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## Comparisons of Captive Gibbons' (Hylobatidae) Intrapair Behaviors Indicative of the Pair Bond

Samantha Jones

Central Washington University, [samantha.jones2@cwu.edu](mailto:samantha.jones2@cwu.edu)

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COMPARISONS OF CAPTIVE GIBBONS' (HYLOBATIDAE)  
INTRAPAIR BEHAVIORS INDICATIVE  
OF THE PAIR BOND

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A Thesis

Presented to

The Graduate Faculty

Central Washington University

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In Partial Fulfillment

of the Requirements for the Degree

Master of Science

Primate Behavior and Ecology

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by

Samantha Schwab Jones

May 2018

CENTRAL WASHINGTON UNIVERSITY

Graduate Studies

We hereby approve the thesis of

Samantha Schwab Jones

Candidate for the degree of Master of Science

APPROVED FOR THE GRADUATE FACULTY

\_\_\_\_\_

\_\_\_\_\_

Dr. Lori K. Sheeran, Committee Chair

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\_\_\_\_\_

Dr. Sofia Blue

\_\_\_\_\_

\_\_\_\_\_

Gabriella Skollar

\_\_\_\_\_

\_\_\_\_\_

Dean of Graduate Studies

## ABSTRACT

### COMPARISONS OF CAPTIVE GIBBONS' (HYLOBATIDAE) INTRAPAIR BEHAVIORS INDICATIVE OF THE PAIR BOND

By

Samantha Schwab Jones

May 2018

I aimed to better understand captive gibbons' pair bonds by studying behaviors that may indicate the relationship's quality. I completed this research at The Gibbon Conservation Center (GCC) in Santa Clarita, California and observed four species: eastern hoolock (*Hoolock leuconedys*), Javan (*Hylobates moloch*), and pileated (*Hylobates pileatus*) gibbons; and a siamang (*Symphalangus syndactylus*). I conducted research from 19 April- 29 May 2017 using scan and focal animal sampling. I focused on nine pairs, and recorded gibbons' grooming bouts, affiliative/agonistic/play behaviors, mating, behavioral synchrony, locomotion, and proximity. Previous researchers focused on duetting in relation to pair bonding more than other qualities of social behavior. The opportunity to study four different species at the same time adds new knowledge to gibbon social behavior. Learning more about captive gibbons' social behavior, in particular pair bonding quality, could help conservation efforts, which is important most gibbons are Endangered. Rehabilitation and reintroduction programs are part of conservation efforts for helping to rebuild gibbon populations in the wild. Success of reintroduction into the wild in rehabilitation and reintroduction programs is measured by survival post-release, maintenance of the pair bond, and reproduction and survival of offspring. If the pairs are successfully cohabiting at the GCC, understanding behaviors

indicating successful bonding may help predict survival once released. My results showed that pairs without offspring were in proximity significantly less and had significantly less occurrences of grooming bouts and affiliative behaviors. I found newly established pairs to be in proximity and behavioral synchrony significantly less than middle and long-term pairs. Newly established pairs had significantly more occurrences of affiliative and play behaviors than middle and long-term pairs. The mixed species pair was significantly in the most pair bonding behaviors. The hoolock pairs had more occurrences and were in grooming bouts significantly longer than other species. My results indicated that pair bonding behaviors might not be mutually exclusive of each other, so more than one behavior needs to be studied when trying to understand these complex social behaviors. I suggest further research into gibbon pair bond behaviors is needed to help staff at rehabilitation and reintroduction centers make decisions about gibbons' release.

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## CHAPTER I

### INTRODUCTION

The scientific objective of my research was to better understand captive gibbon pair bonds by identifying behaviors that indicate the quality of the pair bond. Research on gibbons has focused considerably on the pair bond since they are considered monogamous. I studied a pair from three out of the four gibbon genera: eastern hoolock (*Hoolock leuconedys*), Javan (*Hylobates moloch*), and pileated (*H. pileatus*) gibbons, and siamangs (*Symphalangus syndactylus*). I studied these species at The Gibbon Conservation Center (GCC) in Santa Clarita, California from 19 April- 29 May 2017. Continuous focals, scans, and ad libitum sampling are the observational data collection methods I implemented. I collected data by rotating direct observation and video recording, with a rotation between direct observation and video recording. My study includes a variety of behaviors.

In gibbon behavioral research, the main focus has been on duetting and how it correlates to the quality of a pair bond, but I argue here that it is important to explore a wide range of behaviors to assess pair bond quality, as there may be more to the stability of a pair bond than the mates' duets. I studied affiliative/agonistic/play behaviors, grooming bouts, proximity, behavioral synchrony, mating, and locomotion, and explored how these behaviors are also indicative of pair bond quality. Social bonds between adults can be assessed by rates of affiliative interaction, proximity scores, and a measure of reciprocity between two individuals (Fuentes, 2000; Hinde, 1977).

Assessing these behaviors and establishing that they are indicative of the pair bond will help conservation efforts for gibbons. Most gibbon species are Endangered

mainly due to poaching, deforestation, and the illegal pet trade (Smith, 2011). Rehabilitation and reintroduction programs have been used in efforts to conserve endangered species (Kleiman, 1989; Smith, 2011). The staff of these centers plans to move gibbons back into the forest in their natural social organizations, which comprises of the bonded pair. Reintroduction success is measured by gibbons' survival post-release, maintenance of the pair bond, and reproduction and survival of offspring (Cheyne, 2009). The quality of the pair bond is important in these programs because pair bond maintenance is an important predictor of a gibbons' success in being released. In order for a reintroduction to be successful the gibbons have to stay in the pair and be able to produce offspring. Rehabilitation and reintroduction programs will aid the growth of the populations that are becoming extinct by reintroducing successful pairs back into the wild. These programs can encounter difficulty producing a successful pair once in the wild. Part of this is from a lack in the literature on understanding behaviors that maintain a pair bond (Cheyne, 2004). Information on the behaviors indicative of a strong pair bond will be useful to conservation efforts because it may increase successful reintroductions.

## CHAPTER II

### LITERATURE REVIEW

#### **Gibbon Ecology**

Gibbons are small, arboreal, apes classified in the Hominoidea superfamily with other apes and humans (Kim, Carbone, Becquet & Mootnick, 2011). They are monogamous, but some extra-pair copulations have been observed (Reichard, 1995; Reichard & Sommer 1997; Reichard, 2003). Gibbons are further classified in the family Hylobatidae and are the only smaller bodied apes. Hylobatidae is a separate branch from the large bodied apes (chimpanzees, orangutans, bonobos and gorillas [Zihlman, Mootnick & Underwood, 2011]). Taxonomists recognize four gibbon genera: *Hylobates*, *Hoolock*, *Nomascus*, and *Symphalangus* (Zihlman et al., 2011). Primatologists debate the number of gibbon species, but there are at least 19 known species (Fan et al., 2017). This number sometimes changes, for example with the recent discovery of the new hoolock species “Skywalker” (Fan et al., 2017).

Gibbons inhabit forests in East, South, and Southeast Asia (Kim et al., 2011). Gibbons are frugivorous, and these forests contain the ripe fruit gibbons eat, with 58% of their diet comprised of fruit (Bartlett, 2007). They also eat leaves, insects and flowers to supplement their diet (Bartlett, 2007). They are arboreal and move rapidly by their locomotion style referred to as brachiation, which is one distinctive feature of gibbons. Brachiation is characterized by a pendulum-like swing by their arms (Barlett, 2007). Compared to larger bodied apes, gibbons have a larger cerebellum (Butler & Suddendorf, 2014), which helps in their balance and coordination and is integral to brachiation.

