GESTURAL COMMUNICATION BY WILD CHIMPANZEES

by

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To Hodge… and then to Chopin

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ABSTRACT

GESTURAL COMMUNICATION BY WILD CHIMPANZEES

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Chimpanzees display several gestures in their communicative repertoire, but few data exist regarding how they use and respond to gestures in their natural social and environmental settings. To address this deficiency, I conducted a systematic study of gestural communication by chimpanzees living in an unusually large community at Ngogo in the Kibale National Park, Uganda. Two central goals were to describe the kinds of gestures used by chimpanzees and to evaluate the effect that social relationships have on gesturing behavior.

The Ngogo chimpanzees used 78 gestures in six behavioral contexts. They displayed considerable flexibility in their use, producing single gestures in several contexts and different gestures in the same context. Individuals in three other communities in the wild produce a strikingly similar number of gestures that mirrors the number recorded at Ngogo, an observation consistent with the hypothesis chimpanzees acquire gestures through a process of phylogenetic ritualization.

Chimpanzees form differentiated social relationships. Males are much more gregarious than females are. Adult males also form strong and enduring social bonds with each other. I investigated whether variation in social relationships affected who gestured and responded to whom. Results showed that adult males used and responded to gestures with each other more often than they did when communicating with other individuals. Additional analysis revealed that adult males used and responded to gestures frequently with adult males with whom they formed strong bonds. These findings support an alternative hypothesis that suggests chimpanzees learn gestures via ontogenetic ritualization. I conducted a final series of analyses to examine whether social factors affected the number of gestures adult male chimpanzees used and their patterns of repetition. Adult males used many gestures when they signaled to other adult males. Adult males also repeated gestures more often when signaling to adult males and adolescent males compared with when they gestured to adult females.

In sum, results of this thesis underscore the fact that gesturing is a communicative act involving both signalers and recipients. Understanding how gestures are used requires knowledge of both parties and their social relationships.

CHAPTER I

Introduction

Studies of primates and their behavior remain an integral part of biological anthropology. As our closest living relatives, primates provide information about human uniqueness and the changes that occurred during the course of human evolution. The shared evolutionary history between primates and humans also reveals similarities between them and us. One behavioral similarity exists with respect to communication. Like humans, primates use gestures to communicate with conspecifics (Tomasello et al. 1994; Tanner and Byrne 1996; Liebal et al 2006; Pika et al 2003, 2005; Pollick and DeWaal 2007).

Understanding primate gestural communication is important insofar as it impinges on questions concerning the evolution of language. Language is a hallmark of humankind, but considerable debate exists about its evolution. While many argue that parallels between animal vocal behavior and language provide insights into language origins (Hockett 1963; Steklis 1985; Hauser et al. 1993; Fitch and Hauser 1995), an alternate hypothesis proposes that language may have evolved through an initial stage in which communication was carried out in gestures instead of calls (Hewes 1973; Hockett 1978; Burling 1993; Armstrong et al. 1995). Several lines of evidence support this hypothesis. First, the discontinuity between the apes and other primates suggests that a shift toward a more flexible and intentional communication system characterized our pre-

human ancestors and led to the emergence of language (Taglialatela et al. 2008). Second, apes in captivity have been taught to use gestures in a language-like referential fashion (Savage-Rumbaugh et al. 1986; Gardner et al. 1989). Third, recent research suggests that gesturing provides the cognitive underpinnings for language evolution (McNeill 1992; Nicoladis et al. 1999; Iverson and Goldin-Meadow 1998; Goldin-Meadow et al. 2001). Despite these findings, evaluating the gestural hypothesis of language origins has been difficult given the paucity of observations regarding how our closest living relatives, chimpanzees, use gestures in their natural social and environmental settings. This dissertation attempts to fill this gap in knowledge through a systematic study of gestural communication by wild chimpanzees.

Ape gestural communication

Gestures are defined as expressive body movements and postures that result in a behavioral response (Plooij 1978). Apes are well known to use gestures to communicate, with most previous research limited to captive subjects (gorillas: Tanner and Byrne 1996; Pika et al. 2003; orangutans: Liebal et al 2006; Cartmill and Byrne 2007; bonobos: Savage and Bakeman 1978; Pika et al. 2005; chimpanzees: Tomasello et al. 1985, 1994; Tomasello and Call 1997). These studies reveal that apes produce gestures in several contexts. For example, gorillas use over 30 gestures primarily while playing (Tanner and Byrne 1996). In contrast, one study suggests that bonobos gesture mainly during sexual contexts (Savage and Bakeman 1978). Other studies have shown that chimpanzees use gestures extensively (Goodall 1968; Nishida et al. 1999; Tomasello and Call 2007; Pollick and de Waal 2007). Alternatively, additional research reveals that bonobos

gesture in several situations and use them in ways similar to chimpanzees (deWaal 1988,1989).

In addition to producing gestures in a variety of situations, apes use gestures flexibly between and within contexts. This flexibility is manifest via single gestures being used in multiple contexts and different gestures being used in the same context. For example, an extended 'reach out palm up' gesture can have different meanings depending on whether the signaler is begging for food or seeking coalitionary support during an aggressive interaction (Tomasello and Call 1997; Pollick and deWaal 2007). Alternatively, different gestures are used in the same situation. For instance, a 'self-scratching' gesture and an 'arm raise' gesture may be used to achieve the same goal, to elicit a nearby partner to engage in social grooming (Pika and Mitani 2006). Chimpanzees are not alone in using gestures flexibly, as gorillas (Pika et al 2003) and bonobos (Pika et al. 2005) display similar patterns of use.

Recent research reveals additional variation in how captive apes employ gestures. Chimpanzees continue to gesture if they do not achieve their goal (Leavens et al 2005). Similarly, orangutans adjust their gesturing behavior as a function of how well they are understood. Individuals repeat the same gesture if they are partially understood (Cartmill and Byrne 2007). If recipients misunderstand completely, signalers do not use the same gestures but instead employ new ones (*ibid.*). Apes also modulate their gesturing behavior as a function of the attentional states of recipients. For instance, young chimpanzees are more likely to use visual gestures if recipients are looking at them rather than looking away from them (Tomasello et al 1994). The attentional states of recipients

have also been shown to affect the use of gestures by gorillas and bonobos (Pika et al. 2003, 2005).

The preceding observations illustrate some of the ways apes use gestures. Nevertheless, our understanding of their gesturing behavior, especially in the wild, remains far from complete (Hobaiter and Byrne 2011; Roberts et al. 2012). Specifically, what factors are likely to influence inter-individual variation in the use of and responsiveness to gestures? Here insights are provided by studies of how captive chimpanzees learn gestures via ontogenetic ritualization (Tomasello and Call 1997). In this process animals acquire gestures during repeated social interactions with specific individuals, who shape and alter their behavior. Ontogenetic ritualization depends on relationships formed between specific dyads during development, and thus differs from social learning where animals model their behavior on the actions displayed by multiple individuals. Work with other great apes, such as gorillas (Pika et al 2003) and bonobos (Pika et al 2005), suggests that, like chimpanzees, they too acquire gestures via the process of ontogenetic ritualization. Assuming the generality of this finding, we might expect to find considerable variation in terms of who uses gestures with whom and who responds to whom. Social relationships are likely to play a large and significant role in this regard. In primates, individuals form and maintain differentiated social relationships. Social relationships in chimpanzees have been especially well studied and documented.

Chimpanzee social relationships

Wild chimpanzees live in communities of 20 – 180 individuals, whose members form temporary parties that vary in size and composition (Goodall 1986; Nishida 1990;

Boesch and Boesch-Achermann 2000; Reynolds 2005). Pronounced sex differences in social relationships exist; these have wide-ranging ramifications for several aspects of female and male behavior, including their gestural communication. Male chimpanzees are much more gregarious than are females, and males form differentiated social relationships that are distinct and easily discerned (Mitani 2009). In contrast, relationships between females are not very well developed. Females leave their natal group after reaching sexual maturity and disperse to new communities (Nishida and Kawanaka 1972; Pusey 1979). As a result of this and high levels of feeding competition, female chimpanzees spend considerable time alone and form relatively weak relationships with each other (Murray et al. 2007). After giving birth for the first time, females join a spatially defined subgroup of other females within their communities. These female neighborhoods consist of individuals who frequently associate with each other, but do not necessarily engage in other affiliative and cooperative activities such as grooming and coalitions (Langergraber et al 2009).

Unlike females, male chimpanzees form strong social bonds with each other (Mitani 2009a). These bonds are manifest in affiliative behaviors such as association, grooming, and proximity maintenance (review in Muller and Mitani 2005). Male chimpanzees are also well known for cooperating. They do so in several behavioral contexts, including coalitions, meat sharing, and territorial boundary patrol behavior (review in Mitani 2009b). Males cooperate in these situations to compete with conspecifics both within and between communities. High-ranking individuals form coalitions to acquire and maintain their dominance status (Nishida 1983; Nishida and Hosaka 1996), and high rank, in turn, is positively correlated with reproductive success

(Boesch et al. 2006; Wroblewski et al. 2009; Newton-Fisher et al. 2010). While they strive for status and compete to obtain fitness benefits, male chimpanzees use meat, a scarce and valuable resource, as a tool to obtain coalitionary support (Nishida et al. 1992; Mitani and Watts 2001). Male chimpanzees also cooperate with members of their own community during territorial boundary patrols (Mitani and Watts 2005). Patrolling males occasionally launch lethal coalitionary attacks on individuals of other groups, effectively reducing the collective strength of territorial neighbors in the process (Wilson and Wrangham 2003; Mitani et al. 2010). As they develop over prolonged immature periods, adolescent male chimpanzees attempt to integrate themselves into the adult male social network (Pusey 1990). Their social relationships, as a consequence, are considerably less well developed than those displayed between adult males.

