & N. Creel (Eds.), *The Lesser Apes* (298-323). Edinburgh: University of Edinburgh Press.

Brockelman, W. Y., & Ali, R. (1987). Methods of Surveying and Sampling Forest Primate Populations. In C.W. Marsh & R.A. Mittermeier (Eds.), *Primates Conservation in the Tropical Rain Forest* (pages). New York: Alans R. Liss.

Buckley, C., Nekaris, K. A. I., & Husson, S. J. (2006). Survey of Hylobates agilis albibarbis in a logged peat-swamp forest: Sabangau catchment, Central Kalimantan. *Primates*, *47*(4), 327-335.

Campbell, C. O., Cheyne, S. M., & Rawson, B. M. (2015). Best Practice Guidelines for the Rehabilitation and Translocation of Gibbons. *Occasional Paper of the IUCN Species Survival Commission, 51,* 1-56.

Chatterjee, H. J. (2006). Phylogeny and biogeography of gibbons: a dispersal-variance analysis. *International Journal of Primatology*, *27*(3), 699-712.

Chatterjee, H. J. (2009). Evolutionary relationships among the gibbons: a biogeographic perspective. In S. Lappan. & D. Whittaker (Eds.), *The Gibbons* (pp. 13-36). Springer, New York, NY.

Cheyne, S. M. (2004). *Assessing rehabilitation and reintroduction of captive-raised gibbons in Indonesia.* (Doctoral dissertation, University of Cambridge).

Cheyne, S. M. (2009). Challenges and opportunities of primate rehabilitation—gibbons as a case study. *Endangered Species Research*, *9,* 159-165. Doi: 10.3354/esr00216

Cheyne, S. M. and Brulé, A. (2004). Adaptation of a captive-raised gibbon to the wild. *Folia Primatologica, 75*(1), 37-39.

Cheyne, S. M., Chivers, D. J., & Sugardjito, J. (2007). Covariation in the great calls of rehabilitant and wild gibbons (Hylobates albibarbis). *The Raffles Bulletin of Zoology*, *55*(1), 201-207.

Cheyne, S. M., Thompson, C. J. H., Phillips, A. C., Hill, R. M. C., & Limin, S. H. (2008). Density and Population Estimate of Gibbons (*Hylobates albibarbis*) in the Sabangau Catchment, Central Kalimantan, Indonesia. *Primates, 49*(1), 50-56.

Chivers, D. J., & Hladik, C. M. (1984). Diet and gut morphology in primates. In *Food acquisition and processing in primates* (pp. 213-230). Springer, Boston, MA.

Chivers, D. J. (1991). Guidelines for reintroductions: procedures and problems. *Symposium of the Zoological Society of London, 62,* 89-99.

Clutton-Brock, T. H., & Albon, S. D. (1979). The roaring of red deer and the evolution of honest advertising. *Behavior, 69,* 145-170.

Cowlishaw, G. U. Y. (1992). Song function in gibbons. *Behaviour*, *121*(1), 131-153.

Cunningham, C., & Mootnick, A. (2009). Gibbons. *Current Biology*, *19*(14), R543-R544.

Dallmann, R., & Geissmann, T. (2001). Individuality in the female songs of wild silvery gibbons (Hylobates moloch) on Java, Indonesia. *Contributions to Zoology*, *70*(1), 41-50.

Davies, N. B. & Halliday, T. R. (1978). Deep croaks and fighting assessment in toads *Bufo bufo. Nature, 274,* 683-685.

Ellefson, J. O. (1974). A natural history of white-handed gibbons in the Malayan peninsula. In D. Rumbaugh (Ed.), *Gibbon and siamang vol. 3* (1-136). Basel: S. Karger.

Endangered Primate Rescue Center (2016, February 12). *About Us.* Retrieved from www.eprc.asia.

Erb, W. M., Hodges, J. K., & Hammerschmidt, K. (2013). Individual, contextual, and age-related acoustic variation in simakobu (*Simias concolor*) loud calls. *PLoS One*, *8*(12), e83131

Ey, E., Hammerschmidt, K., Seyfarth, R. M., & Fischer, J. (2007). Age-and sex-related variations in clear calls of *Papio ursinus. International Journal of Primatology, 28,* 947-960.

Fan, P. F., Jiang, X. L., Lui, C. M., Lou, W. S. (2006). Polygynous Mating System and Behavioural Reason of Black Crested Gibbon (*Nomascus concolor jindongensis*) at Dazhizi, Mt. Wuliang, Yunnan, China. *Zoological Research, 27*(2), 216-220.

