All Master's Theses   Master's Theses

Spring 2015

Javan Gibbon (Hylobates moloch) Non-Vocal Social Communication and Gesture Use With Conspecifics

Melanie Bell
Central Washington University, bellm@cwu.edu

Follow this and additional works at: http://digitalcommons.cwu.edu/etd

Part of the Animal Sciences Commons, Animal Studies Commons, Biological and Physical Anthropology Commons, Cognition and Perception Commons, Other Communication Commons, and the Social Psychology Commons

Spring 2015

Javan Gibbon (Hylobates moloch) Non-Vocal Social Communication and Gesture Use With Conspecifics

Melanie Bell
Central Washington University, bellm@cwu.edu

Follow this and additional works at: http://digitalcommons.cwu.edu/etd

Part of the Animal Sciences Commons, Animal Studies Commons, Biological and Physical Anthropology Commons, Cognition and Perception Commons, Other Communication Commons, and the Social Psychology Commons

Recommended Citation

JAVAN GIBBON (*HYLOBATES MOLOCH*) NON-VOCAL SOCIAL

COMMUNICATION AND GESTURE USE WITH CONSPECIFICS

_____

A Thesis

Presented to

The Graduate Faculty

Central Washington University

_____

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

Primate Behavior

_____

by

Melanie Bell

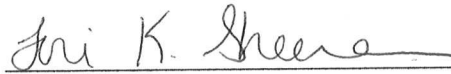April 2015

CENTRAL WASHINGTON UNIVERSITY

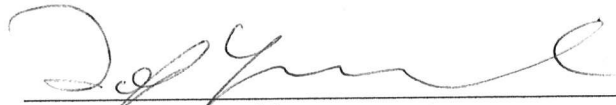Graduate Studies

We hereby approve the thesis of

Melanie Bell

Candidate for the degree of Master of Science

APPROVED FOR THE GRADUATE FACULTY

4/27/15 _____
Dr. Lori K. Sheeran, Committee Chair
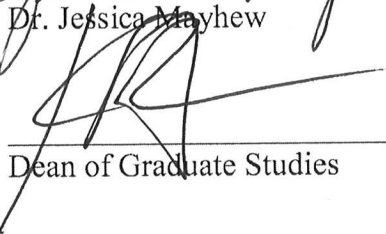
4/27/15 _____
Dr. Ralf Greenwald

4/27/15 _____
Dr. Jessica Mayhew

5/28/15 _____
Dean of Graduate Studies

ii

ABSTRACT

JAVAN GIBBON (*HYLOBATES MOLOCH*) NON-VOCAL SOCIAL

COMMUNICATION AND GESTURE USE WITH CONSPECIFICS

by

Melanie Bell

April 2015

I explored gestures used by captive Javan gibbons (*Hylobates moloch*) at the Gibbon Conservation Center (Santa Clarita, CA). I hypothesized that a sender gibbon's gesture modality would vary with the recipient gibbon's attentional state and the sender would be equally likely to use all modalities (tactile, visual, actions, and facial expressions) when the recipient was attending (facing the sender), but would use more tactile gestures and actions when the recipient was non-attending (oriented away from the sender). I collected data from 10 individuals using all-occurrences sampling and an ethogram to score behaviors from video recordings. In 1,143 interactions, gibbons used visual gestures and facial expressions significantly more when the recipient was attending and tactile gestures significantly more when the recipient was non-attending. There was no significant difference in actions. These data show that juvenile Javan gibbons used gestures appropriate to recipient's attentional state in three out of the four modalities.

ACKNOWLEDGEMENTS

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF FIGURES (Continued)

CHAPTER I

INTRODUCTION

Little information is available concerning small-bodied apes' (Hylobatidae) cognitive and communicative abilities, outside of their duet vocalizations. Some taxonomists recognize 16 gibbon and siamang species (Melfi, 2012), which are collectively called "gibbons" or "small-bodied apes." In the wild, hylobatids are mostly arboreal, making it difficult for researchers to see subtle communication cues such as facial expressions. This results in many more accounts of gibbons' vocal communication, rather than their visual or gestural communication modalities (Maestripieri, 1999). Past research on gibbon cognition suggests that their skills are not complex ones (Tomasello & Call, 1997), particularly in comparison to large-bodied apes. Their taxonomic classification, however, may be reason to conduct further research on small-bodied ape cognition since gibbons are considered to be intermediate to Old World monkeys and large-bodied apes (Cunningham, Anderson & Mootnick, 2006).

Liebal, Pika and Tomasello (2004) studied siamangs' abilities to adjust signals to the recipient's attentional state. They found that siamang senders were equally likely to use tactile and visual gestures, actions, and facial expressions to initiate an interaction with an attending recipient, but were more likely to use tactile gestures and actions with a non-attending recipient. Due to these findings, there is reason to believe the same abilities may occur in other gibbon species.

The Gibbon Conservation Center (GCC) is a behavioral research and breeding facility located in Santa Clarita, California (Cunningham et al., 2006). GCC was established in 1976 by Alan Mootnick and has housed seven different gibbon species.

Currently, the species at GCC include Eastern hoolock (*Hoolock leuconedys)*; Javan (*Hylobates moloch*), Northern white-cheeked (Nomascus leucogenys), and Pileated (*Hylobates pileatus) gibbons*; and siamangs (*Symphalangus* syndactylus). This study focuses on Javan gibbons. This species is endemic to Java, Indonesia. It is estimated that fewer than 4,500 individuals remain in the wild (Nijman, 2004). According to the International Union for Conservation of Nature (IUCN), this species is classified as endangered in the wild (IUCN, 2013).

CHAPTER II

LITERATURE REVIEW

Modes of Ape Communication

Researchers have discovered that communication in large-bodied apes is flexible, dynamic, and complex, incorporating multiple modalities (Goodall, 1986; Ogden & Schildkraut, 1991). Goodall (1986) explains that, in chimpanzees (*Pan troglodytes*), there are four main modalities (or pathways) for the transmission and reception of information. These include visual, tactile, auditory, and olfactory. These modes of information transmission have also been observed in gorillas (*Gorilla gorilla*) and orangutans (*Pongo pygmaeus* and *P. abelii*) (Ogden & Schildkraut, 1991; Cartmill & Byrne, 2007). Ogden and Schildkraut (1991) used scans of location and activity to create an extensive ethogram of gorilla behaviors in regard to different gestural modalities. Tanner and Byrne (1996) examined gesture use in captive lowland gorillas. Each observed gesture was coded as only one instance if it repeated rapidly and in the same form for several instances. They calculated the percent of gestures used while the gesturer had their partner's visual attention (to measure intention) and the percent of gestures used while the partner had a playface (to measure motivation). They found that most gestures occurred in a play context and individuals gestured significantly more when the partner exhibited a playface. They also found significant differences in gesture types based on situational context; for example, a gorilla would be more likely to use a visual gesture while they had their partner's visual attention. Pika, Liebal and Tomasello (2003) also examined the gesture use, learning, and gestural repertoire of young gorillas, which they also later studied in subadult bonobos (*Pan paniscus*) (Pika, Liebal & Tomasello, 2005).

Cartmill and Byrne (2007) observed orangutans modifying their gestural signals according to their audience's comprehension. For example, they would repeat a gesture if they were only partially understood and would use different gestures if they were not understood at all. This showed that orangutans would persist in communication when their goal was not fully met, in a way that would help a recipient fully understand the sender's goal. Chimpanzees that have learned American Sign Language (ASL) have been extensively studied for communication abilities (Gardner & Gardner, 1969; McCarthy, Jensvold & Fouts, 2013). Gardner and Gardner examined the process of teaching ASL to a chimpanzee. In 1966, they began immersing a chimpanzee, Washoe, in an ASL environment. They found that, in the first 22 months, it was evident that Washoe was using ASL as a gestural language and mode of communication. Washoe was able to reproduce the gestures used by her human caregivers and gained a large vocabulary of signs. Her signs were used conversationally, for example, when commenting on her surroundings, asking to perform certain activities, and answering questions.

Theory of mind is an important cognitive ability related to communication. Nystrom and Ashmore (2008) referred to theory of mind as the ability to understand the presence of mental states of another individual, including their beliefs, feelings, intentions, knowledge, etc. and entails the ability to recognize that other individuals also have mental states that may differ from one's own. It may also show the ability to take the perspective of another individual, which is a very important aspect of communication. To begin an interaction, a sender may take the perspective of another individual to interact in a way that is appropriate to where their attention is focused. Call and Tomasello (2008) tested theory of mind through examination of chimpanzees'

4

understanding of human goals. They assessed visual and auditory perspective-taking in chimpanzees and found that chimpanzees made inferences about a human's intentions. McCarthy, Jensvold and Fouts (2013) also found that chimpanzees gestured appropriately to a recipient's behavior and modified their interactions according social cues. They looked at what types of sequences gestures occurred in various gesture modalities, attentional states, gesture sequence lengths, and frequencies of gestures. Slight changes in eye or facial positioning can also impact communication. Hirata, Fuwa, Sugama, Kusunoki and Fujita (2010) described how chimpanzees, much like humans, rely on eyes to understand visual perception, emotion, and communicative intention of others. The researchers used eye tracking to determine how chimpanzees looked at eyes, as opposed to other areas of photographed faces. Tomasello, Call, Nagell, Olguin and Carpenter (1994) studied chimpanzees as well and found that, when it came to similar gesturing by young chimpanzees, commonalities come from the fact that most young chimpanzees have very similar goals as other youngsters and very similar behavioral repertoires since they lack experience with initiating social interactions.

The above studies show the range of research performed on large-bodied ape gesturing and communication capacities and may collectively indicate that these species have a theory of mind, which aids in successful communication. In the present study, I explored whether small-bodied apes, specifically Javan gibbons, share similar abilities through observing gesture use by a sender depending on where a recipient's attention is directed.