Gibbons are also distinguished from other apes by their complex vocal patterns. All gibbons produce loud and long vocal bouts, and in most species they combine species-specific and sex-specific vocals to create duets (Geissmann & Orgeldinger, 2000). Gibbons are the only apes to duet with a mate. Duets can last up to 30 minutes and usually occur in the mornings (Geissmann & Orgeldinger, 2000). The duets vary in sound across the different species of gibbon. Duets are related to mate protection of females by the males (Bartlett, 2007; Palombit 1996; Palombit 1999). Territory defense is also a function of the gibbon duet. Fan, Xiao, Huo & Jiang (2009) found a positive correlation between singing near sleep trees and the distribution of food resources in black crested gibbons (*Nomascus concolor jingdongensis*). Gibbons' average home range is 40 ha and their territory makes up about 82% of this (Bartlett, 2007). Gibbons are territorial within their nuclear families and will defend their home range. Gibbons are considered territorial because intergroup encounters are aggressive in nature (Smith, 2011). In agile gibbons (*Hylobates agilis*), females defend their territory along with support from their mate (Mitani, 1987).

Across all gibbon species, the gestation length is around 7 months (Geissmann, 1991). Females usually give birth to only one infant at a time. *Hylobates* and *Hoolock* reach sexual maturity at 6-8 years (Geissmann, 1991; Tilson, 1979; Tilson, 1981) while *Symphalangus* become sexually mature at around 8-9 years of age (Chivers, 1974). *Nomascus* may start breeding as early as 4 years old (Geissmann 1991). Gibbons start leaving their nuclear families once they reach sexual maturity. The same sexed parent forces the young to leave to find a new territory and a mate (Brockelman, Reichard,

Treesucon & Raemakers, 1998). Gibbons live between 20-40 years in the wild and in captivity (Palombit 1995).

### **Evolutionary History**

Around 18 million years ago, gibbon ancestors split off from the line leading to other apes (Butler & Suddendorf, 2014). The only certain ancestors of the hylobatids are from Asia and date to the Miocene and Pleistocene epochs (Ortiz, Pilbrow & Villamil, 2015). *Yuanmoupithecus* is from the late Miocene and is considered a stem hylobatid, while *Bunopithecus sericus*, another ancestor, is from the Pleistocene epoch (Ortiz et al., 2015).

### ***Hoolock leuconedys***

Primatologists recognize two hoolock species: eastern, *Hoolock leuconedys*, and western, *H. hoolock* (Peng-Fei, Wen, Sheng, Huai-Sen, Tian-Can & Ru-Tao, 2011). Recently, researchers found a new subspecies of western hoolock (Fan et al., 2017). Both males and females are black until the females reach maturity when they turn a buff color (Mootnick, Baker & Nadler, 2006). My study focuses on the eastern hoolock. Eastern hoolocks are found in northeast India, Myanmar, southwestern Yunnan, Lohit District, and Arunachal Pradesh (Mootnick et al., 2006). Conservation experts consider the eastern hoolock Vulnerable (Brockelman and Geissmann, 2008), mainly due to poaching and habitat loss.

### ***Hylobates moloch***

In the Javan or silvery gibbon (*Hylobates moloch*) both sexes are silvery gray with long dense hair and therefore, they are neither sexually dimorphic nor sexually dichromatic (Mootnick et al., 2006). They are endemic to the island of Java in Indonesia

(Kim, Lappan & Choe, 2011). Javan gibbons are considered Endangered with fewer than 2,500 adult individuals left (Andayani, Brockelman, Geissmann, Nijman & Supriatna, 2008). These gibbons are Endangered because of human population growth, which in turn, causes deforestation. Because gibbons are territorial, they rarely move when their habitat is destroyed (Kim et al., 2011). Javan gibbons have a diet similar to other gibbon species: they mostly eat fruit followed by leaves, flowers, and insects (Kim et al., 2011). Javan and Kloss (*H. klossi*) gibbons are the only species that sing separate male and female solo songs instead of duets (Geissmann, 1993; Geissmann and Nijman, 2000; Dallmann and Geissmann, 2001).

### ***Hylobates pileatus***

In *Hylobates pileatus*, the pileated gibbon, adult females are silver-buff with a black throat and triangle on the chest, while adult males are black with a white brow around the face; infant males are buff and start to change color around 10-12 months of age, and females infants remain the same color throughout life (Mootnick et al., 2006). The species is distributed in Cambodia and southeast Thailand (Brockleman, 1975; Brockleman and Gittins, 1984; Marshall and Sugardjito, 1986; Phoonjampa and Brockleman, 2008). They are classified as Endangered due to deforestation and hunting (Brockelman, Geissmann, Timmins & Traeholt, 2008).

### ***Symphalangus syndactylus***

Among the gibbons, the siamangs (*Symphalangus syndactylus*) are the largest and have a throat sac (Mootnick et al., 2006). These gibbons are sexually dimorphic and males are larger than females (Mootnick et al., 2006). They inhabit Sumatra and northwest Malay Peninsula (Mootnick et al., 2006). The siamang is Endangered and the

population has decreased 50% over the last 40 years (Nijman & Geissman, 2008).

Siamangs incorporate a larger amount of leaves in their diet than do other gibbon species (Fischer & Geissman, 1990). Gittins & Raemaekers (1980) found that due to this diet they are generally have more socially cohesive groups. Siamangs are the only gibbon species in which the adult male provides parental care for the infant (Lappan, 2008). The duet of the siamang is also more complex than are those of the other gibbon species (Geissmann & Orgeldinger, 2000).

### **Pair Bonds**

Gibbons are monogamous apes that live in mated adult pairs with one to four offspring (Mitani, 1984). Since they live in pair bonds, an area of focus for researchers has been on behaviors that maintain the pair bond. Fuentes (2002) describes the pair bond as “a long term (over one year) association between two non-kin adults characterized by a set of partner specific affiliative behaviors and there is a closer spatial relationship between the pair” (p. 969). Most of the research published on gibbon pair bonding has explored duetting of pairs as an indicator of pair bond strength. Gibbon song bouts help form and strengthen the pair bond and have a role in intergroup communication that involves territory defense (Cowlshaw, 1992; Dooley and Judge, 2007; Geissmann & Orgeldinger, 2000; Raemaekers & Raemakers, 1985; Mitani, 1984). Fan et al (2009) found mated black crested gibbons to produce more calls and they were more in synchrony when in closer proximity. Geissmann & Orgeldinger (2000) found a positive correlation between pair bonding and duetting in siamangs. Past research shows that duetting is an indicator of pair bond quality, but there are other behaviors to consider that might reflect the pair bond strength.

Social bonds between adults can be assessed by rates of affiliative interaction, proximity scores, and a measure of reciprocity between two individuals (Fuentes, 2000; Hinde, 1977). Affiliative behaviors consist of sociable actions, such as reconciliation and reciprocation with an exchange of grooming (Puga-Gonzalez, Hildenbrandt & Hemelrijk, 2009). Other affiliative behaviors are embracing and being in physical contact with another individual (Palmobit, 1996; Sierra, 2013). Proximity can also be used as an indicator to assess the strength of gibbon pair bonds (Fan et al, 2009). Geissmann and Orgeldinger (2000) found negative correlation between duetting activity and distance between siamang mates.

Grooming is another aspect of affiliative behavior. In a study of chimpanzees (*Pan troglodytes*), Mitani (2009) found that males with the most stable bonds groomed each other more frequently. The number of years the males were bonded was positively correlated with grooming. Mitani (2009) also found strong social bonds were maintained by close proximity in chimpanzees. Grooming and proximity were also determined to be measures of strength in social relationships in other non-human primates such as baboons (*Papio cynocephalus*) (Silk, Altmann & Alberts, 2006). Affiliative/agonistic behaviors, grooming, proximity and behavioral synchrony may also be aspects of pair bond behaviors to examine in studies of gibbon relationships. Therefore, I examined these behaviors, as well as duets, as indicators of the pair bond quality in gibbons.

Little agonistic behavior has been observed in some species of gibbon between pairs. Palmobit (1996) found very little agonistic behavior, like open mouth displays, between the members of siamang and white-handed gibbon (*Hylobates lar*) mated pairs with no direct aggressive behavior.