Fan, P. F., He, K., Chen, X., Ortiz, A., Zhang, B., Zhao, C., Li, Y. Q., Zhang, H. B., Kimock, C., Wang, W. Z., Groves, C., Turvey, S. T., & Roos, C. (2017). Description of a new species of Hoolock gibbon (Primates: Hylobatidae) based on integrative taxonomy. *American Journal of Primatology*, *79*(5), e22631.

Fischer, J., Kitchen, D. M., Seyfarth, R. M., & Cheney, D. L. (2004). Baboon loud calls advertise male quality: acoustic features and their relation to rank, age, and exhaustion. *Behavioral Ecology and Sociobiology, 56,* 140-148.

Fitch, W., & Hauser, M. D. (1995). Vocal production in nonhuman primates: acoustics, physiology, and functional constraints on “honest” advertisement. *American Journal of Primatology, 37*(3), 191-219.

Fitch, W. T., Neubauer, J., & Herzel, H. (2002). Calls out of chaos: the adaptive significance of nonlinear phenomena in mammalian vocal production. *Animal Behaviour, 63*(3), 407-418.

Fleagle, J. G. (1976). Locomotion and posture of the Malayan siamang and implications for hominoid evolution. *Folia primatologica, 26*(4), 245-269.

Geissmann, T. (1984). Inheritance of Song Parameters in the Gibbon Song, Analyzed in 2 Hybrid Gibbons (*Hylobates pileatus* X *Hylobates lar*). *Folia Primatologica, 42*(3-4), 216-235.

Geissmann, T. (2000). *Vietnam Primate Conservation Status Review 2000: Part 1: Gibbons*. Fauna & Flora International, Indochina Programme.

Geissmann, T. (2002). Duet-splitting and the evolution of gibbon songs. *Biological Reviews of the Cambridge Philosophical Society*, *77*(1), 57-76**.**

Gilhooly, L. J., Rayadin, Y., & Cheyne, S. M. (2015). A comparison of hylobatid survey methods using triangulation on Müller's gibbon (Hylobates muelleri) in Sungai Wain Protection Forest, East Kalimantan, Indonesia. *International Journal of Primatology*, *36*(3), 567-582.

Gittins, S. P. (1979). *The behaviour and ecology of the agile gibbon (hylobates agilis)* (Doctoral dissertation, University of Cambridge).

Gittins, S. P. (1980). Territorial behavior in the agile gibbon. *International Journal of Primatology*, *1*(4), 381-399.

Gosling, L. M. (1982). A reassessment of the function of scent marking in territories. *Ethology*, *60*(2), 89-118.

Goustard, M. (1979). Stereotype and plasticity of utterances in gibbons (*Hylobates concolor leycogenys*). *C R Seances Acaddemie Sciences D, 288,* 1615-1618.

Goustard, M. (1983). Organization of loud calls (territorial vocalizations) during puberty, in male gibbon (*Hylobates concolor gabriellae*). *C R Seances Acaddemie Sciences D*, *296*(15), 743-5.

Grafen, A. (1987). The logic of divisively asymmetric contests: respect for ownership and the desperado effect. *Animal Behaviour*, *35*(2), 462-467.

Haimoff, E. H. (1984a). Acoustic and organizational features of gibbon songs. In H. Preuschoft, D. J. Chivers, W. Y. Brockelman, & N. Creel (Eds.), *The lesser apes* (33-353). Edinburgh: Edinburgh University Press.

Haimoff, E. H. (1984b). The organization of song in the Hainan black gibbon (Hylobates concolor hainanus). *Primates, 25*(2), 225-235.

Haimoff, E. H., & Tilson, R. L. (1985). Individuality in the female songs of wild kloss' gibbons (*Hylobates klossii*) on Siberut Island, Indonesia. *Folia Primatologica*, *44,* 129-137.

Hammerschmidt, K., Freundstein, T., & Jurgens, U. (2001). Vocal development in squirrel monkey. *Behaviour, 138,* 1179-1204.

Hauser, M. D. (1993). The evolution of nonhuman primate vocalizations: effects of phylogeny, body weight, and social context. *The American Naturalist, 142*(3), 528-542.

Herring, M. J., Avdalovic, M. V., Quesenberry, C. L., Putney, L. F., Tyler, N. K., Ventimiglia, F. F., St. Georrge, J. A., & Hyde, D. M. (2013). Accelerated structural decrements in the aging female rhesus macaque lung compared with males. *American Journal of Physiology-Lung Cellular and Molecular Physiology*, *304*(2), L125-L134.

Inoue, M. (1988). Age gradations in vocalization and body weight in Japanese monkeys (*Macaca fuscata*). *Folia Primatologica, 51,* 76-86.