Gestural Definitions

When vocalizations or calls are used by a nonhuman primate species, the utterances are often accompanied by gestures. Gestures (or signals), however, may also be used without vocalization. Tanner and Byrne (1999) defined gestures as discrete, non-locomotor limb and head movements, regardless of the modality type (such as visual, auditory, and tactile), that was used when individuals were in proximity to each other and were engaged in an interaction immediately before, after, or during these movements. Pika, Liebal and Tomasello (2005) described that gestures entail the use of limb and/or body motions as a means of expression. Liebal, Call and Tomasello (2004) took another approach by breaking gestures down into three modalities. They define visual gestures as body movements; auditory gestures as non-vocal sounds; and tactile gestures as physical contact. According to Arbib, Liebal and Pika (2008), some important topics that are argued regarding the use of gestures, facial expressions, and vocalizations by nonhuman primates include whether they are used intentionally, how flexibly they are used, whether they have an inherent meaning, whether they are inherited or learned, and whether they are referentially used. Based on the definitions of gestures created by past researchers, I tested qualities of Javan gibbons' gestural communication and whether gesture modality is altered based on the recipient's attentional state.

Attentional State

Several studies have been performed regarding how a sender (or actor) attempts to interact with a receiver depending on where he or she is facing, or where his/her eyes are looking (or where they are "attending"). The recipient's state is referred to as "attentional state" (Theall & Povinelli, 1999). Theall and Povinelli found that chimpanzees

spontaneously followed the gaze direction of humans in response to head and eye movements. Chimpanzees have also been found to alter the locations of their gestures to accommodate to another's attentional state. Location, in their study, referred to food, a distracter object, or a neutral ceiling location, depending on what was being gestured about. Campion, Jensvold and Larsen's (2011) study of gesture sequences in free-living chimpanzees compared the relationship between a recipient's initial attentional state and the signaler's first gesture modality in a sequence. They recorded attentional shifts, which occurred when the recipient's attentional state changed after a signaler gave a gesture. The results showed that a signaler would adjust their gestural modality to accommodate a recipient's attentional state. For example, an auditory gesture was used to get a recipient to turn around, and then visual gestures were used once the signaler had the attention of the recipient. McCarthy, Jensvold and Fouts (2013) examined attentional state and gesture modality during chimpanzee play. They found that a signaler gestured appropriately for the recipient's attentional state. For example, when the recipient was initially attending during play, all actors most frequently used an auditory/tactile gesture. Similarly, when the recipient was initially inattentive during play, all actors most frequently used an auditory or tactile gesture and rarely used a visual gesture. Liebal, Pika, Call and Tomasello (2004) studied how orangutans, gorillas, chimpanzees, and bonobos adjusted to the attentional state of others. An example of their findings is that chimpanzees, when faced with a partner with its back turned, tended to move around to the front of a non-attending partner and then perform a gesture. This showed that the sender (or actor) was aware that he/she would have more success getting the attention of the recipient if they were facing each other. Liebal, Pika and Tomasello's (2004) study on

siamangs (*Symphalangus* syndactylus) (discussed further below) showed that siamangs appropriately adjusted the signals they used to interact with another group member based on the recipient's attentional state. This was referred to as "audience effect." Tomasello and Call (1997) stated that an "audience effect" occurs in situations in which an individual shows an expectation of a particular response from a recipient, or uses a gesture differently depending on the attentional state of the recipient. Tomasello et al. (1997) also discussed how signaling individuals might use different means of reaching a social goal of interest. Those communicative strategies may vary depending on the interactions that the sender previously had with the recipient. These studies show that both large and small-bodied ape signalers/senders have the ability to adjust gesture use appropriate to a recipient's attentional state.

Hylobatid Cognition

The family Hylobatidae consists of 16 gibbon species classified into four genera (*Hylobates*, *Hoolock*, *Nomascus* and *Symphalangus*) (Melfi, 2012). Gibbons form heterosexual pairbonds, evidenced by characteristic affiliative behaviors, such as vocal duetting and joint defense of territory (Bartlett 2011). Hylobatids are found in the rainforest canopies of the countries comprising South and Southeast Asia (Cheyne, 2009). According to Call and Tomasello (2007) little is known about gibbon cognition in comparison to large-bodied ape cognition, perhaps because these apes show a low level of motivation, and previous experimental designs have not taken the unique morphological features of gibbons' hands into consideration. Former experiments did not account for the fact that gibbons are unable to grasp small objects from flat surfaces with their fingers. Gibbon hands are different from other apes in their relatively long fingers

8

and short thumbs, which reduces their dexterity. After experiments were adapted to these differences, most could perform tasks such as pulling a string to obtain food (Beck, 1967).

Although they are different areas of study, cognition relates closely to communication because communication modes depend on an animal's cognitive abilities. For example, one individual may take the perspective of another to understand what he/she would think or feel and adjust communication modalities to match the intended recipient's perspective. Pileated gibbons (*Hylobates pileatus*) have been found to engage in visual co-orientation and appear to have expectations about another individual's attentional state (Horton & Caldwell, 2006). Gibbon cognition has also been measured through object permanence tests. Fedor, Skollár, Szerencsy and Ujhelyi (2008) assessed object permanence abilities of pileated gibbons. Their subjects were successful in single visible displacements (SVDs) and single invisible displacements (SIDs). For SVDs, the experimenter showed an object to a gibbon, put it into an empty box, and then showed his or her empty hand. For SIDs, the experimenter showed the object, closed his/her hand and put it into the box, then showed the gibbon his/her empty hand once more. The researchers scored the trial as correct if the gibbon found the object on his or her first attempt. The study gibbons seemed to have an understanding of each scenario because they scored correctly a significant amount of the time. In a study based at the Gibbon Conservation Center (GCC), Cunningham, Anderson and Mootnick (2006) performed object manipulation tests on hoolock gibbons (*Brunopithecus hoolock*). They explored whether hoolock gibbons could learn to manipulate a tool-like object to obtain a food reward. Zero-order manipulation was the focus, in which an action on one object leads to

9

another action on a second object. This study's results showed that all four subjects were able to obtain the food reward on their first attempt at the task (within a 45 min time limit). Observing object manipulation by a gibbon species is relevant because very few studies on their tool-use have been performed. Anderson (2012) assessed the basic object permanence abilities in gibbons using experiments that required the gibbons to gesture towards the correct container that concealed a food reward that they had previously seen. The gibbons were able to successfully gesture towards the correct container significantly above chance, showing cognitive abilities similar to those of large-bodied apes.

In other tests of cognition, however, gibbons have generally been considered to perform poorly compared to large-bodied apes. Examples of these tests include mirror self-recognition (MSR) and mirror self-exploration (MSE). De Veer and Den Bos (1999) concluded that MSE and MSR tests were negative for the gibbon species studied, including white-handed gibbons (*Hylobates lar*) and agile gibbons (*H. agilis*), noting that, "gibbons may fail to show MSR because they are more auditory than visually focused in communication than chimpanzees" (p.462). De Veer and Den Bos also suggest an alternative to mirror tests for more auditory primates, such as gibbons, by evaluating the their reactions to playback tapes including voices of a stranger, its partner and itself. Suddendorf and Collier-Baker (2009) also found that gibbons failed to use a mirror to find marks on their heads, even though they were able to retrieve visible marks from a mirror's surface itself and their own limbs. Their data suggest that the capacity for visual self-recognition evolved in a common ancestor of great apes, and has not reached the split that led to modern small-bodied apes. Butler and Suddendorf (2014) aimed to create a methodology to compare the brains of hominids (large-bodied apes, including humans)

and their closest relatives, the hylobatids. They examined the brains of 98 humans, 56

chimpanzees, 24 gorillas, 27 orangutans, and 25 gibbons. They found that, based on the

similarities in brain structures, there is great potential for a comparative approach

contributing to the understanding of the neurological bases of visual self-recognition and

other higher cognitive functions.

Hylobatid Communication

Chivers (1976) conducted the first study on siamang (*Symphalangus* syndactylus)

communication. His focus, however, was on auditory signals, such as vocalizations.

Since this study was performed in the wild, non-vocal gestures could not easily be seen.

Subsequent research tended to focus on analyses of duet vocalizations within and

between gibbon groups (Geissmann, 1986, 1999; Geissmann & Orgeldinger, 2000).

Geissmann (1986) studied how mated pairs typically sing together with a patterned duet

that has a partially sex-specific repertoire. Geissmann hypothesized that, if duet

development involves practice, a newly formed siamang pair should spend more time

singing than an established one. Captive pairs were the subjects of this study. At one site,

Geissmann observed that, after a partner exchange, there was an increase in the number

of call bouts per day. At another site, the average song duration decreased only slightly,

therefore resulting in an increased singing time. Geissmann noted that this does not imply

that the siamangs shortened their song bouts after forming a new pair, but merely, that

they would insert additional song bouts into that activity period. Geissmann (1999) also

found a correlation between better-coordinated siamang songs and the occurrences of

first-time copulations. The length of time a pair had been together may also effect duet

durations and frequencies over time. Geissmann and Orgeldinger (2000) noted that gibbon songs function as indicators of relationship quality between mated pairs, such as territory defense and social bond reinforcement.