Specific objectives, study site, and outline of this dissertation

The preceding observations regarding ape gestural communication can be combined with information about the social lives of wild chimpanzees to generate a set of testable hypotheses concerning who gestures, when, and how individuals will respond. To test these hypotheses, I conducted an 18-month field study of wild chimpanzees at Ngogo in the Kibale National Park, Uganda. Ngogo provided an ideal venue to carry out this research, as chimpanzees there have been studied for the past 18 years (Mitani 2009a,b). As a consequence, they were relatively easy to follow, which facilitated documenting some of the fine motor movements that are a part of the chimpanzee gestural communicative repertoire. Chimpanzees at Ngogo live in an extremely large

community, and this furnished another reason to conduct this study there, as I was able to collect observations from relatively large samples of individuals.

Before examining the effects of chimpanzee social relationships on their gestural communication, I constructed an inventory of the kinds of gestures that they employ. Chapter 2 describes the repertoire of gestures used by wild chimpanzees. I compiled this repertoire by conducting behavioral observations of chimpanzees at Ngogo. Using these observations, I found that the Ngogo chimpanzees employed 78 different gestures in 6 behavioral contexts. I compare these findings to those made from studies of three other wild chimpanzee communities and one captive group.

Because chimpanzee social relationships vary, some pairs of individuals are likely to communicate more often than others, resulting in differences in the comprehension of and responsiveness to gestures. Specifically, male chimpanzees interact with each other more often than they do with females, and as a consequence, males are likely to use gestures frequently and comprehend and respond to signals given by the former more readily than those made by the latter. These predictions are tested in Chapters 3 and 4 of this thesis. In Chapter 3, I examine who signaled to whom, how frequently individuals used gestures, and the responses elicited by them. In Chapter 4, I investigate the number of gestures individuals employed and how often they repeated using gestures when communicating with others. The specific goal of these chapters was to evaluate the effects of social relationships on gesturing behavior. Results of my analyses indicate that, as is the case with other aspects of chimpanzee behavior, social relationships have a large and pervasive effect on their gestural communication.

In my final chapter, I summarize the results from Chapters 2, 3 and 4. I then discuss the implications of my findings. Results of this thesis bear on important issues regarding gesture acquisition and intentionality. I conclude by outlining some questions for future research.

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CHAPTER II

Gestural Communication by Wild Chimpanzees:

Repertoire and Behavioral Contexts

ABSTRACT

Few data exist regarding how our closest living relatives, chimpanzees, use gestures in their natural social and environmental settings. To fill this gap in knowledge, I conducted an 18 month field study investigating gestural communication by wild chimpanzees in an unusually large community at Ngogo, Kibale National Park, Uganda. A primary goal was to document the types of gestures chimpanzees produced and the behavioral contexts in which they used them. Results showed that the Ngogo chimpanzees produced 78 gestures in 6 different behavioral contexts. Gestures took 3 different forms, with signalers gesturing to others via sight, sound, or touch. Visual and tactile gestures were produced more frequently than auditory gestures. Visual and tactile gestures were also employed flexibly in multiple contexts more often than they were used in only one situation. Comparisons with other studies revealed that wild chimpanzees in three other communities produced a similar number of gestures as those by the Ngogo chimpanzees. In contrast, wild chimpanzees in all four communities produced considerably more gestures than did those made by individuals in one captive group.

These findings underscore the similarity of gestural repertoires among different populations and underscore the flexible nature of chimpanzee gestural communication. The comparative data across study populations are consistent with the hypothesis that chimpanzees acquire gestures through a process of phylogenetic ritualization.

INTRODUCTION

Chimpanzees have attracted considerable research attention ever since Jane Goodall's (1963) pioneering research, and from the inception of fieldwork, their gestural communication has been a focus of study. Over 40 years ago, Goodall (1968) reported that chimpanzees employ over fifty gestures and postures in their communicative repertoire. Subsequent research conducted in captivity and in the wild has continued to document the kinds of gestures chimpanzees use and they ways they use them (Goodall 1968; Nishida et al 1999; Pollick and de Waal 2007; Hobaiter and Byrne 2011).

One prominent finding of prior research is that chimpanzees use gestures not only extensively, but also in a flexible manner. For instance, chimpanzees modulate their gesturing behavior as a function of the attentional states of recipients. In captivity, captive chimpanzees are more likely to use visual gestures if recipients are looking at them rather than looking away (Tomasello et al 1994). Flexibility is also manifest in the contexts of production, with individuals using single gestures in multiple contexts and different gestures being used in the same context (Tomasello et al 1994; Pollick and de Waal 2007). For example, an extended 'open palm' gesture can have a different meaning depending on whether the signaler is begging for food or seeking coalitionary support

during an aggressive interaction (Tomasello and Call 1997; Pollick and de Waal 2007). The generality of these findings is underscored by comparative research at other sites, which has resulted in the description of the gestural repertoires of chimpanzees at multiple sites (Goodall 1968; Nishida et al 1999; Pollick and de Waal 2007; Hobaiter and Byrne 2011). These comparative data provide a means to ask questions about intraspecific variation in chimpanzee gestural communication and their patterns of use.

In this paper, I provide an additional inventory of gestures utilized by chimpanzees in an extremely large community at Ngogo in the Kibale National Park, Uganda. I document the kinds of gestures produced by the Ngogo chimpanzees and the contexts in which they are produced. I use data on the contexts of production to examine the issue of flexibility. My observations also furnish an opportunity to compare the types of gestures used by chimpanzees at Ngogo with those described for chimpanzees living in different areas in the wild and in captivity. I use these comparative data to evaluate two competing hypotheses that have been advanced to explain how chimpanzees and other apes acquire gestures.

METHODS

Study site and subjects

I conducted behavioral observations of chimpanzees at Ngogo in the Kibale National Park, Uganda, between February 2008 to August 2009. The Ngogo study site lies close to the center of the 766 km^2 Kibale Park and along the equator (00^0, 29’ 53’’ N;

30^0 25’ 30 E) at an altitude of about 1400 m above sea level. The study area is covered with moist, evergreen forest interspersed with patches of *Pennisetum purpureum* grassland. Mean annual rainfall at Ngogo during the two-year study period was 1434 mm, with the site experiencing two dry seasons between January - February and June - July. Average maximum and minimum daily temperatures during 2008 – 2009 were 16.4 C^0 and 23.8 C^0, respectively. Struhsaker (1997) provides a detailed description of the Ngogo study site.

The Ngogo chimpanzee community is extremely large and consisted of about 170 individuals during this study. Chimpanzees at Ngogo have been observed for over 18 years, and as a result, most individuals were well habituated to human presence and relatively easy to follow.

Behavioral observations

Defining and documenting gestures

I followed chimpanzees between 0700 and 1800 hours on 226 days over the 18 month study period. During the first two months of fieldwork, I recorded chimpanzee gesturing behavior *ad libitum*. Using on these observations, I created an inventory of gestures employed by the Ngogo chimpanzees, adapting terms employed in previous research on captive chimpanzees (Tomasello et al. 1985, 1989; deWaal 1988, 1989; Pollick and deWaal 2007). Gestures were defined as bodily and facial movements and postures by one individual directed toward another individual which resulted in a behavioral response (Plooij 1978). Three criteria differentiated gestures from non-

gesturing behavior: (1) whether the signaler waited for a response, (2) whether the recipient alternated his or her gaze or (3) whether the signaler persisted in performing and repeating the gesture (Tomosello et al. 1985, 1989). Gestures were identified when they satisfied any of these criteria, although in practice, most fulfilled two or all three of them.

During observations, I noted the modality in which gestures were produced. Modalities were categorized as visual, auditory, or tactile. Visual gestures involved movements that were seen by others without physical contact. Auditory gestures involved a sound when performed, and tactile gestures included physical contact between signalers and recipients.

Defining behavioral contexts

Prior studies have shown that chimpanzees produce gestures in several contexts. I classified each gesture made by chimpanzees into one of the six following contexts defined by previous researchers (Goodall 1968, 1986; Nishida et al 1999; Pollick and de Waal 2007).

Affliative: Some gestures were produced in an affiliative context when individuals greeted others or sought reassurance. Greeting behavior involved nonaggressive interactions between individuals when meeting after spending time apart. Reassurance was defined as affiliative body contact or invitation for body contact to come into proximity of one another

Agonistic: Gestures were also produced in agonistic contexts that involved aggression, avoidance, frustration, or submission. Agonistic behavior took place when one chimpanzee threatened, physically attacked, or avoided another. Agonism included any

behavior resulting in frustration. Frustration included cases where: (1) a dominant individual interfered with a subordinate or (2) an individual was unable to achieve a goal; Submissive behavior occurred when a low ranking chimpanzee reacted to the approach or presence of a higher ranking chimpanzee.

Food: Gestures were occasionally produced when individuals gathered around another chimpanzee who held or ate food.

Groom: Gestures were produced during bouts of social grooming. Grooming involved individuals using their hands and lips to pull back and pick at the hair and skin of another. Gestures made in this context typically resulted in chimpanzees continuing to groom.

Play: Play occurred when chimpanzees used their hands and bodies in non-agonistic and relaxed ways with others, resulting in a non-agonistic, hyperactive response. Gestures produced in this situation were sometimes used to invite others to continue playing.

Sex: Chimpanzees made gestures during sexual interactions. These occurred while chimpanzees mounted each other and in other situations that led to copulation.

Statistical analysis

Most of the data presented in this paper are descriptive in nature and not suitable for statistical analysis. I conducted one analysis, however, to examine how chimpanzees used gestures at Ngogo. I employed a binomial test to examine whether individuals used single gestures in multiple contexts more often than they did in single contexts. I conducted a chi-square test to examine whether chimpanzees at different study sites produced different types of gestures.

RESULTS

Types of gestures

The Ngogo chimpanzees used 78 gestures. Most gestures were visual (44). Fewer tactile (27) and auditory (7) gestures were produced.

In the following, gestures are described. Visual, tactile, and auditory gestures are listed separately. Each gesture is followed by its field code in parentheses with a description. The behavioral contexts in which each gesture was produced are listed in capital letters.

VISUAL GESTURES (V) (n = 44)

Head Nod (VGA) – looking at an object/direction, then looks at a specific individual, then alternates between object and individual again. The individual rapidly repeats this action more than two times.