International Union for the Conservation of Nature. (2018, March 19). *Version 2017-3*. The IUCN Red List of Threatened Species. www.iucnredlist.org.

Kidney, D., Rawson, B. M., Borchers, D. L., Stevenson, B. C., Marques, T. A., & Thomas, L. (2016). An efficient acoustic density estimation method with human detectors applied to gibbons in Cambodia. *PloS one*, *11*(5), e0155066.

Koda, H., Lemasson, A., Oyakawa, C., Pamungkas, J., & Masataka, N. (2013). Possible role of mother-daughter vocal interactions on the development of species-specific song in gibbons. *PloS one*, *8*(8), e71432.

Konrad, R., & Geissmann, T. (2006). Vocal diversity and taxonomy of Nomascus in Cambodia. *International Journal of Primatology*, *27*(3), 713.

Lappan, S. (2007). Social relationships among males in multimale siamang groups. *International Journal of Primatology*, *28*(2), 369-387.

Maples, E. G., Haraway, M. M., & Hutto, C. W. (1989). Development of coordinated singing in a newly formed siamang pair (*Hylobates syndactylus*). *Zoo biology*, *8*(4), 367-378.

Marshall, J. T., & Sugardjito, J. (1986). Gibbon Systematics. In D. R. Swindler & J. Erwin (Eds.), *Comparative primate biology, volume 1* (137-185). New York: Smithsonian Institution (USA).

Merker, B., & Cox, C. (1999). Development of the female great call in *Hylobates gabriellae*: a case study. *Folia Primatologica*, *70*(2), 97.

Mitani, J. C. (1984). The behavioral regulation of monogamy in gibbons (*Hylobates muelleri*). *Behavioral Ecology and Sociobiology, 15*(3), 225-229.

Mitani, J. C. (1985). Gibbon song duets and intergroup spacing. *Behavior, 92,* 59-96.

Mitani, J. C. (1987). Territoriality and monogamy among agile gibbons (*Hylobates agilis*). *Behavioral Ecology and Sociobiology,20*(4), 265-269.

Mootnick, A. R., & Fan, P. F. (2011). A comparative study of crested gibbons (*Nomascus*). *American Journal of Primatology*, *73*(2), 135-154.

Oyakawa, C., Koda, H., & Sugiura, H. (2007). Acoustic features contributing to the individuality of wild agile gibbon (Hylobates agilis agilis) songs. *American Journal of Primatology, 69*(7), 777-790.

Palombit, R. A. (1994). Extra-pair copulations in a monogamous ape. *Animal Behaviour*, *47*(3), 721-723.

Quanjer, P. H., Stanojevic, S., Cole, T. J., Baur, X., Hall, G. L., Culver, B. H., Enright, P. L., Hankinson, J. L., Ip, M. S. M., Zheng, J., & Stocks, J. (2012). Multi-ethnic reference values for spirometry for the 3–95-yr age range: the global lung function 2012 equations. *European Respiratory Journal*, *40*(6), 1324-1343.

R Development Core Team. 2008. *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Raemaekers, J. J., Raemaekers, P.M., & Haimoff, E.H. (1984). Loud Calls of the Gibbon (*Hylobates lar*): Repertoire, organisation, and context. *Behavior, 91*, 146-189.

Raemaekers, J. J. & Raemaekers, P. W. (1985). Long-range vocal interactions between groups of gibbons (*Hylobates lar*). *Behavior, 95,* 26-44.

Reby, D., & McComb, K. (2003). Anatomical constraints generate honesty: acoustic cues to age and weight in the roars of red deer stags. *Animal Behavior*, *65*, 519-530.

Reichard, U. H., & Barelli, C. (2008). Life history and reproductive strategies of Khao Yai Hylobates lar: implications for social evolution in apes. *International Journal of Primatology*, *29*(4), 823-844.

Roos, C., & Geissmann, T. (2001). Molecular phylogeny of the major hylobatid divisions. *Molecular phylogenetics and evolution*, *19*(3), 486-494.

Roos, C., Thanh, V. N., Walter, L., & Nadler, T. (2007). Molecular systematics of Indochinese primates. *Vietnamese Journal of Primatology, 1*(1), 41-53.

Ruppell, J. C. (2010). Vocal diversity and taxonomy of Nomascus in central Vietnam and southern Laos. *International Journal of Primatology*, *31*(1), 73-94.

Ryan, M. J., & Brenowitz, E. A. (1985). The role of body size, phylogeny, and ambient noise in the evolution of bird song. *The American Naturalist, 126,* 87-100.

Sanvito, S., Galimberti, F., & Miller, E. H. (2007). Vocal signaling of male southern elephant seals is honest but imprecise. *Animal Behavior, 73,* 287-299.