Although more studies have been conducted regarding gibbon communication through vocalizations, some research has been conducted on non-vocal or gestural communication. Horton and Caldwell's (2006) study investigated pileated gibbons' (*Hylobates pileatus*) ability to detect and orient to the attentional states of both conspecifics and humans. Two adult pileated gibbons were observed. A researcher presented the gibbons with the stimuli (photographs) through the glass of their enclosure. According to Horton and Caldwell, the test photographs had three conditions including conspecific (depicting a pileated gibbon also housed at the zoo), human (depicting a human model), and control (depicting an inanimate object, a white box with two adjacent black spots). The data were coded from a video screen, split into four sections, representing different areas of eye gaze. This study revealed that pileated gibbons could detect visual co-orientation of both humans and conspecifics and that they were able to assess another's attentional state. This means that gibbons may have an understanding of how the direction of an individual's visual orientation relates to the location of another object and where that individual's focus lies. Liebal and Kaminski (2012) investigated looking behavior in response to a human who either looked up or at the gibbon in four genera (*Hylobates pileatus*, *H. moloch*, *H. lar*, and *Symphalangus syndactylus*). They found that gibbons looked up more when the experimenter was looking up compared to when they were looking at the gibbons. These findings suggest that gibbons followed human gaze, showing the skill of visual co-orientation. The findings differ from those of

12

large-bodied apes in that gibbons may not take the visual perspective of others. Since the gibbons did not habituate to a human's looking behavior over time, gaze following may be a reflexive behavior, not necessarily representative of perspective-taking.

Liebal, Pika and Tomasello (2004) investigated the social communication of captive gibbons. The study took place in two European zoos. The researchers focused on the use of signals, including tactile and visual gestures, facial expressions, and actions of 14 siamangs (*Symphalangus syndactylus*). Actions, for the purposes of this study, were described as "a complex series of movements for which it was not possible to determine which particular component of this series was initiating a recipient's response" (p. 43). Study gibbons were randomly selected and observed for 10 hours each. Using focal-animal sampling collected through digital video recording, they observed frequencies for 31 different signals, which included 12 tactile gestures, eight visual gestures, seven actions, and four facial expressions. To code these data, the researchers watched the videotapes with a slow-playback function. They used an ethogram to score gibbons' various gestures and signals. They also looked at variation of signal use between groups and whether the gestures between groups were uniform with each other. They observed 3,655 signals in total. From the data, they found that, when siamangs were attending, they used visual and facial expressions the most, followed by actions and facial expressions. When siamangs were non-attending, they used more tactile gestures and actions (visual gestures and facial expressions were rarely used). The study states that siamangs adjusted their signals appropriately for the recipient's attentional state, for example, using visual signals most often when the recipient was attending.

Liebal, Pika and Tomasello's study relates quite closely to my own in its methodology, and mine used portions of their ethogram. Rather than siamangs, however, I studied Javan gibbons and the groups for my study were housed at just one facility. Liebal, Pika and Tomasello's (2004) and my study together fill a gap in knowledge regarding the non-vocal social communication of small-bodied apes.

Javan gibbons (*Hylobates moloch*) were chosen for this particular study to represent the *Hylobates* genus. According to Nijman (2004), they are one of the rarest gibbon species. The Gibbon Conservation Center (GCC) is home to some of the only captive Javan gibbon populations in the world. In nature, this species can be found only in the rainforests of western and central Java, Indonesia and it is estimated that fewer than 4,500 individuals remain in the wild (Nijman, 2004). Like other gibbon species, Javan gibbons form heterosexual pairbonds and live in small family groups (the pair and their offspring). Their diet consists of mostly fruits, followed by leaves, and then flowers (Kim, Lappan & Choe, 2011). According to Hodgkiss et al. (2010), data on Javan gibbon reproductive biology is nearly non-existent, however, they found that females reached sexual maturity around nine years of age, with interbirth intervals of approximately two years. To increase foraging behaviors in captive Javan gibbons, Gronqvist, Kingston-Jones, May & Lehmann (2013) created three enrichment devices (novel object, olfactory, and feeding) to mimic their native environment. The novel objects included boomer balls, plastics fruits and rattling toys, the olfactory enrichment devices were composed of rope mats soaked in tap water and various scents (like peppermint) and the feeding enrichment consisted of wooden foraging boxes. They found that the presence of these enrichment devices significantly increased the frequencies of foraging behaviors, likely because they

increased similarity to their natural habitat. Since other gibbon species have been found to gesture appropriately to a recipient's attentional state and appear to exhibit perspective-taking, there is reason to believe that the same applies to Javan gibbons. I hypothesized that Javan gibbons would be equally likely to use tactile and visual gestures, actions, and facial expressions to initiate an interaction with an attending recipient. If the recipient is non-attending, the sender would be more likely to use tactile gestures and actions.

CHAPTER III

METHODS

Subjects and Study Site

This study was conducted at the Gibbon Conservation Center (GCC) in Santa

Clarita, California. GCC is a behavioral research and breeding facility that houses seven

different gibbon species with approximately 40 individuals. They aim to promote gibbon

conservation and hold educational tours twice every Saturday and Sunday. The

participants of this study included ten captive Javan gibbons (six males and four females)

in three, separately enclosed, family groups. Group 1 included Ivan (unrelated adult

male), Chloe (mother) and Goliath (Chloe's son); Group 2 contained Shelby (father),

Khusus (mother), Oula (daughter) and Winston (son); Group 3 was comprised of Perak

(father), Simpang (mother) and Hercules (son) (Table 1).

Following the methodology of Liebal, Pika, and Tomasello (2004), the gibbon

who performed the gestures, facial expression, or action was labeled the **sender.** The

recipient was the individual who the sender was attempting to interact with based on

who the sender's signal was directed toward. A recipient gibbon was scored as **attending**

"if the recipient had direct eye contact with the signaling individual or if his body

oriented towards the sender and the recipient had him in his field of vision; and **non-**

attending when the recipient's head was turned away from the sender or if his attention

was not directed towards the sender, but distracted by other social partners or incidents in

his environment" (Liebal, Pika & Tomasello, 2004, p. 43).

The sender's behaviors were scored using a modified version of Liebal, Pika, and

Tomasello's (2004) ethogram (Table 2). Previously unlisted behaviors that were observed

were also added to the ethogram. There were four signal modalities: 1) **tactile gestures**: expressive movements of the limbs or head and body postures, including physical contact of the interacting animals; 2) **visual gestures**: expressive movements of the limbs or head and body postures, including distant signals and represented movements of different body parts or specific body postures; 3) **facial expressions**: expressive movements of different parts of the face, such as mouth, lips, and eyes; and 4) **actions**: a complex series of movements for which it was not possible to determine which particular component of this series was initiating a recipient's response (p. 43). Within each signal modality, several behaviors existed. For example, the tactile modality included "slap."

Table 1
Enclosure Numbers, Names, Sexes, Birthdates, and Ages at Time of Study (summer of 2014) for Each Javan Gibbon (*Hylobates moloch*) at GCC.

Enclosure/ Family #	Individual # (for this study)	Name	Sex	D.O.B.	Age (Years)
1	1	Ivan	M	1/1/74	40
1	2	Chloe	F	2/24/90	24
1	3	Goliath	M	4/12/12	2
2	4	Shelby	M	5/18/83	31
2	5	Khusus	F	1/11/95	19
2	6	Oula	F	1/5/09	5
2	7	Winston	M	8/25/11	3
3	8	Perak	M	11/16/01	15
3	9	Simpang	F	5/23/00	14
3	10	Hercules	M	10/15/11	3

Table 2
Ethogram of Gibbon Behaviors and Signal Modalities.

Behavior (Modality)	Definition
Embrace (Tactile)	Sender approaches recipient frontally or laterally and puts one or two of his arms around the body of the recipient.
Embrace with feet (Tactile)	Sender seizes the recipient ventrally or dorsally with both legs.
Formal bite (Tactile)	Sender touches recipient with its open mouth on any body part and bites it with a low intensity.
Gentle touch (Tactile)	Sender touches the social partner softly with hand or foot on any body part.
*Hold hand/foot (Tactile)	Sender grabs the hand or foot of the recipient with their hand and holds for one or more seconds.
Kick (Tactile)	Sender touches the recipient by a fast and forceful movement of foot.
Nudge (Tactile)	Sender touches the recipient by a fast movement of hand; as opposed to 'slap', 'nudge' is not the flat hand, but single fingers or a fist are used.
Pull (Tactile)	Sender grasps any body part of the recipient by hand or foot and then performs a short, forceful movement with it.
Push (Tactile)	Sender pushes any body part of the recipient with a short, vigorous movement away.
Slap (Tactile)	Sender hits the recipient with a flat hand, rarely with a foot, at any body part.
Offer body part (Visual)	Sender lies down on his belly in front of the recipient or offers another body part for grooming; sometimes the sender sits with his body oriented towards the recipient and lowers his head as an invitation for grooming (rare).
Extend arm (Visual)	Sender extends his arm towards the recipient.
*Raise arms (Visual)	Sender holds both arms up over head, usually with hands bent forward.

Table 2 (Continued)

Behavior (Modality)	Definition
Shake object (Visual)	Sender shakes an object.
Throwback head (Visual)	Sender moves his head with a short movement repeatedly back and forth.
Wrist offer (Visual)	Sender approaches the recipient with extended arm and offers him his bent wrist by holding it in front of the face of the recipient.
*Air somersault (Action)	While hanging from caging, sender flips body. Much, like somersault, but suspended.
Biting (Action)	Sender bites the recipient on any body part; as opposed to the 'formal bite' this is not just a hinted signal but is performed with higher intensity.
Chasing (Action)	Sender approaches the recipient by rapid brachiation or running.
*Grab item (Action)	Sender takes item from recipient's hands, typically a toy or food item.
*Groom (Action)	Sender picks through recipient's fur. Usually follows the recipient offering body part.
Jump at (Action)	Sender jumps at the recipient or drops on him out of a hanging position.
*Leap (Action)	Sender hops up from the ground and lands back down.
*Reach for (Action)	Sender extends arm or hand toward recipient with rapid motion, as if trying to grab.
*Rope twirl (Action)	Sender holds onto and twists rope, then spins in circles while suspended.
*Slam body (Action)	Sender hits own body against caging wall while suspended.
Somersault (Action)	Sender tumbles towards the recipient.
Swinging (Action)	Sender hangs in front of the recipient and rocks his body to and fro with rapid movements.