There has not been a long-term field study specifically on pairs bonds in gibbons. Freed (1987) looked at the long-term pair bond of tropical house wrens and studied the dynamics of pair bonds over a long period of time to better understand them. A similar study should be conducted in gibbons to understand long-term pair bonds.

### **Rehabilitation and Reintroduction**

Most gibbon species are Endangered due to deforestation, poaching and the illegal pet trade (Smith, 2011). These non-human primates are in need of conservation support. Conservation efforts on behalf of gibbons can focus on both rehabilitation and reintroduction of wild-born/captive-raised populations and the protection of wild populations (Cheyne, 2004). Rehabilitation and reintroduction programs have been used for some time to help conserve endangered species (Kleiman, 1989; Smith, 2011). Reestablishing gibbons back into the wild through rehabilitation and reintroduction centers may aid the growth of the populations that are becoming extinct.

Some gibbon rehabilitation and reintroduction programs show that pairs do not persist after they are released back into the wild. Reintroduction success is measured by gibbons' survival post-release, maintenance of the pair bond, and reproduction and survival of offspring (Cheyne, 2009). The staff of Kalaweit Gibbon Rehabilitation Centre have established a pair association index, and they test this before and after gibbon pairs are released to see if members of the pair remain together. Cheyne and colleagues were not able to measure the pair association because once released, the members of the pair separated (Cheyne, Chivers & Sugardjito, 2008). They suggest further studies to assess the pair association as a good marker for likelihood of successful reintroduction into the wild.

The quality of the pair bond is important in these programs. The failures of rehabilitation and reintroduction programs arise from a lack of understanding about social, behavioral, and nutritional needs of the gibbons (Cheyne, Campbell & Payne, 2012). It is important to study pair bonding in captive gibbons to understand what behaviors contribute to the quality of a pair bond, and the behaviors that maintain a gibbons' pair bond are not fully understood (Cheyne, 2004). Information on the behaviors indicative of a strong pair bond from my study are useful to rehabilitation and reintroduction programs as it may increase reintroduced gibbons' survival and reproduction. Also, my study investigated mixed species enclosures and adds more literature to the potential benefits of this type of housing. Leonard et al. (2010) found that captive mixed species groups could have socially enriching effects that are beneficial to welfare as long as these enclosures are carefully designed and the environment is managed.

### **Hypothesis and Predictions**

Previous literature has shown that behavioral synchrony, proximity, grooming and affiliative behaviors are indicators of pair bond strength (Fan et al., 2009; Fuentes, 2000; Geissman & Orgeldinger, 2000; Hinde, 1977; Mitani, 2009; Silk, Altmann & Alberts, 2006). My hypothesis was that pairs' behaviors of pair bonds would be different based on the number of years together, species, and presence of offspring. I predicted that behaviors indicative of pair bonds would differ between species. I predicted that pairs who have been together longer and have offspring would show more pair bonding behaviors including: affiliation, behavioral synchrony, grooming and proximity.

## CHAPTER III

### METHODS

#### **Study Subjects and Site**

I studied four different species of gibbons: eastern hoolock, Javan, and pileated gibbons, and a siamang, all housed at The Gibbon Conservation Center (GCC) in Santa Clarita, California. The purpose of The Gibbon Conservation Center is “To promote the conservation, study and care of gibbons through public education and habitat reservation” (<https://www.gibboncenter.org>). Alan Mootnick founded this center in 1976, and these gibbons came from zoos or were born on site. This center houses 41 individuals, and I focused on nine pairs: the mixed species pair consisting of a hoolock and a siamang, and two pileated, three Javan, and four hoolock gibbon pairs (Table 1). I observed affiliative/agonistic/play behaviors in these pairs as well as locomotion, mating, behavioral synchrony, grooming bouts, and proximity. I received approval from Central Washington University’s Institutional Animal Care and Use Committee (IACUC) before I began my data collection (protocol number is A121603).

Table 1

*Study Subjects*

Enclosure	Species	Sex/Age	Offspring	Years at GCC	Years together	Rearing History
1	Javan	M-Ivan(43) F-Chloe(27)	1	21 22	5	Human/peer Parents
3	Javan	M-Perak(16) F-Simpang(17)	1	8 8	8	Parents Parents
5	Pileated	M-Domino(22) F-Tuk(24)	3	9 18	10	Parents Parents
6	Hoolock	M-Win Bo(14) F-Chan Thar(11)	0	6 6	7	Human/peer Human/peer
7	Hoolock	M-U Maung Maung(16) F-Hmawe Ni (13)	0	14 6	5	Human/peer Human/peer
9	Pileated	M-Truman(14) F-Violet(8)	0	14 8	2	Parents Parents
10	Hoolock	M-Kin Maung Win(10) F-Betty(18)	0	10 17	5	Human/peer Human/peer
11	Hoolock	M-Arthur(21) F-Phy Gyi (14)	3	17 6	6	Human/peer Human/peer
14	Hoolock Siamang	M-U Myint Swe(8) F-Marlow(12)	0	8 12	2	Human/peer Parents

**Data Collection**

I collected data from 19 April- 29 May 2017. I observed the gibbons from 0600 h to 1600 h, Monday-Friday, with half days on the weekends. I was not always able to follow this schedule due to cleaning schedules, my volunteer work, and weather. GCC is open to the public on Saturdays and Sundays. The presence of visitors on these days affected the gibbons' behaviors, so I did not collect data then. I used scan sampling, continuous focal animal sampling, and ad libitum observations (Altmann, 1974) to collect the behaviors from an ethogram. I used a video camera on a separate enclosure than the one I was observing, which helped me to efficiently collect more data. I used <https://www.random.org/lists/> (Haahr, 1998) to make sure rotation occurred between the

individuals I was visually observing and the ones I recorded via video. I had Gabriella Skollar, the director of the GCC, make sure I could positively ID my study individuals. I verbally identified each individual in my study enclosures with Gabriella Skollar present.

I collected 10-minute focal animal samples with a randomized schedule created on <https://www.random.org/lists/> (Haahr, 1998). I did not have a randomized lunchtime due to volunteer hours. I recorded every time the focal individual's behavior changed. While making sure the focals were random, I did not collect data on both members of the pair within 30 minutes of each other as this could skew the results. I used 5 minutes between each focal to move between enclosures and set up the video camera on a separate enclosure. I only coded half of my videos and I used the same randomizer for this as I did for my focal schedule. I have the videos saved by individual and day, so I used the randomizer to determine which individual videos to code.

I recorded affiliative/agonistic/play behaviors, mating, grooming, and locomotion during focal samples (Table 2). Affiliative behaviors included individuals being in contact with one another, without grooming, embracing and approaches (Palombit, 1996). Palombit (1996) defined embrace as "stationary ventral-ventral contact, where one individual put its arm around another" (p.326). Agonistic behaviors included open mouth display, bare teeth, slapping and hostile presenting (Mootnick et al., 2006; Palombit, 1996; Smith, 2011). Mootnick et al. 2006 found hostile presenting "consists of anogenital display directed towards humans or conspecifics" (p.814). Play behaviors included nonaggressive rolling, tumbling, and chasing other individuals (Palombit, 1996; Sierra, 2013). For all these behaviors, I collected counts and recorded the behaviors' durations during focals. Most of the behaviors in my ethogram I adapted from other gibbon studies.

Due to the other ethograms being non-comprehensive, in some areas I used my own descriptions from knowledge I gained through reading about gibbon behaviors.

Geissman & Orgeldinger (2000) recorded gibbons' duets during focals by recording the occurrence and duration of the songs. I was going to use this method to record data on duets, but I could not accurately collect data on duetting due to multiple species at different enclosures all singing at once, as well as gibbons' movements during these times were too fast for me to accurately record. Grooming bouts consisted of two or more individuals, and I considered them to have ended if there was no contact for more than 1 minute (Barelli, Reichard & Mundry, 2011). I noted directionality of grooming and changes between individuals; I considered these as within a single grooming bout, provided there were no interruptions that lasted over a minute. I collected ad libitum observations any time two individuals were mating.