Sataloff, R. T., Rosen, D. C., Hawkshaw, M., & Spiegel, J. R. (1997). The aging adult voice. *Journal of Voice, 11*(2), 156-160.

Simpson, G. G. (1945). The principles of classification and a classification of mammals. *Bull. Amer. Museum Nat. History.*, *85*.

Smith, J. M., & Harper, D. (2003). *Animal signals*. Oxford University Press.

Tenaza, R. R. (1976). Songs, choruses and countersinging of Kloss' gibbons (*Hylobates klossii*) in Siberut Island, Indonesia. *Z. Tierpsychol., 40*, 37-52.

Tenaza, R. R. (1985). Songs of hybrid gibbons (*H. lar* x *H. muelleri*). *American Journal of Primatology, 8,* 249-253.

Terleph, T. A., Malaivjitnond, S., & Reichard, U.H. (2015). Lar Gibbon (*Hylobates lar*) Great Call Reveals Individual Caller Identity. *American Journal of Primatology, 77,* 811-821.

Terleph, T. A., Malaivijitnond, S., & Reichard, U. H. (2016). Age related decline in female lar gibbon great call performance suggests that call features correlate with physical condition. *BMC evolutionary biology*, *16*(1), 4.

Thinh, V. N., Mootnick, A. R., Geissmann, T., Li, M., Ziegler, T., Agil, M., Mooisson, P., Nadler, T., Walter, L., & Roos, C. (2010a). Mitochondrial evidence for multiple radiations in the evolutionary history of small apes. *BMC Evolutionary Biology*, *10*(74), 1-9.

Thinh, V. N., Mootnick, A. R., Thanh, V. N., Nadler, T., & Roos, C. (2010b). A new species of crested gibbon from the central Annamite mountain range. *Vietnamese Journal of Primatology, 4,* 1-12.

Thinh, V. N., Rawson, B., Hallam, C., Kenyon, M., Nadler, T., Walter, L., & Roos, C. (2010c). Phylogeny and distribution of crested gibbons (genus Nomascus) based on mitochondrial cytochrome b gene sequence data. *American Journal of Primatology, 72*(12), 1047-1054.

Thinh, V. N., Hallam, C., Roos, C., & Hammerschmidt, K. (2011). Concordance between vocal and genetic diversity in crested gibbons. *BMC evolutionary biology*, *11*(1), 36.

Thorpe, W. H. (1961). Bird-song: the biology of vocal communication and expression in birds. University Press.

Titze, I. R. (1989). On the relation between subglottal pressure and fundamental frequency in phonation. *The Journal of the Acoustical Society of America*, *85*(2), 901-906.

Titze, I. R., & Riede, T. (2010). A cervid vocal fold model suggests greater glottal efficiency in calling at high frequencies. *PLoS Computational Biology*, *6*(8), e1000897.

Trivers, R. (1972). *Parental investment and sexual selection* (Vol. 136, p. 179). Cambridge, MA: Biological Laboratories, Harvard University.

Ulijaszek, S. J. (1992). Human energetics methods in biological anthropology. *American Journal of Physical Anthropology*,*35*(S15), 215-242.

Van Schaik, C. P., & Dunbar, R. I. M. (1990). The evolution of monogamy in large primates: a new hypothesis and some crucial tests. *Behaviour*, *115*(1), 30-61.

Vannoni, E., & McElligott, A. G. (2008). Low frequency groans indicate larger and more dominant fallow deer (Dama dama) males. *PloS one*, *3*(9), e3113.

Vehrencamp, S. L. (2000). Handicap, index, and conventional signal elements of bird song. In G. Rosenqvist, T. Amundsen, & Y. Esprnark (Eds.), *Animal signals: signalling and signal design in animal communication*, 277-300.

Wahba, W. M. (1983). Influence of Aging on Lung Function-Clinical Significance of Changes from Age Twenty. *Anesthesia & Analgesia*, *62*(8), 764-776.

Whittaker, D. J., & Lappan, S. (2009). The diversity of small apes and the importance of population-level studies. In S. Lappan. & D. Whittaker (Eds.), *The Gibbons* (pp. 3-10). Springer, New York, NY.

Wilden, I., Herzel, H., Peters, G., & Tembrock, G. (1998). Subharmonics, biphonation, and deterministic chaos in mammal vocalization. *Bioacoustics*, *9*(3), 171-196.

Zihlman, A. L., Mootnick, A. R., & Underwood, C. E. (2011). Anatomical contributions to hylobatid taxonomy and adaptation. *International journal of primatology*, *32*(4), 865-877.