Table 2 (Continued)

Behavior (Modality)	Definition
*Throw dirt (Action)	Sender throws dirt in the air, usually accompanied by a twirl.
*Twirl (Action)	Sender spins bipedally on ground.
Wrestling (Action)	Sender approaches the recipient and starts to tussle with him; this action can be accompanied by biting or slapping and is performed in a lying, sitting or hanging position.
Grin (Facial expression)	Mouth of the sender is slightly opened and the corners of the mouth are withdrawn with the teeth scarcely visible between the lips.
*Lip smack (Facial expression)	Mouth of sender goes from slightly open to closed (rapidly) several times consecutively.
Mouth-open half (Facial expression)	Mouth is opened slightly, so that the canine teeth are almost completely covered by lips; the shape of the mouth is oval with the corners of the mouth withdrawn very little.
Mouth-open full (Facial expression)	Mouth is opened to the full extent with the canine teeth and the palate visible.

* = Current study

Source: Adapted from Liebal, Pika and Tomasello, 2004: 44-45

Behaviors not observed: Hold tight (T), Rub under arms (T), Shake body part (T), Direct positioning (V), Jerking body movements (V), Present genitals (V), Bluff chase (A), and Pull-a-face (F).

Procedure

I video recorded the gibbons at GCC from 26 June – 25 July 2014. Recordings were made during the times when the gibbons are known to be most active (outside of morning duetting and feedings) and when the temperature was milder (between 0600-1100h). I collected data using all-occurrence focal group sampling (Altmann, 1974), in

20

which one group of animals was observed and their behaviors were scored from an ethogram (Table 2). Each focal gibbon group was video recorded for 15-minutes. Eight (randomly selected) focal gibbon groups were observed each day, making a total of two hours of footage per day. I used randomized sequencing to determine the focal groups. Groups were numbered from one to three and ordered randomly (Table 2). For example, if the selected order was 3, 1, 2, filming started with Group 3 (Perak, Simpang and Hercules), then Group 1 (Ivan, Chloe and Goliath), then Group 2 (Shelby, Khusus, Oula and Winston) and so on until the end was reached when a new random sequence was created. Filming focused on two individuals at a time unless only one gibbon was in the camera's field of vision. If an interaction began between two different individuals, recording focused on interacting gibbons.

From video footage, I recorded onto data sheets video timestamp, sender, recipient, whether the recipient was attending or non-attending, the gesture used, the gesture modality (tactile and visual gestures, facial expressions, or actions), and duration (for state behaviors) (Appendix A).

Reliability

During reconnaissance observations at GCC, I videotaped several hours of the gibbons during the time they were most active. From the reconnaissance footage, I chose from video segments during which most of my ethogram behaviors (Table 2) were exhibited and used these to test intra-observer reliability. I scored the same segments of video (10% of total footage) at the beginning and at the midpoint of the study and compared the number of matches for each behavior and for animal identification, with a

score $\geq$ 85% acceptable for ethogram behaviors, and a score of 100% acceptable for animal identities.

Analysis

Attending Versus Non-Attending (Aggregated Data). For all 10 gibbons, I used a chi square test for independence to test the hypothesis that there was significant variation in modalities used by a sender based upon whether the recipient was attending or non-attending. The total frequencies of gestures used in each modality were compared in attending and non-attending categories.

Attending Versus Non-Attending (Juveniles/Adults). To test the hypothesis that there was significant variation in modalities used by a sender based on whether the recipient was attending or non-attending for each gibbon, I used 10 separate Fisher's Exact Probability tests because some of the values were too low for a chi square to be run.

To determine whether each modality was used significantly more or significantly less when the recipient was attending or non-attending, I used a *t* test. Rates for gestures used in each modality when the recipient was attending and non-attending were calculated for each of the 10 gibbons.

Another *t* test was also used to differentiate between age classes. Rates for gestures used in each modality when the recipient was attending and non-attending were calculated for the four juvenile gibbons, then for the six adult gibbons.

22

CHAPTER IV

RESULTS

Over 20 days, 10 gibbons were observed in three family groups. I collected equal amounts of data for each group (13.33 hours per family, or 40 hours total). In a total of 1,143 interactions 504 were *actions* (44%), 418 were *tactile gestures* (37%), 173 were *facial expressions* (15%), and 48 were *visual gestures* (4%). Modality use while recipient was attending vs. non-attending was as follows: *visual gestures*: $N = 45$ attending (94%), $N = 3$ non-attending (6%); *facial expressions*: $N = 143$ attending (83%), $N = 30$ non-attending (17%); *actions*: $N = 277$ attending (55%), $N = 277$ non-attending (45%); *tactile gestures*; $N = 173$ attending (41%), $N = 245$ non-attending (59%) (Table 3).

Table 3
Occurrences of Signal Use by Each Sender Gibbon While Recipient Was Attending (ATT) vs. Non-Attending (NATT) in Each Modality.

Subjects by Enclosure	Tactile ATT	Tactile NATT	Visual ATT	Visual NATT	Actions ATT	Actions NATT	Facial Exp. ATT	Facial Exp. NATT	TOTAL
Chloe	12	7	3	0	14	14	14	3	67
Goliath	44	48	7	0	36	35	22	3	205
Ivan	18	6	16	0	18	4	13	6	81
Khusus	13	5	1	0	9	1	16	4	49
Oula	14	27	3	2	40	31	16	5	138
Shelby	2	2	0	0	0	1	1	0	6
Winston	21	50	2	0	79	62	9	3	226
Hercules	32	77	10	1	68	59	25	2	274
Perak	11	8	2	0	10	17	18	3	69
Simpang	6	5	1	0	3	3	9	1	28
TOTAL	173	245	45	3	277	227	143	30	1143

Note. Italicized individuals classified as juvenile.

Reliability

To test intra-observer reliability, the same video segments (10% of the total footage) were scored at the beginning and midpoint of the study. The number of matches

for each behavior and animal identification were compared. Ethogram behaviors were 93% (1,093/1,143) and animal identities were 100% (1,143/1,143).

Attending Versus Non-Attending (Aggregated Data)

To test the hypothesis that there was significant variation in modalities used by a sender based upon whether the recipient was attending or non-attending, I ran a chi square test for independence. Total frequencies of gestures used in each modality were compared in attending and non-attending categories (Table 4; $\chi^2 = 113.99$ (3), $p = <0.0001$).

To determine whether or not there was a significant difference between attending and non-attending in each modality, I ran t tests using rates for attending and non-attending in each modality for all 10 gibbons. The results show that gibbon senders used *visual gestures* (t (18) = 2.79, p = 0.01) and *facial expressions* (t (18) = 2.60, p = 0.02) significantly more when the recipient was attending, and *tactile gestures* (t (17) = 2.47, p = 0.02) significantly more when the recipient was non-attending. There was no significant difference in the *actions* modality (t (18) = 0.82, p = 0.43). This shows that a sender gibbon used visual gestures and facial expressions significantly more when the recipient was attending and that a sender gibbon used tactile gestures significantly more when the recipient was non-attending.

Table 4
Total occurrences of signals used in each modality while recipient was attending (ATT) vs. non-attending (NATT).

	Tactile	Visual	Actions	Facial Exp.	Total
ATT	173	45	277	143	638
NATT	245	3	227	30	505
Total	418	48	504	173	1,143

Attending Versus Non-Attending (Juveniles/Adults)

To test the hypothesis that there was significant variation in modalities used by a sender based upon whether the recipient was attending or non-attending, of the 10 gibbons, I used a Fisher's Exact Probability test because some values were too small to be run with chi square. This test showed significant difference in five out of 10 gibbons, four of which were juveniles. Significant values for individuals were as follows: Goliath: $P = <0.0001$, Hercules: $P = <0.0001$, Oula: $P = 0.01$, Perak: $P = 0.003$, and Winston: $P = <0.0001$. Not significant values for individuals were as follows: Chloe: $P = 0.09$, Ivan: $P = 0.07$, Khusus: $P = 0.63$, Shelby: $P = >0.99$, and Simpang: $P = 0.2$.

To determine whether or not there was a significant difference between attending and non-attending in each modality for each age class (juvenile and adult), I ran another t test using rates for each of the 10 individuals. In a total of 843 juvenile sender interactions, 410 were *actions* (49%), 323 were *tactile gestures* (38%), 85 were *facial expressions* (10%), and 25 were *visual gestures* (3%). Modality use while recipient was attending vs. non-attending was as follows: *actions*: $N = 223$ attending (54%), $N = 187$ non-attending (46%); *tactile gestures*: $N = 111$ attending (34%), $N = 212$ non-attending (66%); *facial expressions*: $N = 72$ attending (85%), $N = 13$ non-attending (15%); *visual gestures*: $N = 22$ attending (88%), $N = 3$ non-attending (12%). The *t*-test results showed that juveniles used *visual gestures* ($t(6) = 2.85$, $p = 0.03$) and *facial expressions* ($t(6) = 3.88$, $p = <0.0001$) significantly more while the recipient was attending and *tactile gestures* ($t(6) = 3.67$, $p = 0.01$) significantly more when the recipient was non-attending.

There was no significant difference for juveniles in the *actions* modality (t (6) = 0.83, p = 0.44).