I collected data on proximity and behavioral synchrony during scans. Scans lasted for 5 seconds, which allowed me enough time to see every individual in the enclosure. I completed a scan every minute during focals for proximity data. I scored two individuals as proximate if they were  $< 1$  m from another individual and not proximate if they were  $\geq 1$  m (Palombit, 1996), a meter is approximately a gibbon's arm length. I observed individuals in the enclosure in relation to proximity. To collect data on behavioral synchrony, I used methods adapted from Geissmann & Orgeldinger (2000). I defined behavioral synchrony as any activity performed in unison (King & Cowlshaw, 2009). I used behaviors from my ethogram to mark if the pairs were in unison during the first, middle, and last scan of each focal.

Table 2

*Ethogram.*

Behavior	Description	Code	Source
Feeding <sup>^</sup>	Individual is handling and ingesting food (State)	FE	
Grooming*	Autogrooming, individual is (manipulating, stroking, or picking through own hair) (State)	G	Palombit, 1996
Initiate allogrooming*	Focal animal approaches and initiates (manipulation, stroking, or picking through hair) of another individual (State)	GIA	Palombit, 1996
Receive allogrooming*	Focal animal receives (manipulation, stroking, or picking through hair) from another individual (State)	GRA	Palombit, 1996
Resting*	Sitting or reclining, eyes closed or open (State)	R	Gronquist, 2013
Locomotion *	Moving from one point to another by bipedal walking, brachiating or climbing (State)	L	Sierra, 2013
Play*	Nonaggressive rolling, tumbling or chasing with other individual (State/Event)	P	Sierra, 2013
Agonistic*	Open mouth display, bare-teeth, hostile presenting or slapping (State/Event)	AG	Mootnick et al., 2006 Palombit, 1996 Smith, 2011
Mating <sup>^</sup>	Copulation between any 2 individuals (State/Event)	M	
Duet <sup>^</sup>	Synchronized vocalizations between any individuals (State)	D	
Affiliative*	Approach, embrace, touch or in contact with another group member (State/Event)	AF	Palombit, 1996 Sierra, 2013
Other vocals <sup>^</sup>	Any vocal other than duets (State)	OV	
Other <sup>^</sup>	Any other behavior not listed (State/Event)	O	

*Note:* <sup>^</sup>=my own \* =adapted from source

## **Analysis**

I analyzed my results in the program R with version 1.1.442 (R core team, 2018). The main focus of my study was  $N=18$  individuals, but if they had offspring in the enclosure I recorded their interactions as well. The 18 individuals made up nine pairs: four hoolock, two pileated, two Javan, and one mixed species gibbon pair. For the analysis of my data, I used the generalized linear model (GLM) and the generalized linear mixed model (GLMM), as these were the best methods to analyze my data, since the data were not normally distributed and I had numerous explanatory and predictor variables. When studying pair bond behaviors different factors influence their behavior. These models can account for that, with being able to have fixed and random effects. I used pairs as the random effect and species, offspring, and years together as fixed effects. To work with the GLM and GLMM, I broke the pair's years together down into three categories: newly established, middle, and long-term. Newly established consisted of two pairs that had been together for 1-2 years, middle was four pairs that had been together for 5-6 years, and long-term consisted of 3 pairs that had been together 7, 8, or 10 years.. I randomly gave the pairs a number 1 through 9 to make adding these data into the models easier. I had a model for each of the following behaviors: grooming count, grooming duration, affiliative count, affiliative duration, play count, play duration, mating count, mating duration, proximity and behavioral synchrony. I could not analyze agonistic behaviors because I observed too few agonistic behaviors to include in the analysis.

I used the GLMM models for grooming and affiliative counts, proximity, and behavioral synchrony data. I used the GLM models were used for all other behaviors. For

the GLMM models for grooming and affiliative behavior counts, I used the Poisson Distribution with the log = link function. This distribution describes the probability that a certain number of events occur in a block of time (Zurr, Ieno, Walker, Saveliev and Smith, 2009). The Poisson Distribution works for integers only, and I used it for my count data when I could. I met all of the assumptions for the Poisson Distribution. For proximity and behavioral synchrony GLMM models, I used the Binomial Distribution with the log = logit function. For all durations and the count behaviors that would not work in the GLMM models I used the GLM.

Following Zurr et al. (2009) I began the process of running these models in R. I ran all tests with alpha = 0.05. For all of the models, I first looked for outliers in my variables with Cleveland dot plots and boxplots in R. There were some outliers, but not large enough to need to transform the variables. I then explored my explanatory variables to see if there was any collinearity between them. This is a high correlation between explanatory variables and can lead to inaccurate results (Zurr et al., 2009). This is an issue because collinear variables contain the same information and cannot be disentangled and would skew my results. I used pair plots to look for collinearity and all of my explanatory variables were under 0.6 for correlation, which means none of them were collinear. Next, I checked to make sure there was no homogeneity between variables. I used boxplots for this. I tested my models without pairs as the random effect and then with pairs to see which was the best model. I used the Akaike's Information Criterion scores to test this, and I used the model with the lowest score. In all cases, the model with the lowest score was the model with the random effect. I graphed my

residuals to see if they were normal and tried to transform the residuals, but not all would transform.

The next step was to use Bartlett tests to see if there was homogeneity between variances. There was, and I attempted to run alternate variance structures. None of these worked for my variables, so I went forward using my models, even though they do not meet all of the assumptions. Once I completed my models and observed significant results, I performed a Post Hoc Tukey test. This analysis further shows significance between the different variables in my models. When reading these Post Hoc Tukey test tables it is important to understand how to interpret them. For example, in the grooming count table, if one were investigating the Javan-Hoolock cell one would look at the column next to this titled “estimate”. If the estimate is a negative number then the Javan gibbons groom less than the hoolocks. If the estimate is a positive number then the Javan gibbons groom more than the hoolocks.

## CHAPTER IV

### RESULTS

I observed all individuals for 41 days, with 10-minute focals. The amount each individual was observed ranged from 812 minutes to 1,240 minutes. Every individual was observed at least once a day. The difference in observation time was due to cleaning schedules, tours, and other factors. The total counts and durations for each pair is listed in Table 3, as well as the total number of scans, focals, and significant behaviors for each pair.

Table 3

*Result Table of Pairs' Relevant Information*

ID	Pair	Species	Years	Off.	# of scans	# of focals	# of min total	Groom count and duration	Affil. count and duration	Play count and duration	Mating count and duration	Ag. count and duration	Sig beh.
Arthur Phy Gyi	1	Hoolock	Middle	Yes	853	92	894	C-4 D-217	C-4 D-308	C-0 D-0	C-2 D-206	C-0 D-0	3
Khin Maung Betty	2	Hoolock	Middle	No	1,036	104	939	C-150 D-8012	C-4 D-322	C-2 D-35	C-7 D-73	C-1 D-13	6
Win Bo Chan Thar	3	Hoolock	Long-term	No	1,036	90	830	C-101 D-9607	C-1 D-571	C-0 D-0	C-6 D-67	C-5 D-65	6
Ivan Chloe	4	Javan	Middle	Yes	1,240	113	1,120	C-7 D-791	C-1 D-102	C-0 D-0	C-5 D-73	C-1 D-65	2
Domino Tuk	5	Pileated	Long-term	Yes	870	84	831	C-8 D-449	C-1 D-19	C-0 D-0	C-1 D-7	C-0 D-0	2
U Maung Hmawe Ni	6	Hoolock	Middle	No	1,028	84	817	C-364 D-7327	C-5 D-449	C-0 D-0	C-5 D-70	C-1 D-10	6
U Myint Marlow	7	Mixed	New	No	1,100	100	998	C-22 D-2072	C-13 D-2425	C-11 D-316	C-0 D-0	C-0 D-0	8
Perak Simpang	8	Javan	Long-term	Yes	997	98	948	C-2 D-158	C-0 D-0	C-0 D-0	C-0 D-0	C-0 D-0	2
Truman Violet	9	Pileated	New	No	1,134	103	1,028	C-12 D-1079	C-9 D-508	C-34 D-1838	C-4 D-126	C-2 D-61	6

Note: C = total number of counts. D = total number of durations in seconds

## Behavioral Synchrony

I collected behavioral synchrony data via scans and I used behaviors from my ethogram to mark if the pairs were in unison. Behavioral synchrony is defined as any activity performed in unison (King & Cowlshaw, 2009). I found the mixed pair was in behavioral synchrony significantly more than the hoolock pairs. Newly established pairs were in behavioral synchrony significantly less than pairs of middle and long-term association (Table 4).