AGONISTIC

Glare (VGL) - keeping eye contact with recipient for more than 2 seconds

AFFILIATIVE, AGONISTIC

Directed Scratch (VDS) – while being groomed, the recipient scratches a specific spot/part of the body in front of the groomer. Sometimes, the recipient lifts a body part and exaggerates the scratching in the groomer's line of sight.

GROOM

Reach Out Down (VRD) – lifting an arm away from the body either sideways or in front with the palm of the hand facing down toward the ground. Fingers extended fully.

AFFILIATIVE, AGONISTIC, FOOD, PLAY

Reach Out Side (VRS) – lifting an arm away from the body either sideways or in front with the palm of the hand facing to the side, neither up nor down. Fingers extended fully.

AFFILIATIVE, AGONISTIC, FOOD, PLAY

Reach Out Up (VRU) – lifting an arm away from the body either sideways or in front with the palm of the hand facing upwards. Fingers extended fully.

AFFILIATIVE, AGONISTIC, FOOD, PLAY

Food Interest (VFI) – positioning nose or mouth close to another individual's mouth. The other individual eats a specific type of food while the other individual looks intently at the chewing motion or the food.

FOOD

Self Groom (VSG) – grooming oneself on any part of the body in the presence of another individual.

AFFILIATIVE, AGONISTIC, GROOM

Pirouette (VPI) - spinning entire body on the vertical axis while moving forward

PLAY

Present for Grooming (VPG) – lifting, raising or shoving a body part in the line of site of the groomer or potential groomer.

AFFILIATIVE, AGONISTIC, GROOM

Present Back to Infant (VPB) - presenting back to an infant for jockey style transport.

AFFILIATIVE

Leaf Groom (VLG) – picking off a leaf from a small plant, then folding the leaf, digging into the leaf with nails, then pursing the lips to pick up material from the leaf into the mouth. Folding of and picking from the leaf may happen multiple times.

AGONISTIC, GROOM

Leaf Clip (VLC) – picking off a leaf from a small plant, then placing part of it between the lips and ripping off parts of the leaf with the fingers. Clipping the leaf may happen multiple times.

AGONISTIC, SEX

Bipedal Stand (VBP) – standing erect on two legs with arms to the sides and head lifted high and erect on shoulders.

AFFILIATIVE, AGONISTIC, FOOD, PLAY, SEX

Swagger (VSW) – moving hunched shoulders back and forth at a rapid rate usually during a charge or aggressive interaction. Usually coupled with pilo-erection, branch dragging, branch shaking , branch breaking or branch throwing.

AFFILIATIVE, AGONISTIC, PLAY, SEX

Pilo-erect (VPE) – when hair all over the body stands erect, 'puffing up' the appearance of an individual making them appear larger. Usually occurs with swaggering and during charging displays.

AFFILIATIVE, AGONISTIC, SEX

Drag Branch (VDB) – dragging a branch or log during a charging display.

AFFILIATIVE, AGONISTIC, PLAY, SEX

Shake Branch (VSB) – shaking a branch at another individual during an aggressive interaction.

AGONISTIC, PLAY, SEX

Break Branch (VBB) – breaking a branch off a tree or dead wood during a charging display.

AGONISTIC, SEX

Throw Branch (VTB) – throwing a branch away from the body usually during a charging display and accompanied by pilo-erection and swaggering.

AGONISTIC, PLAY, SEX

Arm Raise (VAR) – lifting or raising of an arm or both arms straight above the head and holding them above the head.

AGONISTIC, FOOD, PLAY, SEX

Lunge (VLU) – lower body planted on the ground but quickly shooting the upper body forward toward another individual. May happen multiple times in succession.

AGONISTIC, PLAY, SEX

Flap (VFL) – raising or lifting an arm forward away from the body with the palm facing down (Reach Out Down) but forcefully motioning the arm down toward the ground moving vegetation along with the motion.

AGONISTIC

Stamp Ground (VST) – slapping a foot or both feet on the ground in a repeated manner. Can occur with jumping or arm swinging.

AGONISTIC

Somersault (VSO) - body tucked tightly while forward motion with feet over head movement

AGONISTIC, PLAY

Crouch (VCR) – hunching down posture with arms and legs close to the body and head lowered. Usually occurs as a submissive behavior.

AFFILIATIVE, AGONISTIC

Bow (VBW) – moving the upper body and head downward toward the ground on the approach of another individual. Arms can be splayed out at the sides or in front of the head or can be tucked close to the stomach. Face either pointing downward or forward. Usually occurs as submissive behavior.

AFFILIATIVE, AGONISTIC, FOOD

Bob (VBB) - alternating movement of the upper body and head downward and upward on the approach of another individual. Arms can be splayed out at the sides or in front of the head or can be tucked close to the stomach. Face either pointing downward or forward. Usually occurs as submissive behavior.

AFFILIATIVE, AGONISTIC, FOOD

Slap Ground (VSL) – slapping or hitting the ground with an open palm. May happen multiple times in succession.

AGONISTIC, PLAY

Bend Away (VBA) – moving the upper body away from an approaching individual. Usually occurs as submissive behavior.

AGONISTIC, SEX

Wrist Bend (VWB) – raising or lifting an arm extended away from the body with the wrist flexed toward the body or pointed downward toward the ground. Usually occurs when another individual approaches.

AFFILIATIVE, AGONISTIC, FOOD

Pout Face (VPF) – pursing of the lips and furrowing of the brow. Usually occurs between an infant and mother.

AGONISTIC, FOOD, PLAY

Relaxed Open Mouth (VOM) – protruding lower jaw and/or lower lip hanging down with open mouth.

ALL

Grin (VFG) – taught lips pulled back to the ears showing teeth and squinting eyes. Usually occurs during fright, flight or reassurance.

ALL

Hit Away (VHA) – flinging an arm toward another individual with the back of the hand.

AGONISTIC, SEX

Head Tip (VHE) – subtle, rapid up and down repeated movement of the head on approach to another individual. Usually performed by dominant males.

AFFILIATIVE, AGONISTIC

Arm Wave (VAW) – raising or lifting one or two arms above the head and rapidly moving them back and forth medio-laterally. Usually occurs during excitement.

AFFILIATIVE, AGONISTIC, PLAY, SEX

Beg w/ Hand (VBG) – lifting an arm forward toward another individual with coveted food. Palm of the hand is facing upward close to the other individual's mouth.

AGONISTIC, FOOD

Finger Flex (VFF) – the repeated flexion and extension of the fingers only. Usually occurs during rest or play.

GROOM, PLAY

Beckon (VBE) – lifting an arm anterior or medially with the palm facing up, down or to the side toward another individual, but with fingers flexed.

AFFILIATIVE, FOOD, PLAY

Play Chase (VPC) – chasing another individual in a playful or nonaggressive manner usually around a small tree.

PLAY

Play Face (VPF) – eyebrows raised widely and opening of the mouth toward another individual to initiate play. Usually paired with other play gestures

PLAY

Self-Scratch (VSS) – using the finger nails to visibly scratch a part of the body.

ALL

Yawn (VYA) - opening of the mouth accompanied with deep breath toward another individual

ALL

AUDITORY GESTURES (A) (n = 7)

Teeth Chatter (ATC) – rapid up and down movement of the lower jaw clacking against the upper jaw with lower and upper teeth contact. Occurs during the context of grooming.

GROOM

Lip Smack (ALS) – loud and rapid smacking of the lips with the tongue. Occurs during the context of grooming.

GROOM

Lip Bob (ALB) – rapid up and down movement of the lower lip smacking against the upper lip accompanied with popping sound. The tongue is not used. Occurs during the context of grooming.

GROOM

Sputter (ASP) – rapid pursing of the lips with the explosive pushing out of air. Similar to a spitting behavior and accompanied by loud spitting sound. Occurs during the context of grooming.

GROOM

Buttress Drum (ABD) – open palm or plantar surface of foot hitting or smacking a large buttress of a tree. Often smacking is used in repeated succession to produce large booming noises. Usually occurs during traveling or extreme excitement.

AFFILIATIVE, AGONISTIC, PLAY

Leaf Clip (ALC) - picking off a leaf from a small plant, then placing part of it between the lips and ripping off parts of the leaf with the fingers. Clipping the leaf may happen multiple times. The ripping sound from the leaf is a distinct sound.

AGONISTIC, SEX

Self-Scratch (ASS) – using the finger nails to produce scratching sounds on a part of the body.

ALL

TACTILE GESTURES (T) (n = 27)

Embrace/Hug (TEM) – wrapping arms and hands around another individual in a hugging behavior. Can occur facing one another (ventral-ventral) or from behind another individual (ventral-dorsal).

AFFILIATIVE, PLAY

Slap/Hit (TSL) – forcefully striking another individual with an open palm or closed fist.

AGONISTIC, SEX

Play Slap/Hit (TPH) – playfully striking another individual with an open palm or dorsum of the hand during initiation or maintenance of play.

PLAY

Gentle Touch (TGT) – lightly touching another individual in a vulnerable part of the body ie genitalia or face. Usually occurs between mother – infant interactions or during grooming.

AFFILIATIVE, AGONISTIC, GROOM

Hard Touch (THT) – forceful pressured touching of another individual in a usually non-vulnerable part of the body. Usually occurs during reassurance, fright or aggressive interactions.

ALL

Sniff Body Part (TSN) – positioning the nose in contact with another individual's body part and holding the position for a few seconds.

AFFILIATIVE, AGONISTIC, FOOD, SEX

Move Body Part (TMV) – forcefully moving another individual's body part during the context of grooming

GROOM, PLAY, SEX

Hand Clasp (THC) – lifting an arm above the head and grasping another individual's fingers, palm or wrist with the hand during grooming.

GROOM

Extend Leg (TEL) – directing a leg away with partially extended knee toward another individual.

AFFILIATIVE, PLAY

Hold Leg (THL) – holding a leg with extended knee of another individual.

AFFILIATIVE, PLAY

Hold Hand (THH) – holding the hand of another individual with the hand. Usually occurs during reassurance or rest.