In a total of 300 adult sender interactions, 94 were *actions* (32%), 95 were *tactile gestures* (31%), 88 were *facial expressions* (29%), and 23 were *visual gestures* (8%). Modality use while recipient was attending vs. non-attending was as follows: *actions*: N = 54 attending (57%), N = 40 non-attending (43%); *tactile gestures*: N = 62 attending (65%), N = 33 non-attending; *facial expressions*: N = 71 attending (81%), N = 17 non-attending (19%); *visual gestures*: N = 23 attending (100%), N = 0 non-attending (0%). The *t*-test results showed that adults used *facial expressions* (t (10) = 2.25, p = 0.05) significantly more while the recipient was attending. There was no significant difference in *tactile gestures* (t (10) = 1.01, p = 0.34), *visual gestures* (t (10) = 2.13, p = 0.06), or *actions* (t (10) = 1.72, p = 0.12).
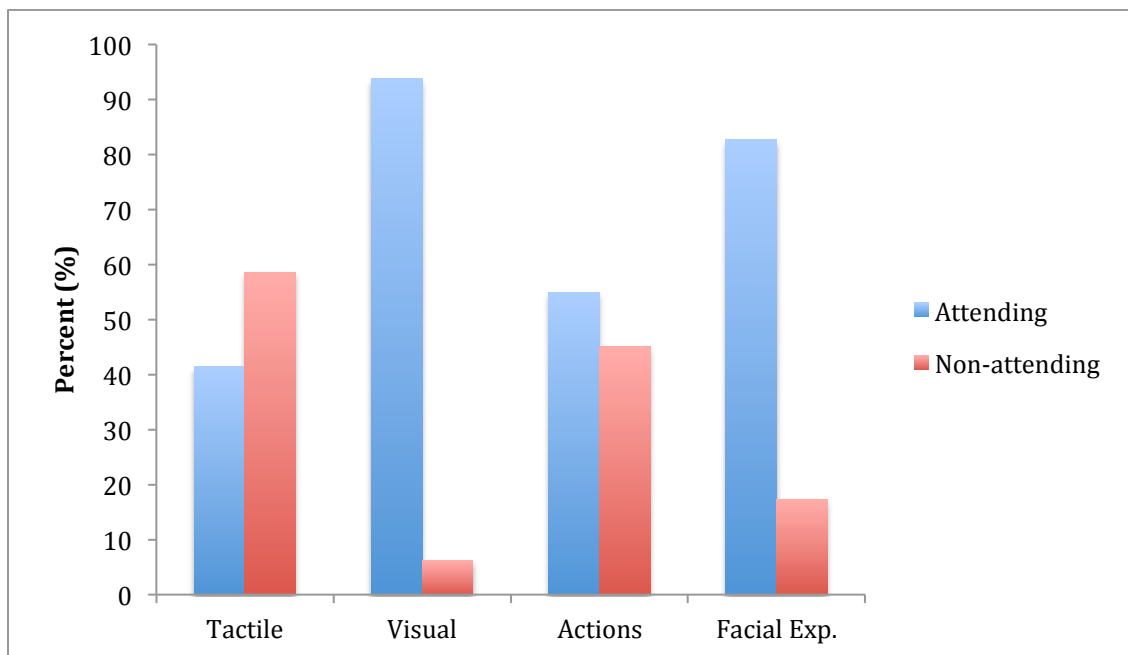
Figure 1. Bar graph of signal use when recipient was attending vs. non-attending in each modality.
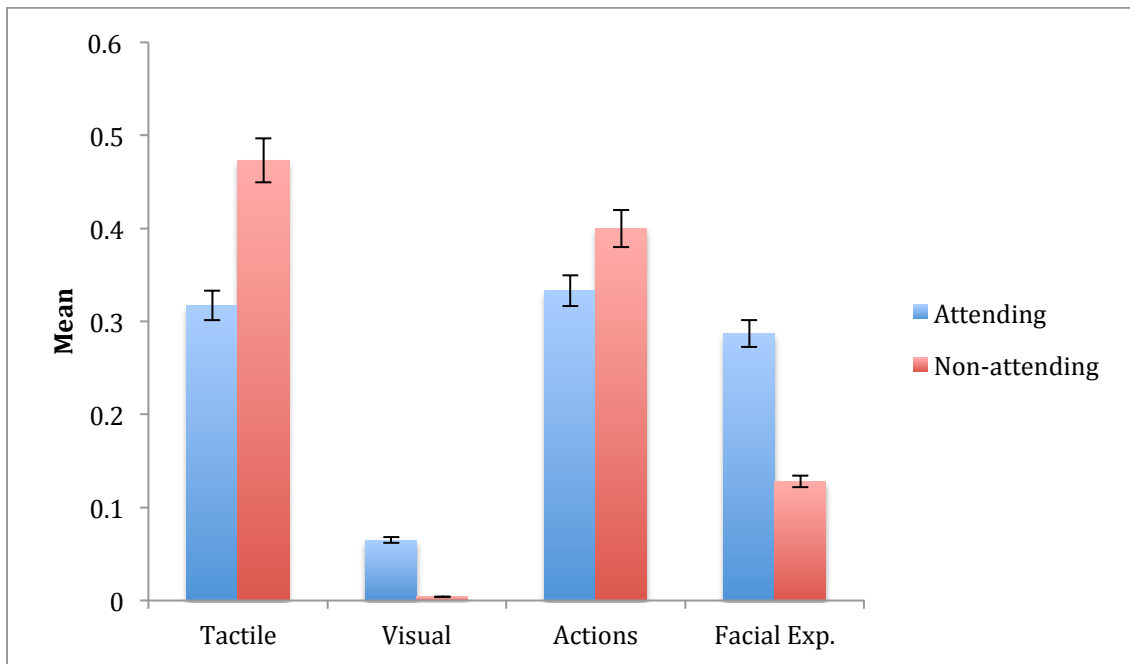
Figure 2. Bar graph of means for signal use when the recipient was attending vs. non-attending in each modality. Error bars represent 95% CI.

Figure 3. Bar graph of signal use by juveniles in each gesture modality.

Figure 4. Bar graph of means for signals used by juveniles in each gesture modality. Error bars represent 95% CI.