Table 4

*GLMM Behavioral Synchrony in Gibbon Pairs*

Gibbons being compared	Estimate	Std. Error	Z value	P value
Javan-Hoolock	0.525	0.292	1.803	0.251
Mixed-Hoolock	1.484	0.481	3.085	<b>0.009</b>
Pileated-Hoolock	0.893	0.377	2.372	0.745
Mixed-Javan	0.958	0.415	2.312	0.086
Pileated-Javan	0.368	0.287	1.282	0.549
Pileated-Mixed	-0.590	0.300	-1.974	0.181
Yes-No (offspring)	-0.469	0.271	-1.728	0.084
New-Middle	-1.232	0.484	-2.546	<b>0.025</b>
Long-Middle	-0.282	0.199	-1.417	0.304
Long-New	0.950	0.410	2.317	<b>0.046</b>

*Note:* Bold indicates significant results.

## Proximity

I used scan data to measure proximity. I marked the gibbons proximate if they were < 1m from each other. The mixed pair was significantly proximate in more scans than the Javan and pileated gibbon pairs (Table 5). The pileated gibbon pairs were proximate significantly more in scans than the Javan gibbon pairs. The pairs with offspring spent a

significantly less amount of time in proximity than the pairs without offspring. Newly established pairs were in proximity significantly less than the middle and long-term pairs.

Table 5

*GLMM Proximity in Gibbon Pairs*

Gibbons being compared	Estimate	Std. Error	Z value	P value
Javan-Hoolock	-0.231	0.138	-1.676	0.315
Mixed-Hoolock	0.461	0.203	2.273	0.095
Pileated-Hoolock	0.969	0.168	0.577	0.935
Mixed-Javan	0.692	0.174	3.982	< <b>0.001</b>
Pileated-Javan	0.327	0.131	2.496	<b>0.055</b>
Pileated-Mixed	-0.364	0.114	-3.200	<b>0.006</b>
Yes-No (offspring)	-1.4308	0.1211	-11.81	< <b>0.001</b>
New-middle	-1.098	0.204	-5.393	< <b>0.001</b>
Long-middle	0.162	0.0745	2.175	0.065
Long-new	1.259	0.1792	7.031	< <b>0.001</b>

*Note:* Bold indicates significant results.

### Grooming

I used focal samples to collect grooming, affiliative, mating, and play behaviors. For grooming counts the hoolocks groomed significantly more often than the Javan gibbon pairs. The gibbon pairs with offspring groomed significantly less than pairs without offspring. Grooming frequency did not significantly differ in pairs based on the number of years the pairs had been together (Table 6).

For grooming durations, Javan and pileated gibbon pairs spent significantly less time in grooming bouts than did the hoolocks (Table 7). Again, gibbon pairs with offspring spent significantly less time grooming than did the pairs without offspring. Grooming duration did not significantly differ in pairs based on number of years the pairs had been together.

Table 6

*GLMM Grooming Counts in Gibbon Pairs*

Gibbons being compared	Estimate	Std. Error	Z value	P value
Javan-Hoolock	-3.045	1.050	-2.898	<b>0.019</b>
Mixed-Hoolock	-1.354	1.293	-1.047	0.717
Pileated-Hoolock	-2.104	1.015	-2.073	0.158
Mixed-Javan	1.691	1.451	1.165	0.643
Pileated-Javan	0.940	1.211	0.776	0.862
Pileated-Mixed	-0.750	1.425	-0.527	0.951
Yes-No (offspring)	-2.703	0.7553	-3.579	<b>&lt;0.001</b>
New-Middle	-0.957	1.411	-0.678	0.775
Long-Middle	-1.110	1.256	-0.883	0.650
Long-New	-0.153	1.499	-0.102	0.994

*Note:* Bold indicates significant results.

Table 7

*GLM Grooming Duration in Gibbon Pairs*

Gibbons being compared	Estimate	Std. Error	Z value	P value
Javan-Hoolock	-68.687	23.814	-2.884	<b>0.019</b>
Mixed-Hoolock	-52.496	30.756	-1.707	0.314
Pileated-Hoolock	-65.074	23.907	-2.722	<b>0.032</b>
Mixed-Javan	16.192	33.634	0.481	0.962
Pileated-Javan	3.613	27.511	0.131	1.000
Pileated-Mixed	-12.579	33.700	-0.373	0.982
Yes-No (offspring)	-59.88	20.23	-2.96	<b>0.003</b>
New-Middle	-32.50	35.00	-0.929	0.621
Long-Middle	-10.10	30.92	-0.327	0.943
Long-New	22.40	36.91	0.607	0.816

*Note:* Bold indicates significant results.

### **Affiliative Behaviors Combined**

For all affiliative behaviors combined, the mixed pair had a significantly larger number of occurrences than did the hoolocks or Javan gibbons (Table 8). The pairs with offspring had significantly fewer occurrences in affiliative behaviors than the pairs

without offspring. The newly established pairs had significantly more occurrences of affiliative behaviors than the middle and long-term pairs.

The mixed pair spent significantly more time engaging in combined affiliative behaviors than did the hoolocks and the Javan and pileated gibbons (Table 9). I found a significantly larger amount of time spent in combined affiliative behaviors if the pairs did not have offspring. There was no significant difference in the number of years the pairs had been together and the durations of their combined affiliative behaviors. Pairs did not differ in durations of combined affiliation based on how long they had been together.

Table 8

*GLMM Combined Affiliative Behavior Counts in Gibbon Pairs*

Gibbons being compared	Estimate	Std. Error	Z value	P value
Javan-Hoolock	-2.174	1.033	-2.105	0.137
Mixed-Hoolock	1.128	0.378	2.976	<b>0.013</b>
Pileated-Hoolock	0.249	0.408	0.611	0.922
Mixed-Javan	3.302	1.038	3.182	<b>0.007</b>
Pileated-Javan	2.423	1.049	2.311	0.085
Pileated-Mixed	-0.878	0.421	-2.088	0.142
Yes-No (offspring)	-1.49	0.53	-2.82	<b>&lt;0.005</b>
New-Middle	1.082	0.342	3.165	<b>0.004</b>
Long-Middle	-1.198	0.636	-1.883	0.136
Long-New	-2.280	0.616	-3.705	<b>&lt;0.001</b>

*Note:* Bold indicates significant results.

Table 9

*GLM Combined Affiliative Behaviors Duration in Gibbon Pairs*

Gibbons being compared	Estimate	Std. Error	Z value	P value
Javan-Hoolock	-5.708	4.017	-1.421	0.480
Mixed-Hoolock	17.818	5.216	3.416	<b>0.004</b>
Pileated-Hoolock	-3.373	4.176	-0.808	0.848
Mixed-Javan	23.526	5.605	4.197	<b>&lt;0.001</b>
Pileated-Javan	2.335	4.653	0.502	0.958
Pileated-Mixed	-21.192	5.721	-3.704	<b>0.001</b>
Yes-No (offspring)	-9.107	3.964	-2.298	<b>0.022</b>
New-Middle	11.267	5.003	2.522	0.062
Long-Middle	1.170	4.521	0.259	0.964
Long-New	-10.097	5.319	-1.898	0.138

*Note:* Bold indicates significant results.