AFFILIATIVE, PLAY

Hold Foot (THF) - holding the foot of another individual with the hand. Usually occurs during rest.

AFFILIATIVE, PLAY

Present for Mating (TPS) – positioning the hind end or perineal swelling toward another individual during estrous or reassurance.

AFFILIATIVE, AGONISTIC

Mount (TMM) – positioning the body into a bipedal stand behind another individual with hands placed upon the other individual's back. Accompanied by rapid back and forth thrusting of the pelvis with or without intromission. Usually occurs during the contexts of sex or reassurance.

AFFILIATIVE, AGONISTIC, SEX

Play Mount (TPM) – positioning the body into a bipedal stand behind another individual with hands placed upon the other individual's back. Accompanied by rapid back and forth thrusting of the midsection without intromission. Occurs during the context of play.

PLAY

Stamp Back (TST) – forcefully slapping the plantar surface of the foot down on the back of another individual. May be repeated multiple times in succession.

AGONISTIC, SEX

Lift (TLI) – raising or lifting another individual from the ground with the arms during an aggressive interaction.

AGONISTIC, SEX

Slam (TSM) – forcing another individual down toward the ground during an aggressive interaction. Usually follows the gesture of lifting.

AGONISTIC, SEX

Drag (TDR) – pulling or dragging another individual away from their previous stationary position during an aggressive interaction.

AGONISTIC, SEX

Bite (TBI) – sinking the teeth into a part of the body of another individual during an aggressive interaction.

AGONISTIC, SEX

Play Bite (TPB) – the gumming or light use of teeth on another individual's body part during play.

PLAY

Kiss (TKS) – touching lips to another individual's body part.

ALL

Wrist Bend (TWB) – raising or lifting an arm extended with the wrist flexed inward toward the body or pointed downward toward the ground *in contact* of another individual. Usually occurs when another individual approaches.

AFFILIATIVE, AGONISTIC, FOOD

Dab (TDB) – light touching of another individual with the knuckles of a flexed hand. Can be repeated multiple times in rapid succession.

AFFILIATIVE, AGONISTIC, PLAY

Hunch Over (THO) – coming up behind another individual and placing an out stretched arm around them while hunching the shoulders and back. Usually occurs during fright, reassurance or aggressive interactions.

AFFILIATIVE, AGONISTIC

Pat (TPT) – repeated up and down movement of palmar surface of the hand on another individual's body part.

PLAY

Play Wrestle (TPW) – to lock arms and legs around the arms, legs or torso of another individual in a tumbling manner during play.

PLAY

Behavioral Contexts of Gestures

The Ngogo chimpanzees produced gestures in six behavioral contexts, but they did not do so with equal frequency. Chimpanzees used gestures most often in the contexts of agonism, affiliation, and play (Table 2.1). Visual and tactile gestures were used often in the four contexts of affiliation, agonism, play, and sex (Table 2.1). In contrast, visual gestures were employed frequently in the food context, while auditory gestures were made often while individuals were grooming (Table 2.1). The chimpanzees used single gestures in multiple contexts more often than they used single gestures in single contexts (binomial test: $P < 0.001$). In sum, chimpanzees use multiple gestures in each of the six behavioral contexts (Table 2.2). In fact, a few (7) were used extensively across all of the situations (Table 2.2).

Comparison of Gestural Repertoires

Table 2.3 provides a comparison of the gestures produced by chimpanzees living at three additional study sites in the wild (Budongo, Gombe, Mahale) and one captive colony (Yerkes). A total of 105 gestures have been described from these four groups, including the Ngogo chimpanzees (Table 2.3).

Chimpanzees produced a similar number of gestures across the four field sites, with 78, 70, 69, and 77 documented at Ngogo, Sonso, Gombe, and Mahale, respectively (Table 2.4). In contrast, the captive chimpanzees at Yerkes produced substantially fewer gestures (33 gestures) than chimpanzees in the wild (Table 2.4). Despite this difference in the total number of gestures produced by wild and captive chimpanzees, similar types of gestures were displayed across all five sites. Visual gestures predominated followed by tactile and auditory gestures. There was no heterogeneity between study site and type of gesture produced (Pearson's chi-squared test: $X^2 = 4.661$, df =8 $P = 0.79$).

There was also considerable overlap in the precise types of gestures used by chimpanzees across all sites. The majority all 105 gestures that have been described were used at three or more sites (> 3 sites: 71.4% = 75/105 gestures). Forty percent of all gestures described have been described at five (17.1% = 18/105) or four sites (22.9% = 24/105). About a fifth of all gestures were unique and limited to only one site (17.1% = 18/105 gestures). Fifteen percent of all gestures were found strictly at all four field sites (15.2% = 16/105 gestures), while only one gesture was limited to captivity (< 1% = 1/105 gestures).

DISCUSSION

The observations presented here provide novel data on the gestural communication of wild chimpanzees. At Ngogo, chimpanzees produced 78 gestures in 6 different behavioral contexts. Gestures were made using three sensory modalities via sight, sound, and touch. Visual and tactile gestures were produced more frequently than auditory gestures. Visual and tactile gestures were also employed flexibly in multiple contexts more often than they were used in only one situation. Comparative data provided from three other communities indicate that chimpanzees utilize a similar number of gestures and in similar ways across all study sites. This pattern differs markedly from the one shown in captivity, where chimpanzees produce fewer gestures.

Prior studies regarding gestural communication by apes consistently show how these animals use gestures flexibly, with single gestures frequently employed in multiple contexts (Pika 2003,2005; Liebal 2006; Call and Tomasello 2007; Pollick and de Waal 2007). The observations presented here are consistent with these previous findings, and reveal that visual and tactile gestures are used in this fashion more so than those that are made by sound. One simple reason for this difference may lie in the fact that chimpanzees produce many more visual and tactile gestures than they do auditory gestures, and that the use of the former in multiple contexts arises by chance alone. This is unlikely to be the case, however, given the clear skew in the contexts of production (Table 2.2).

The distances over which gestures are typically utilized provide another potential hypothesis to explain the observed difference in use of gestures. Visual and tactile gestures are usually employed when signalers and recipients are close together and attending to each other, while auditory gestures are given when recipients may be further away and not looking at signalers (Tomasello et al 1994; Pika et al. 2003, 2005; Tomasello and Call 2007). Proximity is likely to create a variety of situations within which to use gestures for communicative purposes. In contrast, separated individuals may be constrained in the types of activities in which they can engage. Because two individuals cannot play when separated, gestures used in this context often utilize sight and touch. Similarly, affiliation usually demands close contact between individuals, which again may place a limitation on the use of auditory gestures. In sum, it remains unclear why some types of gestures are used more often than others. Additional study will be required to clarify this issue.

My observations from Ngogo provide data that can be used for comparative purposes. Prior studies have described the gestures used by chimpanzees in three additional communities in the wild (Sonso: Hobaiter and Byrne 2011; Gombe: Goodall 1968, 1986; Mahale: Nishida et al 1999) and in one captive group (Yerkes: Pollick and de Waal 2007). Chimpanzees in all five groups use a surprisingly similar number of visual, auditory, and tactile gestures relative to the total number produced. Most gestures are shared across sites, with only a few made uniquely at only a single site. In addition, chimpanzees produced gestures in the same ways across populations, giving more visual and tactile gestures than auditory ones. Finally, one striking difference revealed by the

comparative data is that chimpanzees in the wild produced many more gestures than those in captivity.

What accounts for the strikingly smaller repertoire of gestures displayed by chimpanzees in captivity? Environmental and social factors furnish an obvious reason for the large disparity. Chimpanzees in captivity operate in a limited number of ecological settings with relatively few social partners, all of which are likely to constrain the number and kinds of gestures that they use. Developmental factors may also contribute to the observed difference in repertoire size. Unlike chimpanzees in the wild, captive chimpanzees may not have grown up together. Without having done so, individuals may lack the experiences necessary to forge bonds and communicate with each other, which in turn may influence the kinds of gestures they produce.

Findings of this study provide potential insights into a current controversy regarding how chimpanzees and other apes acquire gestures during development. One hypothesis proposes that apes learn gestures individually via ontogenetic ritualization (Tomasello and Call 1997). In this process animals acquire gestures during repeated social interactions with specific individuals, who shape and alter their behavior. According to this hypothesis, gestures will frequently be used idiosyncratically between specific pairs of individuals. An alternative, phylogenetic ritualization hypothesis suggests that ape gestures undergo little modification over time. Instead, gestures appear fully formed in individuals, presumably at birth (Genty et al 2009). While not definitive, the comparative data presented here are more in line with the phylogenetic ritualization hypothesis, as the strikingly similar number of gestures produced across study sites in the wild does not conform to the process of ontogenetic ritualization. Moreover, the

ontogenetic ritualization predicts that gestures will be employed idiosyncratically between pairs of individuals, but such gestures do not appear to be widespread across groups.

Taken together, the results presented here highlight the flexible nature of chimpanzee gestural communication and contribute to a current debate regarding the acquisition of gestures. Several questions, however, remain to be investigated. Despite the similarity in the overall number of gestures used across populations, are there variations in how chimpanzees use and respond to them? Do some individuals use gestures more frequently than others? Why? Is there variation in responsiveness? Who responds to whom and under what circumstances? These questions constitute fertile areas for future investigation.

Table 2.1. Types of gestures produced in six behavioral contexts**.**

Behavioral Context	**Visual (44)**	**Auditory (7)**	**Tactile (27)**	**Total (78)**
Affiliative	22 (50%)	2 (29%)	14 (52%)	**38 (49%)**
Agonistic	35 (80%)	3 (43%)	15 (56%)	**53 (68%)**
Food	15 (34%)	1 (14%)	4 (15%)	**20 (26%)**
Groom	9 (20%)	5 (71%)	5 (19%)	**19 (24%)**
Play	23 (52%)	2 (29%)	13 (48%)	**38 (49%)**
Sex	17 (39%)	2 (29%)	11 (41%)	**30 (38%)**
All Contexts	4 (9%)	1 (14%)	2 (7%)	**7 (9%)**

Table 2.2. Gesture usage in single contexts vs. multiple contexts.