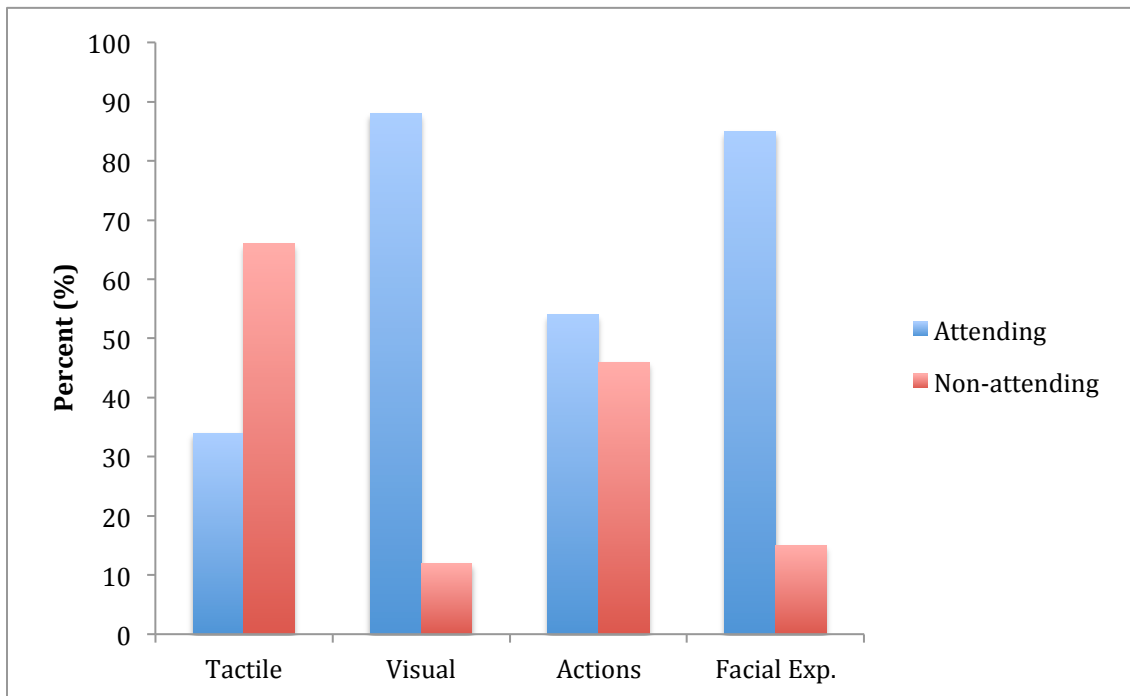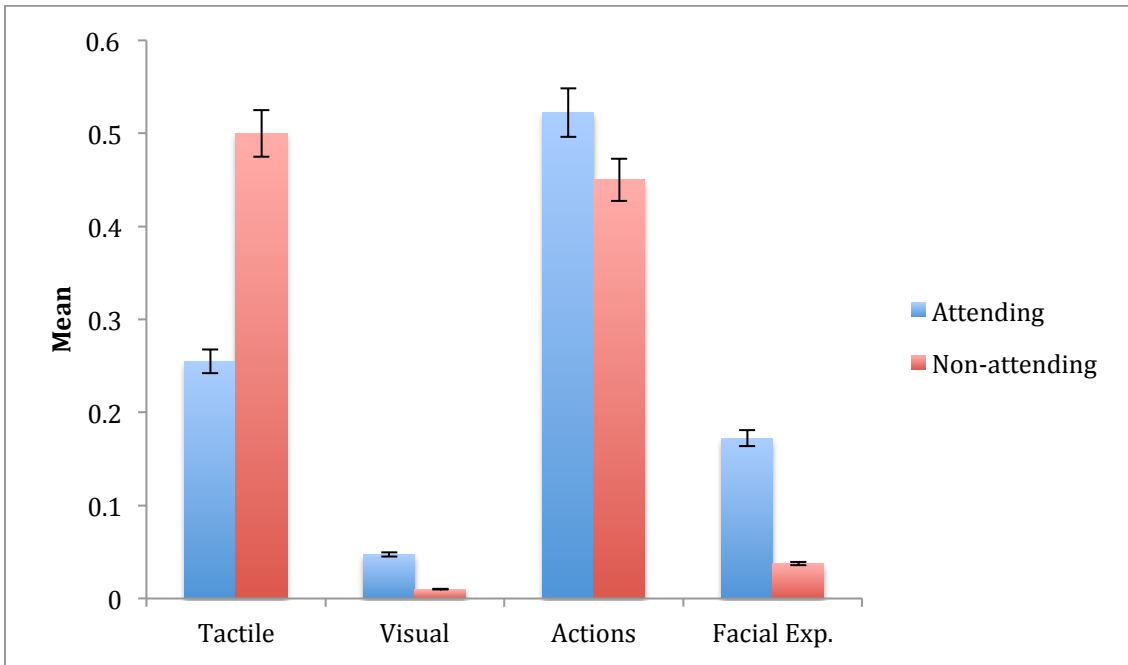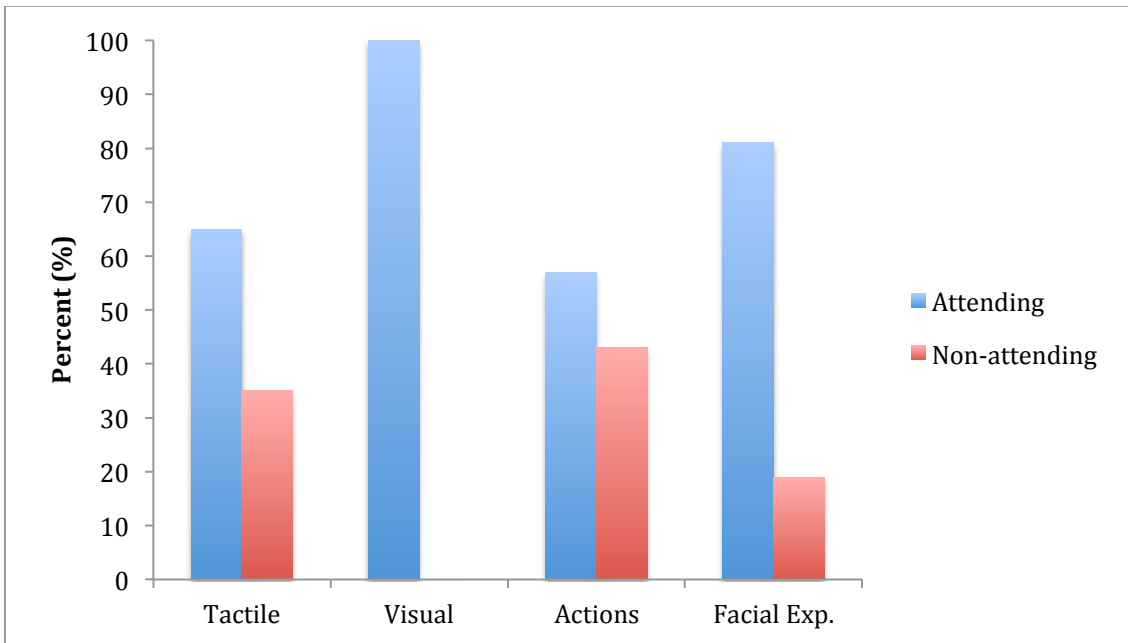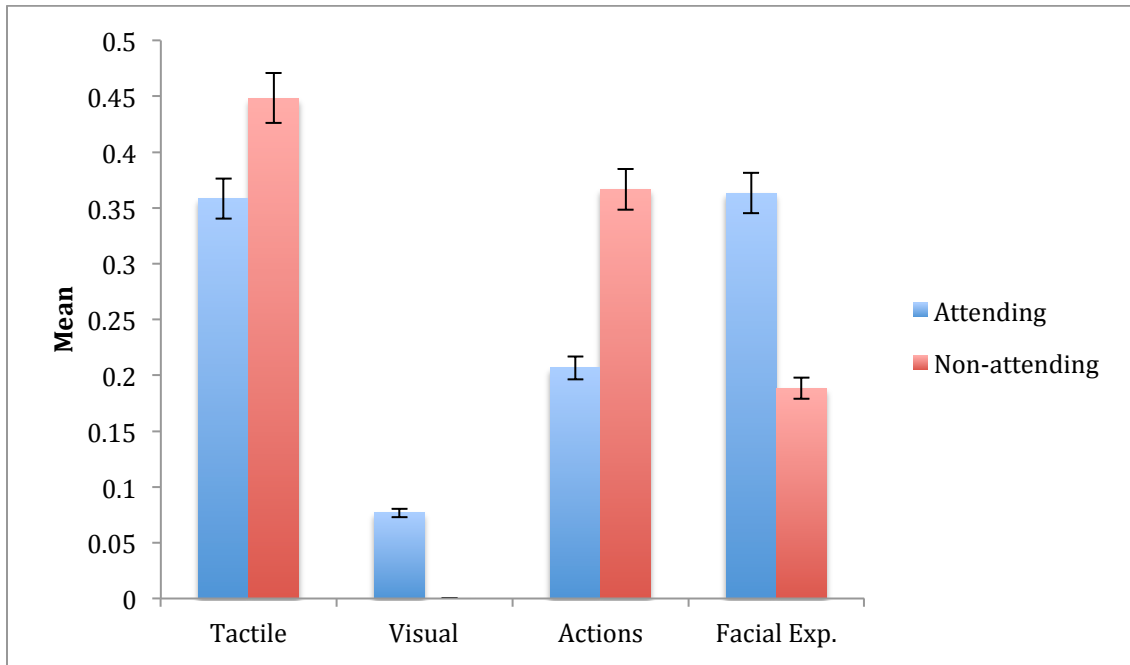*Figure 5.* Bar graph of signal use by adults in each gesture modality.

Figure 6. Bar graph of means for signals used by adults in each gesture modality. Error bars represent 95% CI.

CHAPTER V

DISCUSSION

Large-bodied ape cognition and communication have been extensively studied (for example, Goodall, 1986; Ogden & Schildkraut, 1991; Cartmill & Byrne, 2007; Pika, Liebal & Tomasello, 2005; Gardner & Gardner, 1969; McCarthy, Jensvold & Fouts, 2013), but less is known regarding cognition and communication in small-bodied apes. This study aimed to determine whether small-bodied apes exhibit behaviors and abilities similar to those documented in large-bodied apes. Generally, small-bodied apes perform poorly in cognition studies that use object permanence tests compared to large-bodied apes, but this might be partly due to their anatomy. The structure of gibbon hands may make it difficult for them to pick up objects from a flat surface, which may explain their poor performance in object permanence tests. (Beck, 1967; Hill, Collier-Baker & Suddendorf, 2011). Other studies, however, have shown them to have cognitive abilities similar to those of large-bodied apes. (Liebal, Pika & Tomasello, 2004; Cunningham, Anderson & Mootnick, 2006; Horton & Caldwell, 2006; Ujhelyi, 2008; Anderson, 2012; D'agostino & Cunningham, 2015).

The mode in which an individual communicates is a key aspect of ape cognition. According to some researchers, the way individuals communicate may indicate that they have a theory of mind or perspective-taking: the ability for an individual to understand the goals and take the perspective of another individual, whether human or conspecific (Nystom & Ashmore, 2008). Theory of mind has been inferred in several studies for several species (*Pan troglodytes*: McCarthy, Jensvold & Fouts, 2013; Hirata et al., 2010;

Call & Tomasello, 2008; Tomasello et al., 1994; *Pongo pygmaeus*: Cartmill & Byrne, 2007; *Gorilla gorilla*: Tanner & Byrne, 1996).

A sender gesturing appropriately to a recipient's attentional state appears to be an imperative aspect of non-vocal social communication in both large and small-bodied apes and shows that the sender may have an understanding of a recipient's perception of the signal being sent. This is seen in the results of numerous studies (*Pan troglodytes*: McCarthy, Jensvold & Fouts, 2013; Campion, Jensvold & Larsen, 2011; Theall & Povinelli, 1999; *Gorilla gorilla*: Tanner & Byrne, 1996; *Pongo pygmaeus*, *Gorilla gorilla*, *Pan troglodytes*, and *Pan paniscus*: Liebal, Pika, Call & Tomasello, 2004; *Symphalangus syndactylus*: Liebal, Pika & Tomasello, 2004). The present study also showed that sender gibbons gestured appropriately to a recipient's attentional state in three out of four communication modalities, but this was more descriptive of juvenile than of adult gibbons in my sample.

<center>Attending Versus Non-Attending (Aggregated Data)</center>

For all 10 gibbons, a chi square test for independence showed a significant difference between attending and non-attending categories, meaning the distribution between gestural modalities was likely not due to chance. After obtaining these results, I ran a *t* test to determine whether a there was significant difference in the use of gestures while the recipient was attending versus non-attending between each modality (tactile gestures, visual gestures, actions, and facial expressions). Gibbon senders used visual gestures and facial expressions significantly more when the recipient was attending, showing that they may understand that the recipient is able to see their gestures. Senders also used tactile gestures significantly more when the recipient was non-attending. This

<center>31</center>

may show that the senders understand that the recipient cannot see the senders; therefore a visual gesture or facial expression would be ineffective. There was no significant difference between attending and non-attending in the actions modality. The reason for the insignificant results may be because of the category itself. "Actions" ended up being a miscellaneous category and included many behaviors that could have been separated into different categories. For example, "wrestle" was coded as an action, when it could have been coded as a tactile gesture. If this category was eliminated and its behaviors were distributed into the other three modalities, the results may have been different. "Actions" were left as a category to mirror the methodology of Liebal, Pika and Tomasello (2004).