**Mating**

I found no significant results of mating for counts (Table 10) or durations (Table 11) of this behavior. This could be due to rarity of mating behaviors in my data set. Pairs without offspring had more mating occurrences than pairs with offspring, but this difference was not significant. There were no significant results in mating based on the different number of years the pairs have been together.

Table 10

*GLM Mating Counts in Gibbon Pairs*

Gibbons being compared	Estimate	Std. Error	Z value	P value
Javan-Hoolock	-0.037	0.019	-1.942	0.206
Mixed-Hoolock	-0.061	0.025	-2.443	0.067
Pileated-Hoolock	-0.034	0.020	-1.716	0.309
Mixed-Javan	-0.024	-0.027	-0.881	0.811
Pileated-Javan	0.003	0.022	0.136	1.000
Pileated-Mixed	0.027	0.027	0.975	0.760
Yes-No (offspring)	-0.031	0.0173	-1.76	0.078
New-Middle	-0.030	0.023	-1.299	0.394
Long-Middle	-0.016	0.021	-0.783	0.712
Long-New	0.013	0.025	0.5553	0.843

Note: Bold indicates significant results.

Table 11

*GLM Mating Duration in Gibbon Pairs*

Gibbons being compared	Estimate	Std. Error	Z value	P value
Javan-Hoolock	-1.087	0.652	-1.668	0.335
Mixed-Hoolock	-1.433	0.847	-1.693	0.322
Pileated-Hoolock	-0.722	0.678	-1.065	0.706
Mixed-Javan	-0.346	0.909	-0.380	0.981
Pileated-Javan	0.365	0.755	0.484	0.962
Pileated-Mixed	0.711	0.929	0.766	0.867
Yes-No (offspring)	-0.185	0.517	-0.357	0.721
New-Middle	-0.484	0.653	-0.741	0.738
Long-Middle	-0.462	0.598	-0.77	0.719
Long-New	0.022	0.698	0.032	1.00

Note: Bold indicates significant results.

**Play Behaviors**

I found no significant differences for counts of play behaviors across the different species (Table 12). This could be because I observed 47 occurrences of play throughout

the entirety of my study. Newly established pairs had significantly more occurrences of play than did pairs of middle and long-term (Table 13). The newly established pairs were in play behaviors longer than pairs of middle and long-term association. I found no significant results for play duration and species, or for pairs with and without offspring. The newly established pairs played significantly longer than any other pairs.

Table 12

*GLM Play Counts in Gibbon Pairs*

Gibbons being compared	Estimate	Std. Error	Z value	P value
Javan-Hoolock	-0.005	0.067	-0.080	1.000
Mixed-Hoolock	0.103	0.086	1.198	0.623
Pileated-Hoolock	0.163	0.067	2.420	0.071
Mixed-Javan	0.109	0.094	1.154	0.650
Pileated-Javan	0.169	0.077	2.181	0.125
Pileated-Mixed	0.059	0.095	0.631	0.921
Yes-No (offspring)	-0.093	0.063	-1.475	0.140
New-Middle	0.215	0.046	4.630	<b>&lt;.001</b>
Long-Middle	-0.005	0.042	-0.127	0.991
Long-New	-0.219	0.049	-4.476	<b>&lt;.001</b>

*Note:* Bold indicates significant results.

Table 13

*GLM Play Duration in Gibbon Pairs*

Gibbons being compared	Estimate	Std. Error	Z value	P value
Javan-Hoolock	-0.094	3.611	-0.026	1.000
Mixed-Hoolock	3.034	4.665	0.651	0.913
Pileated-Hoolock	9.005	3.638	2.475	0.062
Mixed-Javan	3.129	5.093	0.614	0.926
Pileated-Javan	9.09	4.173	2.180	0.125
Pileated-Mixed	6.00	5.113	1.168	0.642
Yes-No (offspring)	-4.315	3.465	-1.245	0.213
New-Middle	10.412	3.043	3.421	<b>0.002</b>
Long-Middle	-0.093	2.711	-0.034	1.00
Long-New	-10.505	3.219	-3.264	<b>0.003</b>

*Note:* Bold indicates significant results.

### Agonistic Behaviors

I saw 10 occurrences of agonistic behavior throughout my entire study. I could not analyze these results due to the low occurrence of this behavior.

### Pair Comparison

After looking at all of my results I calculated the total number of significant behaviors for each pair. For example, if I were looking at the mixed species pair, I would give them a mark in the behavioral synchrony category because they were in synchrony the most in my study. I found that the mixed species had the most significant pair bonding behaviors out of all of the GCC gibbon pairs with a total of 8. Next, the three hoolock gibbon pairs without offspring had 6 significant behaviors. The newly established pileated pair had 6 significant behaviors as well. The hoolock pair with offspring followed with 3 significant behaviors. Both Javan gibbon pairs were at the

bottom with 2 significant behaviors, as well as the pileated pair with offspring. Table 14 shows all of these results.

Table 14

*Pairs' Significant Behaviors*

ID	Species (a)	Offspring (b)	Years (c)	Synch	Prox	Groom	Affil	Play	Behaviors
U Myint Marlow	Mixed	No	New	a	a,b	b	a,b,c	c	8
Khin Maung Betty	Hoolock	No	Middle	c	b,c	a,b	b		6
Win Bo Chan Thar	Hoolock	No	Long-term	c	b,c	a,b	b		6
U Maung Hmawe Ni	Hoolock	No	Middle	c	b,c	a,b	b		6
Truman Violet	Pileated	No	New		b,c	b	b,c	c	6
Arthur Phy Gyi	Hoolock	Yes	Middle	c	c	a			3
Ivan Chloe	Javan	Yes	Middle	c	c				2
Domino Tuk	Pileated	Yes	Long-term	c	c				2
Perak Simpang	Javan	Yes	Long-term	c	c				2

## CHAPTER V

### DISCUSSION

The purpose of my research was to better understand captive gibbons' pair bond behaviors by studying behaviors that may indicate the relationship's quality. Previous research has been rare on this topic and has mainly focused on duetting in relation to pair bonds (Cowlshaw, 1992; Dooley and Judge, 2007; Fan et al., 2009; Geissmann & Orgeldinger, 2000; Raemaekers & Raemakers, 1985; Mitani, 1984). I aimed to examine a variety of behaviors so as to better assess and understand the quality of the pair bonds in these apes. My results show that the quality of a pair bond cannot be determined from just one particular behavior. I wanted to identify whether different factors such as species, the presence of offspring in enclosures, and the number of years the pair has been together affect these behaviors. This is the first study to look at pair bonds in gibbons that includes four different species and examines a wide range of behaviors.

#### **Behavioral synchrony**

Behavioral synchrony is defined as any activity performed in unison (King & Cowlshaw, 2009). I used behaviors from my ethogram to mark if the pairs were in unison during my study. The only prior research examining behavioral synchrony in gibbons was by Fan et al. (2009), who studied four groups of wild black crested gibbons, and Geissmann & Orgeldinger (2000), who studied ten groups of captive siamangs. Both sets of researchers found that gibbons produced more calls when they were in synchrony and when they were in closer proximity. I found that the mixed species pair was in behavioral synchrony significantly more than were the hoolock gibbon pairs, but that newly established pairs in my study were in synchrony significantly less than were the

middle and long-term pairs. The mixed species pair is under the newly established category. The reason for this skew of results could be the fact the other newly established pair in this category was in behavioral synchrony so little. To further understand why middle and long-term pairs are in behavioral synchrony more longitudinal studies need to be done. Freed (1987) looked at the long-term pair bond of tropical house wrens and studied the dynamics of pair bonds over a long period of time to better understand their mechanisms. A similar study should be conducted in gibbons to understand long-term pair bonds. The high rate of behavioral synchrony in the middle and long-term pairs could indicate that the pairs are compatible: they are in synchrony more because they have been together longer and are more bonded. Mitani (2009) found the strongest social bonds were positively correlated with the number of years together and the amount of time spent grooming. Similar results could also apply for the case of behavioral synchrony in gibbons.