Modality (# of gestures)	**Single context**	**Multiple contexts**
Visual (44)	9 (20%)	35 (80%)
Auditory (7)	4 (57%)	3 (43%)
Tactile (27)	6 (22%)	21 (78%)
Total (78)	**19 (24%)**	**59 (76%)**

Table 2.3. Gestures produced by chimpanzees in different groups.

Gesture (Ngogo)	**Definition (Ngogo unless specified)**	**Ngogo (wild)**	**Sonso (wild) a**	**Gombe (wild) b**	**Mahale (wild) c**	**Yerkes (captive) d**
Arm Raise	lifting or raising of an arm or both arms straight above the head and holding them above the head for a few seconds.	X	X	X	X	X
Arm Shake*	(Sonso) 'small repeated back and forth motion of the arm'	0	X	0	0	0
Arm Swing *	(Sonso) 'large back and forth movement of the arm held below the shoulder'	0	X	0	0	X
Arm Wave	raising or lifting one or two arms above the head and rapidly moving them back and forth. Usually occurs during excitement.	X	X	0	0	X
Beckon	lifting an arm forward with the palm facing up, down or to the side toward another individual.	X	X	X	0	X
Beg w/ Hand	lifting an arm forward toward another individual with coveted food. Palm of the hand is facing upward close to the other individual's mouth.	X	X	X	X	X
Bend Away	moving the upper body away from an approaching individual. Usually occurs as submissive behavior.	X	0	X	X	?
Bipedal Stand	standing erect on two legs with arms to the sides and head lifted high and erect on shoulders.	X	0	X	X	?

Bite	sinking the teeth into a part of the body of another individual during an aggressive interaction.	X	X	X	X	0
Bob	alternating movement of the upper body and head downward and upward on the approach of another individual. Arms can be splayed out at the sides or in front of the head or can be tucked close to the stomach. Face either pointing downward or forward. Usually occurs as submissive behavior.	X	0	X	X	?
Bow	moving the upper body and head downward toward the ground on the approach of another individual. Arms can be splayed out at the sides or in front of the head or can be tucked close to the stomach. Face either pointing downward or forward. Usually occurs as submissive behavior.	X	X	X	X	0
Break Branch	breaking a branch off a tree or dead wood during a charging display.	X	X	X	X	?
Buttress Drum	open palm or foot hitting or smacking of a large buttress to a tree. Often times smacking is in repeated succession to produce large booming noise. Usually occurs during traveling or extreme excitement.	X	X	X	X	0
Clap*	(Sonso) 'both palms moved towards each other and are	0	X	0	0	X

	brought together with and audible contact'					
Crouch	hunching down posture with arms and legs close to the body and head lowered. Usually occurs as a submissive behavior.	X	0	X	0	0
Dab	light touching of another individual with flexed fingers or knuckles. Can be repeated multiple times in rapid succession.	X	0	X	X	X
Dangle*	(Sonso) 'to hang from one or both arms from a branch above another individual, this audible as there is normally significant disturbance of the canopy'	0	X	X	X	0
Directed Scratch*	during grooming, the recipient adamantly scratches a specific spot on/part of his body in front of the groomer. Sometimes, the recipient lifts up the body part and exaggerates the scratching in the groomer's line of site.	X	0	0	0	0
Drag	pulling and dragging another individual during an aggressive interaction.	X	X	X	X	X
Drag Branch	dragging a branch or log during a charging display.	X	X	X	X	X
Drum Belly*	(Mahale) 'Slapped his belly with his right hand to make drum-like sounds'	0	0	0	X	0
Drum Other*	(Sonso) 'short hard audible contact of alternate palms against recipient's body'	0	X	0	0	0

Embrace/ Hug	wrapping arms and hands around another individual in a hugging behavior. Can occur facing one another or from behind another individual.	X	X	X	X	0
Extend Leg/Foot	extending a leg away from the body toward another individual.	X	X	0	0	0
Fear Grin	taught lips pulled back to the ears showing teeth and squinting eyes. Usually occurs	X	0	X	X	?
Feet Shake*	(Sonso) 'repeated back and forth movement of feet from the ankles'	0	X	0	0	0
Finger Flex	the back and forth motion of the fingers only. Usually occurs during rest or play.	X	0	X	X	X
Flap	raising or lifting an arm forward away from the body with the palm facing down (Reach Out Down) but forcefully motion the arm down toward the ground moving vegetation along with the motion.	X	X	X	X	0
Food Interest	positioning nose or mouth close to another individual's mouth. The other individual is eating a specific type of food while the other individual looks intently at the chewing motion or the food.	X	X	0	0	X
Foot Present*	(Sonso) 'sole of the foot is presented to the recipient'	0	X	0	0	0
Gallop	An exaggerated running movement where the contact of the hands and	0	X	X	X	0

	feet is deliberately audible					
Gentle Touch	lightly touching another individual in a vulnerable part of the body i.e. genitalia or face. Usually occurs between mother – infant interactions or grooming.	X	X	X	X	X
Glare	keeping eye contact with other for more than 2 seconds	X	X	X	X	X
Hand Clasp	lifting an arm above the head and holding or locking with another individual's hand or wrist during the context of grooming.	X	X	0	X	?
Hard Touch	forceful pressure touch of another individual in a usually non-vulnerable part of the body. Usually occurs during reassurance, fright or aggressive interactions.	X	X	X	X	X
Head Butt*	(Sonso) 'head is briefly and firmly pushed into the body of the recipient'	0	X	0	0	0
Head Nod	looking at an object/direction, then looks at a specific individual, then alternates between object and individual again. The individual repeats this action more than two times.	X	X	0	0	X
Head Stand*	(Sonso) 'signaler bends forward and places head on the ground'	0	X	0	0	0
Head Tip	subtle, rapid up and down movement of the head on approach to another individual. Usually	X	0	X	X	0

	performed by dominant males.					
Hide Face*	(Sonso) 'face is hidden by the hands and/or arms'	0	X	0	0	0
Hit Away	flinging an arm toward another individual with the palm facing away .	X	X	X	X	X
Hit with Object*	(Sonso) 'an object is brought into short hard contact with the body of the recipient'	0	X	0	X	0
Hold Foot	holding the foot of another individual. Usually occurs during rest.	X	0	X	X	X
Hold Hand	holding the hand of another individual. Usually occurs during reassurance or rest.	X	X	X	X	X
Hold Leg	holding an extended leg of another individual.	X	0	X	X	?
Hunch Over	coming up behind another individual and placing an out stretched arm around them while hunching the shoulders and back. Usually occurs during fright, reassurance or aggressive interactions.	X	X	X	X	X
Jump*	(Sonso) 'while bipedal both feet leave the ground simultaneously, accompanied by horizontal displacement through the air'	0	X	0	X	0
Kick	Foot is brought into short hard contact with the recipient's body in a movement from the hip with a horizontal element	0	X	X	X	0
Kiss	touching lips to another individual’s body part.	X	X	X	X	0

Knock Object*	(Sonso) 'back of the hand or knuckles are brought into short hard audible contact with an object'	0	X	0	X	X
Leaf Clip – Auditory	picking off a leaf from a small plant, then placing part of it between the lips and ripping off parts of the leaf with the fingers. Clipping the leaf may happen multiple times. The ripping sound from the leaf is a distinct sound in the wild.	X	X	0	X	0
Leaf Clip – Visual	picking off a leaf from a small plant, then placing part of it between the lips and ripping off parts of the leaf with the fingers. Clipping the leaf may happen multiple times.	X	X	0	X	0
Leaf Groom	picking off a leaf from a small plant, then folding the leaf, digging into the leaf with nails, then pursing the lips to pick up material from the leaf into the mouth. Folding of and picking from the leaf may happen multiple times.	X	0	X	X	0
Leg Swing*	(Sonso) 'large back and forth movement of the leg from the hip'	0	X	0	0	0
Lift	raising or lifting object from the ground during an aggressive or playful interaction.	X	0	X	X	?
Lip Bob*	rapid up and down movement of the lower lip smacking against the upper	X	0	?	0	?

	lip accompanied with popping sound. The tongue is not used. Occurs during the context of grooming.					
Lip Smack	loud and rapid smacking of the lips with the tongue. Occurs during the context of grooming.	X	0	?	X	?
Lunge	lower body planted on the ground but quickly shooting the upper body forward toward another individual. May happen multiple times in succession.	X	0	X	X	?
Mount	positioning the body into a bipedal stand behind another individual with hands placed upon the other individual's back. Accompanied by rapid back and forth thrusting of the midsection. Usually occurs during the contexts of sex or reassurance.	X	0	X	X	?
Move Body Part*	forcefully moving another individual's body part during the context of grooming	X	0	0	0	?
Object in Mouth Approach*	(Sonso) 'signaler approaches recipient while carrying an object in the mouth (e.g. small branch)'	0	X	0	0	0
Pat	repeated up and down movement of open palm on another individual's body part.	X	X	X	X	0
Pilo-erect	when hair all over the body stands erect, 'puffing up' the appearance of an individual making them	X	X	X	X	?

	appear larger. Usually occurs with swaggering and during charging displays.					
Pirouette	spinning entire body on vertical axis while moving forward	X	X	X	X	0
Play Bite	the gumming or light use of teeth on another individual's body part during play.	X	0	X	X	?
Play Chase	chasing another individual in a playful manner or nonaggressive manner usually around a small tree.	X	0	X	X	?
Play Face	opening of the mouth toward another individual to initiate play. Usually paired with other play gestures	X	0	X	X	?
Play Mount	positioning the body into a bipedal stand behind another individual with hands placed upon the other individual's back. Accompanied by rapid back and forth thrusting of the midsection. Occurs during the context of play.	X	0	X	X	?
Play Slap/Hit	to smack with either the palm or back of the hand in a playful manner to initiate or maintain play.	X	0	X	X	?
Play Wrestle	to lock arms and legs with another individual in a tumbling manner during play.	X	0	X	X	?
Pout Face	pursing of the lips and furrowing of the brow. Usually occurs between and infant and mother.	X	0	X	X	?