These results support the hypotheses in that sender gibbons used visual gestures and facial expressions more when the recipient was attending, and used tactile gestures more when the recipient was non-attending. Significant results were found in three out of the four modality categories. This shows that gibbons may use gestures appropriate to a recipient's attentional state, much like what was found by Liebal, Pika and Tomasello (2004) in siamangs (*Symphalangus syndactylus*). From the data, they found that, when siamangs were attending, they used visual and facial expressions the most, followed by actions and facial expressions. When siamangs were non-attending, they used significantly more tactile gestures and actions. Similar to in the present study, visual gestures and facial expressions were directed significantly more often towards an attending recipient than were tactile gestures and actions. Liebal, Pika and Tomasello (2004), however, found no significant difference between attentional state in tactile gestures or actions, whereas my study showed that senders used tactile gestures significantly more when a recipient was non-attending. These differences may be due to

32

variation in sample sizes, levels of activity in individual gibbons, or differences in enclosure types/sizes.

<div align="center">Attending Versus Non-Attending (Juveniles/Adults)</div>

To test the hypothesis that there was significant variation in modalities used by a sender based upon whether the recipient was attending or non-attending, I ran a Fisher's Exact Probability test because some values (such as zero occurrences in the visual modality) were too small to be run with chi square. This test showed significant differences in five out of 10 gibbons, four of which were juveniles. Since all four juvenile gibbons and only one of the six adults showed a significant p-value, I decided to separate the data for the gibbons and analyze according to age class (juvenile or adult). Past literature has mentioned differences in the amounts of interaction performed by juvenile and adult mammals in a play context. Oliveira, Rossi, Silva, Lau and Barreto (2009), for example, stated that immature individuals play and interact more than adults. This may be because the juvenile stage coincides with the most important period of physical, hormonal, and social development in a mammal. Being more "playful" could account for an increase in frequencies of certain communicative behaviors and mark the beginnings of perspective-taking. There may also be developmental differences between large and small-bodied apes, especially in studies on theory of mind. De Veer and Den Bos (1999) discussed that large-bodied apes tend to only pass mirror self-recognition tests after a certain age.

To determine whether or not there was a significant difference between attending and non-attending in each modality for each age class (juvenile and adult), I ran another *t* test using rates of gesturing for each of the 10 individuals. There were 843 interactions by

<div align="center">33</div>

four juveniles and 300 interactions by six adults. The *t*-test results showed that juveniles used visual gestures and facial expressions significantly more while the recipient was attending and tactile gestures significantly more when the recipient was non-attending. There was no significant difference for juveniles in the actions modality, likely for the same reason as in the aggregated data: that "actions" acted as a miscellaneous category. Adults showed significant difference in only the facial expressions category, in that facial expressions were used significantly more when the recipient was attending. Juvenile gibbons appeared to gesture much more frequently than did adults. This may be because juveniles are in a crucial stage of development and expending their higher levels of energy, particularly in a play context (Oliveira et al., 2009). Liebal, Pika and Tomasello (2004), however, did not observe more interactions in their sample of juvenile siamangs.

These results reflect those of the aggregated data and show that juvenile gibbons may gesture appropriately to a recipient's attentional state. The *t*-test results also showed that adults used facial expressions significantly more when the recipient was attending, but there was no significant difference in tactile gestures, visual gestures or actions. Since the occurrences of gestures by the juvenile gibbons was almost three times that of the adults, these data may not accurately represent the abilities of adult Javan gibbons. Adults may gesture less because of their bond duration: if bonded for a long period of time, they may not need to use effective communication to understand one another. Increased age may also mean decreased activity. I noticed that some of the older individuals, like Shelby, were not very energetic and infrequently interacted with others. Younger individuals appeared more curious and were attempting to interact very frequently.

Conclusion and Future Recommendations

In conclusion, the juvenile Javan gibbons at the Gibbon Conservation Center appear to gesture appropriately to a recipient's attentional state in three out of four categories and adults gesture appropriately in one out of four categories. When the pooled data were aggregated, gibbon senders used visual gestures and facial expressions significantly more when the recipient was attending and tactile gestures significantly more when the recipient was non-attending. No significant difference was found in the actions modality. The same results were seen in juvenile gibbons; however, adults only showed significant difference in the facial expressions modality while the recipient was attending. The results of juveniles in this study show a possibility of perspective taking in small-bodied apes, much like what has been observed in large-bodied apes.

Recommendations for Future Research

For future research, I recommend that the amount of recorded data increase. Liebal, Pika and Tomasello's (2004) study recorded a total of 140 hours of data, whereas my study had 40 hours of recorded data. They also had a total of 14 individuals, whereas mine had 10. These may reasons for the differences in our data on adult gibbons. Data should be recorded for at least three months as opposed to one to have a longer sampling period. Collection should also happen in the spring when the weather is milder. During the summer (when this study was performed), temperatures reached up to about 43 degrees Celsius, which appeared to be uncomfortable for the gibbons. In a cooler temperature, the gibbons may be more active, and therefore gesture more frequently. I would also expand the study to include other gibbon taxa. Some gibbon taxa may be

35

more gregarious than others, for example. According to Chivers (1976), this is true of siamangs.

In another analysis, sex and/or dominance class should be taken into account so see if males gesture differently from females and vice versa, or if more or less dominant individuals gesture differently. There may be contextual differences found as well (agonistic, affiliative, play, etc.). A social network analysis may also be performed to show who gestures with whom.

The actions modality ended up being more of a miscellaneous category in this study; however, it was used in order to make my data comparable to published research (Liebal, Pika & Tomasello, 2004). If the actions modality was eliminated, and the gestures within it were distributed into the other three modalities, the results may be altered and show higher levels of significance. This could potentially also resolve the differences between frequencies in juveniles versus adults.

Two gibbons were outliers in my dataset: Simpang and Shelby. During the time of this study, Simpang, the adult female of her group (enclosure #3), was suffering from a bladder stone, which was surgically removed after this study was completed. Because of this, she was more lethargic and did not engage in as many interactions as she likely would have under healthier circumstances. Shelby, the adult male of his group (enclosure #2), was the gibbon who interacted the least out of all individuals. He usually kept to himself as the other three gibbons in that enclosure spent time with one another. At 31 years of age, Shelby was the second oldest of the observed gibbons, therefore, he could have had less energy than the other members of his family group. Any other reasons for his lack of participation are unknown.

REFERENCES

Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, *49*(3). 227- 266.

Anderson, M. R. (2012). Comprehension of object permanence and single transposition in gibbons. *Behaviour*, *149*, 441-459.

Arbib, M. A., Liebal, K., & Pika, S. (2008). Primate vocalization, gesture, and the evolution of human language. *Current Anthropology*, *49*(6), 1053-1076.

Bartlett, T. Q. (2011). The Hylobatidae: Small Apes of Asia. In C. J. Campbell, A. Fuentes, K. C. Mckinnon, M. Panger & S. K. Bearder (Eds.), *Primates in perspective* (pp. 300-312). Oxford: Oxford University Press.

Beck, B. B. (1967). A study of problem solving by gibbons. *Behaviour*, *29*, 95-109.

Butler, D. & Suddendorf, T. (2014). Reducing the neural search space for hominid cognition: What distinguishes human and great ape brains from those of small apes? *Psychonomic Bulletin & Review*, *21*(3), 590-619.

Call, J. & Tomasello M. (Eds.) (2007). *The gestural communication of apes and monkeys*. Mahwah, N.J.: Lawrence Erlbaum.

Call, J. & Tomasello M. (2008). Does the chimpanzee have a theory of mind? 30 years later. *Trends in Cognitive Sciences*, *12*(5), 187-192.

Campion, T.L., Jensvold, M.L., & Larsen, G. (2011). Use of gesture sequences in free-living chimpanzees *(Pan troglodytes schweinfurthii)* in Gombe National Park, Tanzania. *American Journal of Primatology, 73*(1), 97.

Cartmill, E. A. & Byrne, R. W. (2007). Orangutans modify their gestural signaling according to their audience's comprehension. *Current Biology*, *17*, 1345-1348.

Cheyne, S. M. (2009) Studying social development and cognitive abilities in gibbons (*Hylobates* SPP): Methods and applications. In Potocki, E. & Kransiñski, J. (Eds.), Primatology: Theories, Methods and Research, pp. 129-152. Nova Science Publishers, Inc.

Chivers, D. J. (1976). Communication within and between family groups of siamang (*Symphalangus syndactylus*). *Behaviour*, *57*, 116-135.

Cunningham, C.L., Anderson, J.R. & Mootnick, A.R. (2006). Object manipulation to obtain food reward in hoolock gibbons, *Bunopithecus hoolock. Animal Behaviour*, *71*, 621-629.

D'agostino, J. & Cunningham, C. (2015). Preliminary investigation of flexibility in learning color-reward associations in gibbons (Hylobatidae). *American Journal of Primatology*, DOI: 10.1002/ajp.22410.

De Veer, M. W. & Van Den Bos, R. (1999) A critical review of methodology and interpretation of mirror self-recognition research in nonhuman primates. *Animal Behaviour*, *58*, 459-468.

Fedor, A., Skollár, G., Szerencsy, N, & Ujhelyi, M. (2008). Object permanence tests on gibbons (Hylobatidae). *Journal of Comparative Psychology*, *122*(4), 403-417.

Gardner, R.A. & Gardner, B.T. (1969). Teaching sign language to a chimpanzee. *Science*, *165*, 664-672.