### **Proximity**

Proximity has been used in several studies to evaluate the quality of social bonds in non-human primates. All individuals in the enclosure were observed in relation to proximity. I scored two individuals as proximate if they were  $< 1$  m from another individual and not proximate if they were  $\geq 1$  m (Palombit, 1996). A meter is approximately a gibbon's arm length. Mitani (2009) discovered that in chimpanzees, the strongest male social bonds were maintained by close proximity. Fan et al. (2009) noted that gibbons produced more calls when they were closer in proximity. Silk, Altmann & Alberts (2006) found that proximity was a measure of social bond strength in baboons.

I found that the mixed species pair was in proximity significantly more than the Javan and pileated gibbons pairs. Palombit (1996) found siamangs spent significantly more time in proximity to each other than white-handed gibbons. This could be why the mixed pair is in proximity more, since the female in the pair is a siamang. The Javan and pileated gibbon pairs are classified in genus *Hylobates*, so there may be genus difference in proximity. Gittins & Raemaekers (1980) argued that because of siamangs' more folivorous diet, they generally have more socially cohesive groups.

Gibbon pairs with offspring were in proximity significantly less than pairs without offspring. The mixed species pair in my study did not have offspring, while both Javan gibbon pairs and one pileated gibbon pair did. This could be another reason why the mixed species pair is in proximity more. Pairs without offspring may be in proximity significantly more, because the mother is occupied with the children more than the adult females in pairs without offspring. For example, the pairs Tuk and Domino and Arthur and Phy Gyi each have three offspring in their enclosures. Tuk and Domino have an infant, Howard, in their enclosure and he was almost always clinging to Tuk. Juveniles, Nyi Ma Suu and Alan Mootnick Jr. followed Phy Gyi during many of my focals. Sheldon (2017) found that Nyi Ma Suu spent significantly more time in proximity to Phy Gyi than any other gibbon in the enclosure. This shows that young offspring spend a large amount of time in proximity to their mother. The presence of offspring in the enclosure can therefore negatively alter proximity between members of mated pairs, specifically by increasing distance between them.

Newly established pairs were significantly in proximity less than the middle and long-term pairs. Proximity could be correlated with the number of years of the bond, but

further studies would need to be done to understand this. For example, Mitani (2009) found that in chimpanzees' years of the bond was positively correlated with grooming. Proximity has been studied alongside grooming and therefore, as is true of grooming, proximity could be correlated with the number of years of association.

Fan et al. (2009) stated that proximity could be used as an indicator to assess the strength of gibbon pair bonds. My data indicates that proximity is an important factor, but not the sole determinate, of what contributes to be a strong pair bond. The presence of offspring can be a major factor affecting pair bond behaviors. Cheyne (2009) reports that reproduction and survival of offspring are factors considered when assessing the success of gibbon reintroduction programs. That a pair has reproduced is a sign of success in many cases, but as shown in my study, a child can alter their parents' proximity to one another, and thereby affect their pair bond. Proximity should be considered in addition to other pair bond behaviors and further studies should be completed since there is no research published on proximity that includes the affect that offspring have on gibbon groups.

### **Grooming**

When collecting my data, I categorized grooming as a separate behavior rather than combining it with other affiliative behaviors. Primatologists have often viewed grooming as indicative of the bond strength between grooming partners. Grooming bouts consist of two or more individuals, with an initiator and a receiver. Grooming bouts in my study ended if there was no contact between partners for more than 1 minute (Barelli, Reichard & Mundry, 2011). Grooming was determined to be a good measure of social relationships in baboons (Silk, Altmann & Alberts, 2006). Mitani (2009) found that male

chimpanzees with the most stable bonds groomed each other more frequently. In my study, hoolock pairs had significantly more occurrences of grooming than did the Javan gibbon pairs. Also, they had longer grooming bouts than did the mixed species and Javan and pileated gibbon pairs. Fischer & Gesissmann (1990) studied siamangs and white-handed gibbons. Their results showed the siamangs to have longer grooming bouts than the white-handed gibbons. Barelli & Reichard (2001) found white-handed gibbons groomed 7% of the day. Bartlett (2003) studied white-handed gibbons, were they found to have a lack of social interactions. Overall, it appears that white-handed gibbons do not engage in much grooming/social behaviors. There are no research articles on hoolock, Javan, or pileated gibbons' grooming behaviors, so I cannot compare my data to field studies for these taxa. As was the case for my findings of proximity, the lower frequency of grooming I observed in Javan gibbons could be due to their classification in the genus *Hylobates*.

More than 30 years ago, Brockelmann & Gittins (1984) noted the lack of information on gibbon social behavior. When comparing pair bond behaviors, one needs to consider a breadth of behaviors and understand that we cannot assume because we see a behavior in one species, it will be equivalent in the next species. For example, if hoolocks have a high rate of grooming and this is consistent with a good pair bond, we cannot assume that high grooming rates indicates a strong pair bond across all species. There could be other species-specific variables we need to explore to understand bonding behaviors.

In my dataset, gibbon pairs with offspring had fewer grooming occurrences and were in grooming bouts significantly less than the pairs without offspring. Out of the four

hoolock gibbon pairs, three did not have offspring in the enclosure. Offspring could be affecting grooming in gibbon pairs, similar to what I found with proximity. Anecdotally, I often witnessed offspring interrupting pairs, and the members of the pair interacted more if no offspring were in the enclosure interrupting them.

I found no significant relationships between the number of years the pairs have been together and their grooming. Mitani (2009) found the number of years the male chimpanzees in his study were bonded was positively correlated with their grooming. My results are not consistent with Mitani, perhaps because of the dramatically different social organizations of these two apes. Further research needs to be done on gibbon species and on their different social behaviors to see whether the pattern I observed is consistent across other taxa.

### **Affiliative Behaviors Combined**

Gibbons' affiliative behaviors consist of embracing, holding each other, and being in physical contact, resting next and touching with another individual (Palombit, 1996). I used Palombit's description of affiliative behaviors to assess these behaviors in the pairs in my study. Multiple studies have shown that affiliative interactions can be used to assess social bonds between adult non-human primates (Fuentes, 2000; Hinde, 1977). The mixed species pair in my dataset had significantly more occurrences of affiliative behaviors than the hoolock or Javan gibbon pairs and a longer duration of these behaviors than all other pairs. This is very interesting since the one mixed species pair shows significantly more behaviors than the other hoolock and Javan gibbon pairs combined. Further studies on species' social behaviors need to be investigated to understand this. Palombit (1996) found that siamangs spent significantly more time in proximity to each

other than white-handed gibbons, and Fischer & Gesissmann (1990) stated that grooming bouts were longer in siamangs. This coincides with the fact that the female in the mixed species pair in my study is a siamang and she specifically may be influencing the frequency of the behaviors I observed.

Pairs with offspring have significantly less occurrences and shorter durations of affiliative behaviors than pairs without offspring. This can relate back to proximity and grooming when thinking about how offspring affect the behaviors of their parents. Offspring in the enclosure, especially infants, can affect how much the members of the pair interact. This is not necessarily negative, as members of the pair have been successful in producing offspring. It may merely mean that other behaviors need to be examined to assess pair bond strength when studying pairs with young offspring.

The newly established pairs had more occurrences of affiliative behaviors than the middle and long-term pairs. The mixed species pair is newly established, and their songs are different since gibbons' songs are species-specific. One reason why they engaged in more affiliative behaviors could be to compensate for their lack of duetting. Also, the newly established pairs could be still establishing a pair bond, so they engage in more affiliative behaviors. Further research is needed to investigate the amount of pair bonding behaviors in a newly established pair versus a long-term pair.

It is interesting that hoolocks significantly groomed the most, but the mixed species pair had significantly more occurrences of affiliative behaviors. This difference reinforces my observation that different behaviors need to be studied to better understand pair bonding.