Pounce*	(Sonso) 'signaler displaces through the air to land quadrupedally on the body of the recipient'	0	X	0	0	0
Present Back to Infant	presenting back to infant for jockey style transport.	X	X	X	0	0
Present for Grooming	lifting or raising or shoving of a body part in the line of site of the groomer or potential groomer.	X	X	X	X	X
Present for Mating	positioning the hind end toward another individual during estrous or reassurance.	X	X	X	X	?
Pull Through Stem*	(Mahale) 'pull the leafy branch of - a shrub or a clump of grass stems through the hand by a rapid upwards movement of the forearm. Produces a conspicuous sound'	0	0	0	X	0
Reach out down	lifting an arm away from the body either sideways or in front with the palm of the hand facing down toward the ground.	X	X	X	X	X
Reach Out Side	lifting an arm away from the body either sideways or in front with the palm of the hand facing to the side, neither up nor down.	X	X	X	X	X
Reach Out Up	lifting an arm away from the body either sideways or in front with the palm of the hand facing up to the sky.	X	X	X	X	X
Relaxed Open Mouth	protruding lower jaw and/or lower lip hanging down with open mouth.	X	0	X	X	?

Roll Over*	(Sonso) 'the signaler rolls onto their back exposing their stomach, normally accompanied by repeated movements of the arms and/or legs'	0	X	X	0	0
Rump Rub*	(Sonso) 'push/rub rump against the body/swelling of recipient'	0	X	X	0	0
Self Groom	grooming oneself on any part of the body in the presence of another individual.	X	0	X	X	?
Self-Scratch – Auditory	using the finger nails to produce distinct scratching sounds on a part of the body.	X	X	X	X	0
Self-Scratch – Visual	using the finger nails to visibly scratch a part of the body.	X	X	X	X	0
Shake Branch	shaking a branch at another individual during an aggressive interaction.	X	X	X	X	0
Side Roulade*	(Sonso) 'body is rotated around the head-feet axis while lying on the ground with horizontal displacement along the ground'	0	X	0	0	0
Slam	forcefully heaving another individual down toward the ground during an aggressive interaction. Usually follows the gesture of lifting.	X	X	?	X	X
Slap Ground	slapping or hitting the ground with an open palm. May happen multiple times in succession.	X	X	?	X	X

Slap Object with Object*	(Sonso) 'as (Slap Ground) but the hand holds an object which is brought into contact with another object (e.g. a branch is slapped against a tree)'	0	X	X	X	0
Slap/Hit	forcefully smacking another individual with an open palm or closed fist.	X	X	X	X	X
Sniff Body Part	positioning the nose in contact with another individual's body part and holding the position for a few seconds.	X	0	X	X	?
Somersault	body tucked tightly while forward motion with feet over head movement	X	X	X	X	0
Spit Water*	(Yerkes) 'subject spits water at other to invite play'	0	0	0	0	X
Sputter	rapid pursing of the lips with the explosive pushing out of air. Similar to a spitting behavior and accompanied by loud spitting sound. Occurs during the context of grooming.	X	0	?	X	?
Stamp Back	forcefully slamming the flat part of the foot down on the back of another individual. May be repeated multiple times in succession.	X	X	X	X	X
Stamp Ground	slapping a foot or both feet on the ground in a repeated manner. Can occur with jumping or arm swinging.	X	X	X	X	X

Swagger	moving hunched shoulders back and forth at a rapid rate usually during a charge or aggressive interaction. Usually coupled with pilo-erection, branch dragging, branch shaking , branch breaking or branch throwing.	X	X	X	0	0
Tap Object*	(Sonso) 'movement of the arm from the wrist or elbow, with firm short contact of the fingers to the object'	0	X	0	0	0
Teeth Chatter	rapid up and down movement of the lower jaw smacking against the upper jaw with lower and upper teeth contact. Occurs during the context of grooming.	X	0	?	X	?
Throw Branch	throwing a branch away from the body usually during a charging display and accompanied by pilo-erection and swaggering.	X	X	X	X	X
Water Splash*	(Sonso) 'hand is moved vigorously through the water so that there is audible displacement of the water'	0	X	0	X	0
Wrist Bend – Tactile	lifting an arm away from the body with the wrist sticking out and hand pointed inward toward the body or pointed downward toward the ground in contact of another individual. occurs with approaching individual.	X	0	X	X	X

Wrist Bend – Visual	lifting an arm away from the body with the wrist sticking out and hand pointed inward toward the body or pointed downward toward the ground. occurs with approaching individual.	X	0	X	X	X
Yawn	opening of the mouth and deep breath	X	X	X	X	X

The gestural repertoire of the Ngogo chimpanzees in comparison with three wild groups and one captive group

a Hobaiter and Byrne (2011)
b Goodall (1968,1986); Plooij (1984)
c Nishida et al. (1999)
d Tomasello et al. (1989, 1994); Pollick and De Waal (2007)

X = gesture present; 0 = gesture absent;
? = unknown
* depicts uniqueness at labeled field site

Table 2.4. Comparison of types of gestures produced by chimpanzees in different groups

Study Group	Visual	Auditory	Tactile	Total
Ngogo	44 (56%)	7 (9%)	27 (35%)	**78**
Sonso	46 (66%)	5 (7%)	19 (27%)	**70**
Gombe	43 (62%)	2 (3%)	24 (35%)	**69**
Mahale	43 (56%)	8 (10%)	26 (34%)	**77**
Yerkes	21 (64%)	2 (6%)	10 (30%)	**33**

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CHAPTER III

Gestural Communication by Wild Chimpanzees:

Use and Response

ABSTRACT

Chimpanzees display several postures and gestures in their communicative repertoire, but few data exist regarding how they use and respond to gestures in their natural social and environmental settings. To fill this gap in knowledge, I conducted an 18 month field study investigating gestural communication by wild chimpanzees in an unusually large community at Ngogo, Kibale National Park, Uganda. I observed 29 adult males, 12 adolescent males, 39 adult females, and 16 adolescent females and collected data concerning who signaled to whom, how frequently individuals used gestures, and the responses elicited by them. A primary goal was to examine the effects of social relationships on gesturing behavior. Results showed that adult males used and responded to gestures with each other more often than they did with adolescents or females. Additional analysis revealed that adult males used and responded to gestures frequently with adult males with whom they formed strong bonds compared with others with whom they shared weaker bonds. In contrast, adult females did not alter their gesturing behavior

between bonded and non-bonded individuals. These findings indicate that, as is the case with other aspects of chimpanzee behavior, social relationships have a large and pervasive effect on gestural communication. This result is also consistent with the hypothesis that chimpanzees acquire gestures through a process of ontogenetic ritualization.

INTRODUCTION

The vocal behavior of animals has been the focus of considerable ethological study. A large body of theoretical and empirical research has yielded important insights into the proximate causes, development, and function of animal vocal communication (Catchpole and Slater 1995; Bradbury and Vehrencamp 1998; Gerhardt and Huber 2002; Maynard Smith and Harper 2003; Seyfarth and Cheney 2003; Nowicki and Searcy 2005). In contrast, we know substantially less about how animals use gestures to communicate with conspecifics, especially in the wild. Our closest living relatives, chimpanzees (*Pan troglodytes*) provide a model organism to investigate gestural communication in animals. Chimpanzees are well known to possess a rich array of gestures and postures. Over 40 years ago, Goodall (1968) suggested that chimpanzees use over 50 gestures and postures for communicative purposes. Despite these early observations, our understanding of how chimpanzees use gestures in their natural social and environmental settings remains limited (but see Hobaiter and Byrne 2011).

To date, most research on the gesturing behavior of chimpanzees and other apes has been conducted in captivity (review in Zuberbuhler 2012). One prominent finding

derived from these studies is that apes use gestures with surprising flexibility. This flexibility is manifest in two different ways, with individuals using the same gestures in different contexts and different gestures in the same context (Pika et al 2003; Pika et al 2005; Leibal et al 2006; Call and Tomasello 2007; Pollick and deWaal 2007). Flexibility is also revealed in the kinds of gestures that apes use and the ways they use them. For instance, apes modulate their gesturing behavior as a function of the attentional states of recipients; captive chimpanzees, gorillas, and bonobos are more likely to use visual gestures if recipients are looking at them rather than looking away (Tomasello et al 1994; Pika et al. 2003, 2005). Additional research shows that chimpanzees continue to gesture if they do not achieve their goal (Leavens et al. 2005). Similarly, orangutans adjust their gesturing behavior as a function of how well they are understood. Individuals repeat the same gesture if they are partially understood (Cartmill and Byrne 2007). If recipients misunderstand completely, signalers do not use the same gestures but instead employ new ones (*ibid.*).

While these findings shed light on how apes use gestures in captivity, the factors that influence how they use and respond to gestures in the wild remain unclear. Here social relationships are likely to play a large and significant role. Primates are well known for developing and maintaining differentiated social relationships (Hinde 1983). These relationships have an important effect not only on the behavior of individuals, but also influence their physiology and fitness in significant ways (Seyfarth and Cheney 2011; Silk 2012). For example, individuals experience relatively high levels of stress following the loss of particularly important social partners, and animals who form strong

social bonds with others produce more infants and live longer than do individuals who develop only weak bonds with others (*ibid*.).

Chimpanzees are particularly apt subjects to investigate the effect of social relationships on gesturing behavior, as they are well known for forming differentiated social relationships. Adult male chimpanzees in particular are quite gregarious. Specific pairs of males form strong and long-lasting social bonds that can have important fitness consequences (review in Muller and Mitani 2005). In contrast, members of other age-sex classes are less social and typically develop relatively weak bonds with others (*ibid*.). Insofar as communication mediates social interactions and relationships, the observed patterns of variation in chimpanzee social relationships is likely to have important consequences for who gestures to whom and who responds to whom.