Geissmann, T. (1986). Mate change enhances duetting activity in the siamang gibbon (*Hylobates syndactylus*). *Behaviour*, *96*, 17-27.

Geissmann, T. (1999). Duet songs of the siamang, *Hylobates syndactylus*: II. Testing the pair-bonding hypothesis during a partner exchange. *Behavior*, *136*(8), 1005-1039.

Geissmann, T. & Orgeldinger, M. (2000). The relationship between duet songs and pair

    bonds in siamangs, *Hylobates syndactylus. Animal Behaviour*, *60*, 805-809.

Goodall, J. (1986). *The chimpanzees of Gombe: Patterns of behavior*. Cambridge, MA:

    Harvard University Press.

Gronqvist, G., Kingston-Jones, M., May, A. & Lehmann, J. (2013). The effects of three

    types of environmental enrichment on the behaviour of captive Javan gibbons

    (*Hylobates moloch*). *Applied Animal Behaviour Science*, *147*, 214-223.

Hill, A., Collier-Baker, E. & Suddendorf, T. (2011). Inferential reasoning by exclusion in

    great apes, lesser apes, and spider monkeys. *Journal of Comparative Psychology*,

    125(1), 91-103.

Hirata, S., Fuwa, K., Sugama, K., Kusunoki, K., & Fujita, S. (2010). Facial perception of

    conspecifics: Chimpanzees (*Pan troglodytes*) preferentially attend to proper

    orientation and open eyes. *Animal Cognition*, *13*, 679-688.

Hodgkiss, S., Thetford, E., Waitt, C.D. & Nijman, V. (2010). Female reproductive

    parameters in the Javan gibbon (*Hylobates moloch*). *Zoo Biology*, *29*, 449-456.

Horton, K. E. & Caldwell C.A. (2006). Visual co-orientation and expectations about

    attentional orientation in pileated gibbons (*Hylobates pileatus*). *Behavioural*

    Processes, *72*, 65-73.

IUCN Red List of Threatened Species. Version 2013.2 <www.iucnredlist.org>.

    Downloaded on 28 April 2014).

Kim, S., Lappan, S. & Choe, J.E. (2011). Diet and ranging behavior of the endangered

    javan gibbon (*Hylobates moloch*) in submontane tropical rainforest. *American*

    Journal of Primatology, *73*, 270-280.

Liebal, K., Call, J., & Tomasello, M. (2004). Use of gesture sequences in chimpanzees. *American Journal of Primatology*, *64*, 377-396.

Liebal, K. & Kaminski, J. (2012). Gibbons (*Hylobates pileatus*, *H. moloch*, *H. lar*, *Symphalangus syndactylus*) follow human gaze, but do not take the visual perspective of others. *Animal Cognition*, *15*(6), 1211-1216.

Liebal, K., Pika, S., & Tomasello, M. (2004). Social communication in siamangs (*Symphalangus syndactylus*): Use of gestures and facial expressions. *Primates*, *45*, 41-57.

Liebal, K., Pika, S., Call, J., & Tomasello, M. (2004). To move or not to move: How apes adjust to the attentional state of others'. *Interaction Studies*, *5*(2), 199-219.

Maestripieri, D. (1999). Primate social organization, gestural repertoire size, and communication dynamics: a comparative study of macaques. In: King BJ (ed) The evolution of language: assessing the evidence from nonhuman primates. School of American Research, Santa Fe, pp. 55–77.

McCarthy, M. S., Jensvold, M. L. A., & Fouts, D. H. (2013). Use of gesture sequences in captive chimpanzee (*Pan troglodytes*) play. *Animal Cognition*, *16*, 471-481.

Melfi, V. A. (2012). Gibbons: Probably the most endangered primates in the world. *International Zoo Yearbook*, *46*, 239-240.

Nijman, V. (2004). Conservation of the Javan gibbon *Hylobates moloch*: Population estimates, local extinctions, and conservation priorities. *The Raffles Bulletin of Zoology*, *52*, 271-280.

Nystrom, P. & Ashmore, P. (2008). The primate brain and complex behavior. In P. Nystom & P. Ashmore (Eds.), *The life of primates* (pp. 325-350). Upper Saddle

River, N.J.: Pearson Prentice Hall.

Ogden, J. & Schildkraut, D (1991). Compilation of gorilla ethograms. Atlanta: Gorilla Behavior Advisory Group.

Oliveira, A. F. S., Rossi, A.O., Silva, L. F. R., Lau, M. C., Barreto, R. E. (2010). Play behaviour in nonhuman animals and the animal welfare issue. *Journal of Ethology*. *28*, 1-5.

Pika, S., Liebal, K., & Tomasello, M. (2003). Gestural communication in young gorillas (*Gorilla gorilla*): Gestural repertoire, learning, and use. *American Journal of Primatology*, *60*, 95-111.

Pika, S., Liebal, K., & Tomasello, M. (2005). Gestural communication in subadult bonobos (*Pan paniscus*): Repertoire and use. *American Journal of Primatology*, *65*, 39-61.

Suddendorf, T. & Collier-Baker, E. (2009). The evolution of primate visual self-recognition: Evidence of absence in lesser apes. *Proceedings of the Royal Society B*, *276*, 1671-1677.

Tanner, J. E. & Byrne, R. W. (1996). Representation of action through iconic gesture in captive lowland gorilla. *Current Anthropology*, *37*(1), 162-173.

Tanner, J. E. & Byrne, R. W. (1999). The development of spontaneous gestural communication in a group of zoo-living gorillas. In S.T. Parker, R.W. Mitchell & H. L. Miles (Eds.) *The mentalities of gorillas and orangutans: Comparative perspectives* (pp. 211-239). New York: Cambridge University Press.

Theall, L. A., & Povinelli, D. J. (1999). Do chimpanzees tailor their gestural signals to fit the attentional states of others? *Animal Cognition*, *2*, 207-214.

Tomasello, M. & Call, J. (1997). Primate cognition. New York: Oxford University Press.

Tomasello, M., Call, J., Nagell, K., Olguin, R., & Carpenter, M. (1994). The learning and
use of gestural signals by young chimpanzees: A trans-generational study.
Primates, *35*(2), 137-154.

Tomasello, M., Call, J., Warren, J., Frost T., Carpenter, M., Nagell, K. (1997). The
ontogeny of chimpanzee gestural signals: A comparison across groups and
generations. *Evolution of Communication*, *1*, 223–253.

Appendix A

Sample Data Sheet

	TIME	SENDER	RECIPIENT	R's ATTEN. STATE	GESTURE	GESTURE TYPE
1	NO INTERACTION	NO INTERACTION	NO INTERACTION	NO INTERACTION	NO INTERACTION	NO INTERACTION
1	0:02:32	Goliath	Ivan	NATT	Reach for	Action
1	NO INTERACTION	NO INTERACTION	NO INTERACTION	NO INTERACTION	NO INTERACTION	NO INTERACTION
1	0:02:54	Chloe	Goliath	NATT	Gentle touch	Tactile
1	0:11:35	Goliath	Chloe	NATT	Shake object	Action
1	0:12:43	Goliath	Chloe	NATT	Slap	Tactile
1	0:12:46	Goliath	Chloe	NATT	Shake object	Action
1	0:12:57	Chloe	Goliath	NATT	Nudge	Tactile
2	0:08:36	Oula	Winston	NATT	Chasing	Action
2	0:08:37	Oula	Winston	NATT	Wrestle	Tactile
2	0:10:20	Winston	Oula	NATT	Embrace	Tactile
1	0:02:05	Chloe	Ivan	NATT	Chasing	Action
1	0:02:06	Chloe	Ivan	ATT	Slap	Tactile
1	0:02:06	Ivan	Chloe	ATT	Mouth-open half	Facial expression
1	0:02:07	Ivan	Chloe	NATT	Chasing	Action
1	0:03:45	Goliath	Ivan	NATT	Nudge	Tactile
1	0:03:47	Ivan	Goliath	ATT	Nudge	Tactile
1	0:05:42	Ivan	Goliath	ATT	Chasing	Action
1	0:08:53	Ivan	Goliath	ATT	Chasing	Action
1	0:11:20	Ivan	Goliath	ATT	Chasing	Action
1	0:13:30	Goliath	Chloe	ATT	Swinging	Action

43

Appendix B

Facial Expression Photos

Figure 1B. Mouth-open full performed by Ivan.

Figure 3B. Grin performed by Perak.

Figure 2B. Mouth-open half performed by Winston.

Figure 4B. Wrist offer performed by Ivan.

Photos of Individuals

Enclosure #1:

Figure 1C: Ivan (M)

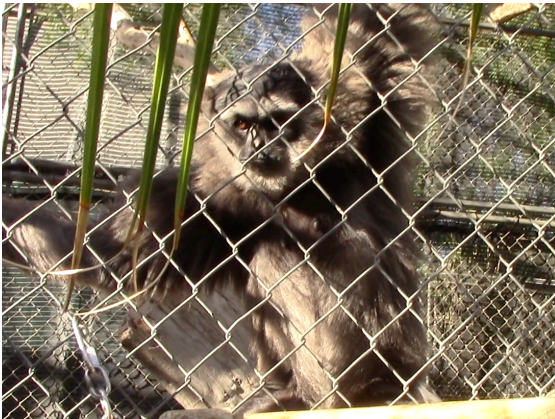*Figure 2C*: Chloe (F)

Figure 3C: Goliath (M)

Enclosure #2:

Figure 4C: Shelby (M)

Figure 7C: Winston (M)

Figure 5C: Khusus (F)

Figure 6C: Oula (F)

Enclosure #3:

Figure 8C: Simpang (F)

Figure 9C: Perak (M)

Figure 10C: Hercules (M)