## **Mating**

I found no significant results for mating. I recorded individuals as mating if they were engaging in copulation. Overall, I observed only 30 occurrences of mating across the pairs, and the lack of significant results could be from such a small sample size of occurrences. Mating happened at least once in all of the pairs except for the mixed species pair and one Javan gibbon pair.

## **Play Behaviors**

Play behaviors included nonaggressive rolling, tumbling, and chasing other individuals (Palombit, 1996; Sierra, 2013). I defined embrace as stationary ventral-ventral contact, where one individual put its arm around another following (Palombit, 1996). Bartlett (2003) found that play behavior in gibbons was primarily displayed by juveniles and adolescents. In my study, for count and duration play data, the newly established pairs played significantly more than middle and long-term pairs. The mixed species pair is a newly established pair. The female is 12 years old and the male is 8 years old. The other newly established pair is around the same age range. They are not juvenile or adolescent, but they are among the younger-aged pairs at the GCC. The fact that the newly established pairs are younger could be the primary reason why they express more play behaviors. This corresponds with other observations that gibbon play involved infants, juveniles, adolescents, and sub-adults more than adults (Brockelman & Reichard, 1998).

## **Agonistic Behaviors**

Agonistic behaviors included open mouth display, bare teeth, slapping, and hostile presenting (Mootnick et al., 2006; Palombit, 1996; Smith, 2011). I could not

analyze agonistic behaviors due to the fact there were only ten occurrences of agonism during my study. Bartlett (2003) noted that within-group aggression is rare in white-handed gibbons. There was little agonistic behavior in siamang and white-handed gibbon pairs in research conducted by Palombit (1996). Agonism could be rare for all species, since so little agonistic behaviors were seen in my six week research, but further research needs to be done on this aspect of gibbon behavior. The agonistic behavior counts I observed were distributed across five out of nine pairs. One pair, Chan Thar and Win Bo, had five out of ten of my counts of agonistic behaviors.

### **Duetting**

All gibbons produce loud and long vocal bouts, and in most species they combine species-specific and sex-specific vocals to create duets (Geissmann & Orgeldinger, 2000). Gibbons are the only apes to duet with a mate. Duets can last up to 30 minutes and usually occur in the mornings (Geissmann & Orgeldinger, 2000). Duetting is the most studied pair bond behavior (Cowlshaw, 1992; Dooley and Judge, 2007; Fan et al., 2009; Geissmann & Orgeldinger, 2000; Raemaekers & Raemakers, 1985; Mitani, 1984). Gibbons at the GCC often vocalize at the same time. I could not accurately collect data on duetting due to multiple species at different enclosures all singing at once. I suggest future researchers at the GCC conduct a separate study on duetting so it can be accurately evaluated as part of pair bonding behavior.

### **Pair comparison**

It is important to understand captive gibbons' pair bond behaviors so that managers of rehabilitation and reintroduction programs can make informed decisions about mated pairs' release. The issue remains that some pairs from these programs

separate when released back into the wild. Reintroduction success is measured by gibbons' survival post-release, maintenance of the pair bond, and reproduction and survival of offspring (Cheyne, 2009). Understanding pair bond behaviors is important for reintroduction success. The purpose of my study was to understand these pair bonding behaviors better and to see what factors might affect them.

When looking at the GCC pairs in my dataset, the mixed species pair had eight significant behaviors, which is the most out of any of the pairs in my study. Based on this, they would be the most bonded pair at the GCC. This result indicates to staff at sanctuaries and zoos with single housed individuals that they can be placed with individuals from other species instead of isolating them. In a study examining behavior and welfare in capuchins and squirrel monkeys, Leonard et al. (2010) found that captive mixed species groups could have socially enriching effects that are beneficial to welfare as long as these enclosures are carefully designed the environment is managed.

All of the Javan gibbon pairs are at the bottom of this list. This result is interesting because Javan gibbons are one of the only gibbon species to not duet, which is a known signal of pair bond strength. It is perhaps significant that the Javan gibbons do not duet with their mates and show the least amount of other pair bond behaviors. More research should be done in this area to understand the lack of bonding behaviors in this species.

Analysis of my data may answer the question, "what makes a pair bond" but it also invites further query. Are the hoolocks the "best" pairs because they groom the most, or is the mixed species pair the most strongly bonded because they are in proximity the most and exhibit the most behavioral synchrony, and other affiliative behaviors? Or are the pairs with the most offspring the most bonded? I agree that my results indicate that a

strong pair bond in gibbons is a combination of all of these behaviors, dependent upon and varying from species to species.

I hypothesized that pairs' behaviors of pair bonds would be different based on the number of years together, species, and presence of offspring. I predicted that behaviors indicative of pair bonds would differ between species. I predicted that pairs who have been together longer and have offspring would show more pair bonding behaviors including: affiliation, behavioral synchrony, grooming and proximity. My results aligned with my prediction of a difference in behaviors between species. There were species differences, such as the hoolocks had more occurrences of grooming, the Javans displayed a lack of pair bonding behaviors, and the mixed species had a wide range of behaviors. My results aligned with my prediction that pairs who have been together longer would show more pair bonding behaviors only for proximity and behavioral synchrony data. Lastly, my prediction of pairs with offspring would show more pair bonding behaviors did not align with my results, as the pairs with offspring were in fewer behaviors.

### **Research Limitations**

One thing that could have affected my research is the presence of more hoolock gibbon pairs in the study than any other: four of my nine pairs were hoolocks. The environment could be affecting the pairs' behaviors as well. For example, being in enclosures next to different species they would not normally see in the wild and hearing different duets may affect their behavior. Anecdotally, I saw some pairs watching other enclosures habitually, which could result in increased stress. Individual personalities play a major factor in behavior as well, and I did not include the rearing history in my

analysis, which may affect behaviors as well. I collected data on proximity even though GCC gibbons live in enclosures, whereas if they were in the wild they would have a more natural proximity. If pairs in my study did not want to be together, they would move to opposite ends of the enclosure. I included proximity in this study because I felt it was an important behavior to record when looking at pair bond behaviors, even though wild gibbons would have a wider range of possible proximity distances. Marlow, a member of the mixed species pair, was sick from 5/9/2017-4/30/2017 and this could have affected her behavior during part of my study. I do not have an equal amount of focals and scans for each individual, which could skew my results. Lastly, I coded only half of the video footage I took, so I am missing behaviors that occurred in some videos. However, this is not likely to influence my results because the footage I scored was randomly selected for each pair.

## CHAPTER VI

### CONCLUSION

Pair bonding behaviors may not be mutually exclusive of each other, so more than one behavior needs to be studied when trying to understand these complex social behaviors. Factors such as species, presence of offspring, years together, environment, and personalities also affect these behaviors. I reviewed previous literature on pair bonding behaviors in gibbons to study pair bonding of the gibbon pairs at the GCC. There is a lack of social behavior information for many gibbon species, with the white-handed gibbons and siamangs studied the most. More research is needed in social behavior in gibbons to understand pair bonds better. The mixed species pair displayed a wide variety of pair bonding behaviors significantly more than of all the pairs in my study. This may mean at more sanctuaries and zoos, individuals who are housed alone can have a more enriched life being housed with others, even if they are of different species.

The relationship between behaviors and other factors than can affect them need to be taken into consideration when researching pair bonding. Proximity can be affected by offspring, but offspring makes the pair successful. There appears to be a species difference that may be related to evolved differences in ecology in social behaviors that needs to be further studied. Gibbons songs are species-specific, and therefore, as my study suggests, other pair bond behaviors may be as well. Overall, multiple variables and numerous behaviors need to be examined when studying the quality of pair bonds in gibbons. I suggest further research into gibbon species' pair bond behaviors is needed to help staff of rehabilitation and reintroduction centers make informed decision about

quality of a pairs' bond, and whether the bond is likely to endure when that pair is released.

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