In this paper, I investigate how chimpanzees at Ngogo, Kibale National Park, Uganda, use and respond to gestures. Specifically, I examine the effects that social relationships have on the use of and responsiveness to gestures produced by members of different age-sex classes. Prior research at Ngogo has documented the social relationships of adult male and female chimpanzees, laying the groundwork for this study (e.g. Wakefield 2008; Langergraber et al. 2009; Mitani 2009). In addition, the exceptionally large community of chimpanzees there provides unusually large numbers of individuals to observe, creating an ideal situation to examine the effects of social relationships on gesturing behavior.

METHODS

Study site and subjects

I conducted behavioral observations of chimpanzees at Ngogo in the Kibale National Park, Uganda, over 18 months during February 2008 to August 2009. The Ngogo study site lies close to the center of the 766 km^2 Kibale Park and along the equator (00^0, 29' 53'' N; 30^0 25' 30 E) at an altitude of about 1400 m above sea level. The study area is covered with moist, evergreen forest interspersed with patches of *Pennisetum purpureum* grassland. Mean annual rainfall at Ngogo during the two-year study period was 1434 mm, with the site experiencing two dry seasons between January - February and June - July. Average maximum and minimum daily temperatures during 2008 – 2009 were 16.4 C^0 and 23.8 C^0, respectively. Struhsaker (1997) provides a detailed description of the Ngogo study site.

The Ngogo chimpanzee community is extremely large and consisted of about 170 individuals during this study. Chimpanzees at Ngogo have been observed for over 18 years, and as a result, most individuals were well habituated to human presence and relatively easy to follow. To assign age-sex classes of individuals, I used a classification system developed by Goodall (1986), who distinguished adult males (> 15 years), adult females (>14 years), adolescent males (8 - 15 years), and adolescent females (8 – 14 years). Using these age-sex class designations, I collected data on 29 adult males, 39 adult females, 12 adolescent males, and 16 adolescent females.

Behavioral data collection

I observed chimpanzees between 0700 and 1800 hours on 226 days over the 18 month study period. Focal chimpanzees were selected randomly and followed during hour-long sampling sessions. I collected 1262 h of focal data on gesturing and social behavior (Table 3.1). One Ugandan field assistant recorded an additional 2262 h of behavioral observations used in the analysis of social bonds (Table 3.1). Adult male chimpanzees are more gregarious than members of any other age-sex class, while some of the adolescent females in this study were shy and sometimes difficult to follow. As a consequence, I collected more data on gesturing and social behavior for adult males than members of any age-sex class (Table 3.1). The fewest observations were obtained for adolescent females (Table 3.1). Because relatively few behavioral observations were collected on adolescent females, I limit the analysis of social bonds to adults only.

Defining chimpanzee social bonds

Tests of my hypotheses required information on chimpanzee social bonds. To collect these data, I recorded interactions between individuals, including who associated, groomed, and maintained proximity with whom. The identities of individuals who associated with focal subjects were recorded at the start of each observation session. Proximity and grooming were recorded during point samples every 10 minutes within the focal sampling session. I assessed social bonds between adult males and between adult females using these behavioral observations. Specifically, I computed a composite sociality index (SI) between adult male dyads following Silk et al. (2006). Numerically this index is:

$$\frac{\frac{A_{i,j}}{A_{x,y}} + \frac{P_{i,j}}{P_{x,y}} + \frac{G_{i,j}}{G_{x,j}}}{3}$$

where $A_{i,j}$ = the frequency of association between individual i and individual j and $A_{x,y}$ = the median frequency of association between all of possible dyads (Silk et al 2006). Proximity (P) and grooming (G) frequencies were computed in the same manner.

I performed a similar computation to determine a composite sociality index (SI) for adult females. Because females rarely groomed each other, however, I employed only observations of association and proximity for this purpose. Numerically this index is:

$$\frac{\frac{A_{i,j}}{A_{x,y}} + \frac{P_{i,j}}{P_{x,y}}}{2}$$

where $A_{i,j}$ = the frequency of association between individual i and individual j and $_{x,y}$ = the median frequency of association between all possible dyads.

Defining and documenting gestures

I recorded data on the types of gestures individual chimpanzees used, how often they used them, the patterns of use, and responses given to them by recipients. In the first two months of fieldwork, I created an inventory of gestures displayed by the Ngogo chimpanzees adapting terms employed in previous research on captive chimpanzees (Savage-Rumbaugh et al. 1977; Savage and Bakeman 1978; Tomasello et al. 1985, 1989; deWaal 1988, 1989; Pika et al. 2003, 2005, see Chapter 2). Following Plooij (1978), I defined gestures as body and facial movements and postures by one individual that were directed toward another individual and that resulted in a behavioral response. Three

criteria differentiated gestures from non-gesturing behavior. Gestures involved: (1) signalers waiting for a response; (2) recipients alternating his or her gaze; and (3) signalers persisting in performing and repeating the gesture (cf. Tomasello et al. 1985, 1989). Gestures were identified by any one of these criteria, although in practice, most fulfilled two or all three. Using this definition and criteria, I documented 78 different gestures used by the Ngogo chimpanzees (Chapter 2).

To collect data on gestures, I followed focal subjects and counted and recorded all gestures and gesturing bouts. During these sampling sessions, I continuously noted the signaler, gestures and their modalities, and recipients. Gesture modalities were categorized as visual, auditory, or tactile. Visual gestures involved movements that were seen by others without physical contact. Auditory gestures involved sounds, and tactile gestures included physical contact between signalers and recipients. I defined the recipient of a gesture as the individual to whom the signaler directed the gesture. It proved difficult to record observations of gesturing and social behavior simultaneously, and because of this, I recorded responses to gestures only from other adult males in the vicinity of focal subjects. This limitation also served to maximize the sample of responses from other chimpanzees, as adult males are more social than members of other age-sex classes.

Timed focal samples allowed me to compute how often individuals used gestures. To record frequencies of use, I scored the number of times individuals displayed gestures per unit time, i.e. 60 minutes. Most gestures were executed by chimpanzees as one time actions, e.g. *reach out and up,* and ended when the individual paused for 3 seconds or more or gave a new gesture (Tomasello et al 1985; Pika et al. 2003). A small number of

gestures (16.7% = 13/78 gestures), e.g. *self scratching*, were difficult to count individually as they were produced rapidly over short periods. In these cases, I counted the entire gesture bout as a single gesture. A bout was defined to begin with the initial use of a single gesture and to end when the signaler stopped using that same gesture or the signaler paused for at least 3 seconds (Tomasello et al 1985; Pika et al. 2003). For example, if more than 3 seconds passed between an individual performing a rapid fire *self-scratching* gesture, a new bout was scored. If the individual switched to a different gesture, then a new single gesture or gesture bout was scored. Scoring bouts as single gestures potentially introduces bias in calculating frequencies of use by underestimating the number of gestures used by specific individuals. Because response waiting occurred after each gesturing bout, however, treating bouts as single gestures provided a behaviorally relevant way to assay gesture use between individuals.

I also noted the type of response given to gestures by recipients. Responses were scored in three ways, either by: (1) a change in the attentional state of the recipient or (2) the recipient's physical reaction to signals or (3) by no response at all. Changes in the attentional state of recipients included making direct eye contact and turning the head toward the signaler. These two types of responses were defined as passive. Previous studies have recorded how far individuals turn their heads toward signalers (Pika et al. 2003, 2005). Due to difficult observation conditions in the forest, I was only able to reliably record whether individuals turned their heads toward signalers or lifted their heads to make eye contact. Physical reactions to gestures included recipients gesturing back to signalers or recipients interacting socially with signalers. These types of responses were defined as active and were quite easy to record. The final type of response

was no response. In these, recipients responded neither actively nor passively to signalers by not moving or changing body position or by continuing the same behavior before the signaler began to gesture.

Statistical analysis

To evaluate social bonds between adult males, I counted the number of point samples each dyad associated, were in proximity, and groomed. I then divided these values by the number of hours I observed each pair to calculate frequencies. The sociality index (SI) measured the degree to which association, proximity, and grooming between particular dyads deviated from all other pairs in the community. High values indicated strong bonds between dyads, while low values reflected weaker bonds. For adult males, dyads with a sociality index larger than 3.19, a value equal to the mean plus one standard deviation, were considered bonded males (X + SD = 1.55 + 1.64, N = 406 dyads). I considered all other dyads non-bonded (SI = 0.0 – 3.0). Using to these criteria, pairs that fell in the highest 14% of all dyads were bonded. I used the same methods to evaluate social bonds between 14 adult females for whom I had 15 hours or more data on social behavior (Table 3.1). Dyads with a sociality index larger than 2.55 (9% of all dyads), a value equal to the mean plus one standard deviation (X + SD = 1.00 + 1.55, N = 91), were considered bonded females. All other dyads were considered non-bonded.

To assess how frequently individuals used gestures with members of different age-sex classes, I calculated the number of gestures performed per focal hour for each chimpanzee. I compared these frequencies using parametric nested analysis of variance.

In these analyses, I sampled all 72 chimpanzees, who performed gestures during data collection. To evaluate response frequencies to gestures performed by members of different age-sex classes, I counted the number of times adult males responded to gestures and divided this by the number of hours focal subjects were observed. I used Student's *t* tests to ascertain whether adult males responded differentially to members of different age-sex classes. To ensure adequate samples for purposes of these analyses, I included only those individuals who I observed frequently. This included adult males, adult females, and adolescent males who I followed more than 20, 15, and 14 hours, respectively.

I conducted another series of analyses to examine whether social bonds influenced how chimpanzees used gestures and responded to them. Of the 29 adult males in my sample, 17 males had 3 or more strongly bonded partners, 9 males had only two partners, and 3 males had no partners. Because only 14% of dyads were strongly bonded, every adult male had substantially fewer bonded partners than non-bonded ones. Including individuals with fewer than three partners could potentially skew the results of analyses investigating how males used gestures, and I excluded them as a result. For the remaining 17 individuals, I calculated the number of times they gestured per focal hour of observation. I then computed and compared two usage frequencies for each adult male, one with bonded males and another with non-bonded males. Rates of association potentially differ between strongly bonded dyads and those that possessed weaker bonds, which introduces another potential confound. Specifically, bonded dyads are likely to have many more opportunities to gesture to one another, while non-bonded dyads will have fewer chances. To reduce this possible bias, I calculated the average frequency

males associated with bonded males and the average frequency males associated with non-bonded males. I then divided gesture usage frequencies with bonded and non-bonded males by the corresponding average association frequency. I used parametric paired Student's *t* tests to compare frequencies of use with bonded males and non-bonded males. I used the same methods to compare frequencies of use with bonded females and non-bonded females.

To assay how often adult males responded to gestures produced by bonded males and non-bonded males, I computed the number of times adult males responded per focal hour of observation. I then compared response frequencies to bonded and non-bonded adult males using parametric paired samples *t* tests. In all of the following analyses, parametric tests were performed only after confirming that the data were normally distributed using a Kolmogorov-Smirnov test.

RESULTS

Adult chimpanzee social relationships

The sociality Index (SI) between males ranged from 0.00 to 11.06 (X + SD = 1.55 + 1.64, N = 406 dyads; Fig. 3.1). The scores, however, were strongly skewed to the left. The majority of dyads fell below 3.19. Using this cut-off, 57 pairs (14%) formed strong bonds with each other, with the number of partners varying from 2 to 10 individuals per male. The SI between adult females ranged from 0.00 to 9.37 (X + SD = 1.00 + 1.55, N = 91; Fig. 3.2). Scores were strongly skewed to the left with the majority of dyads falling

below 2.55, suggesting that they generally formed weaker bonds than those between males. In fact, the SI values between females were significantly lower than those between males ($F_{1,496} = 8.56$, $P = 0.004$). The SI between females exceeded 2.55 in only 9% of all dyads, and in these, females formed strong bonds with 1 to 3 partners.

Use of gestures

Adult males produced more gestures than members of any other age-sex class, 5,044 times over 719 hours (X + SD = 0.12 + 0.16 gestures/hr). Adolescent males produced fewer gestures than adult males (X + SD = 0.07 + 0.11 gestures/hr). Adult females gave 702 gestures over 290 hours (X + SD = 0.05 + 0.09 gestures/hr), while adolescent females made the fewest gestures of individuals in any age-sex class (X + SD = 0.02 + 0.04 gestures/hr).

I conducted a series of nested analyses of variance to investigate whether chimpanzees gestured equally often to members of different age-sex classes. Chimpanzees in different age-sex classes displayed significant variability in their frequency of use of gestures ($F_{3,71}$= 2.40, $P < 0.001$; Fig. 3.3). Adult males used gestures more frequently with one another than they did with adult females ($P < 0.001$), adolescent males ($P = 0.002$), or adolescent females ($P < 0.001$). Similar patterns in the frequency of use of gestures did not emerge between adult females, adolescent males, and adolescent females. Individuals in each of these age-sex classes gestured to other members in their same age-sex class as often as they did to chimpanzees in different age-sex classes ($P > 0.40$ for all three comparisons).

Additional analyses indicated that adult males gestured more often to males with whom they shared strong bonds compared with males with whom they shared weaker bonds ($t_{16} = 2.48$, $P = 0.025$; Fig. 3.4). In contrast, the strength of social bonds did not affect the use of gestures by adult females; adult females signaled equally often to other adult females with whom they shared strong bonds and those with whom they formed weaker bonds ($t_{13} = 0.75$, $P = 0.469$; Fig. 3.5).

Responses to gestures

Effects of age-sex classes

Adult males differed in how they responded to gestures performed by other adult males, adult females, and adolescent males. When considering *all* types of responses, adult males responded significantly more often to gestures given by other adult males (X + SD = 3.97 + 2.52) than to those produced by adult females (X + SD = 1.01 + 0.79; $t_{35.788} = 5.68$, $P < 0.001$; Fig. 3.6) and by adolescent males (X + SD = 1.68 + 1.82; $t_{36} = 2.63$, $P = 0.013$; Fig. 3.6). Adult males also responded actively more often to gestures from other adult males (X + SD = 3.65 + 2.36; Fig. 3.6) than to those given by adult females (X + SD = 0.91 + 0.79; $t_{36.535} = 5.55$, $P < 0.001$; Fig. 3.6) and by adolescent males (X + SD = 1.58 + 1.83; $t_{36} = 2.50$, $P = 0.017$; Fig. 3.6). Similarly, adult males responded passively more frequently to gestures given by other adult males (X + SD = 0.32 + 0.23; Fig. 3.6) than they did to gestures produced by adult females (X + SD = 0.11 + 0.14; $t_{38.640} = 3.803$, P < 0.001; Fig. 3.6) and by adolescent males (X + SD = 0.10 + 0.10; $t_{34.928} = 4.10$, P < 0.001; Fig. 3.6). In sum, adult males were more likely to respond

to gestures given by other adult males than to those made by individuals of other age-sex classes.

Additional analyses indicated that adult males responded to gestures from other adult males (X + SD = 4.85 + 2.43) more frequently than they failed to respond (X + SD = 3.38 + 1.31; $t_{27} = 3.52$, $P = 0.002$; Fig. 3.6). When adult males responded to other adult males, they did so actively (X + SD = 4.44 + 2.25) more than passively (X + SD = 0.41 + 0.28; $t_{27} = 10.15$, $P < 0.001$; Fig. 3.6). Active responses by adult males to gestures made by other adult males also exceeded the number of times they did not respond ($t_{27} = 2.67$, $P = 0.013$; Fig. 3.6). In contrast, adult males failed to respond to gestures more frequently than the number of times they responded passively ($t_{27} = -13.08$, $P < 0.001$; Fig. 3.6).

Responses by adult males to gestures produced by adult females and adolescent males differed from those that they gave to gestures made by other adult males. Adult males responded to gestures given by adult females (X + SD = 1.01 + 0.79; Fig. 3.6) as often as they failed to respond (X + SD = 0.68 + 0.68; $t_{13} = 1.48$, $P = 0.162$; Fig. 3.6). When adult males did respond to the gestures of adult females, however, they did so actively (X + SD = 0.91 + 0.79; Fig. 3.6) more often than passively (X + SD = 0.11 + 0.14; $t_{13} = 3.71$, $P = 0.003$; Fig. 3.6). Passive responses to gestures occurred significantly less often than no response ($t_{13} = -3.14$, P = 0.008; Fig. 3.6). Adult males responded to the gestures of adolescent males (X + SD = 1.68 + 1.82; Fig. 3.6) as often as they failed to respond (X + SD = 2.10 + 0.91; $t_9 = -1.02$, $P = 0.333$; Fig 3.6). When adult males did respond to adolescent males, though, they did so actively (X + SD = 1.58 + 1.83; Fig. 3.6) more than passively (X + SD = 0.10 + 0.10; $t_9 = 2.53$, $P = 0.032$; Fig. 3.6). Adult males failed to respond to the gestures made by adolescent males (X + SD = 2.10 + 0.91; Fig.

3.6) more often than the number of times they responded passively (X + SD = 0.10 + 0.10; $t_9 = -6.70$, $P < 0.001$; Fig. 3.6).

Effects of social bonds

Social bonds between males also influenced their responsiveness to gestures. Adult males responded to gestures given by strongly bonded males (X + SD = 4.31 +1.80; Fig. 3.7) more often than they did to those given by non-bonded males (X + SD = 1.90 + 0.76; $t_{16} = 4.92$, $P < 0.001$; Fig. 3.7). In addition, males responded actively to the gestures of bonded partners (X + SD = 4.01 + 1.67; Fig. 3.7) more frequently to those performed by non-bonded individuals (X + SD = 1.68 + 0.74; $t_{16} = 5.05$, $P < 0.001$; Fig. 3.7). In contrast, there was no difference in the passive responses given to gestures produced by males in the two groups (bonded males, X + SD = 0.30 + 0.25; non-bonded males, X + SD = 0.21 + 0.11; $t_{16} = 1.31$, $P = 0.210$; Fig. 3.7).

Adult males responded to gestures given by strongly bonded males (X + SD = 4.31 + 1.80; Fig. 3.7) more often than they failed to respond (X + SD = 2.24 + 1.14; $t_{16} = 6.65$, $P < 0.001$; Fig. 3.7). In contrast, males responded to non-bonded males (X + SD = 1.90 + 0.76; Fig. 3.7) the same number of times they did not respond (X + SD = 1.51 + 0.77; $t_{16} = 1.62$, $P = 0.125$; Fig. 3.7). Adult males in both groups responded actively to one another more often than they did so passively (strongly bonded males: active responses X + SD = 4.01 + 1.67, passive responses X + SD = 0.30 + 0.25; $t_{16} = 9.71$, $P < 0.001$; non-bonded males: active responses X + SD = 1.68 + 0.74, passive responses X + SD = 0.21 + 0.11; $t_{16} = 8.23$, $P < 0.001$; Fig. 3.7). Adult males who shared strong social bonds responded actively to one another significantly more often than not at all ($t_{16} =$

5.99, $P < 0.001$; Fig. 3.7), while non-bonded males showed no difference ($t_{16} = 0.74$, $P = 0.473$; Fig. 3.7). In contrast, both groups responded passively to one another significantly more often than not (strongly bonded males: passive responses X + SD = 0.30 + 0.25, no responses X + SD = 2.24 + 0.11: $t_{16} = -7.66$, $P < 0.001$; Fig. 3.7; non-bonded males: passive responses X + SD = 0.21 + 0.11, no responses X + SD = 1.51 + 0.77: $t_{16} = -6.80$, $P < 0.001$; Fig. 3.7).

DISCUSSION

Results presented here furnish novel insights into how social relationships influence the use of and responses to gestures by wild chimpanzees. Social relationships among chimpanzees vary extensively. Using measures of party association, proximity maintenance, and social grooming, several pairs of adult males formed strong social bonds. Fewer pairs of adult females maintained strong bonds. Additional analyses indicated that variation in chimpanzee social relationships affected their gestural communication. Adult males used and responded to gestures produced by adult males more frequently than they did to those given by members of other age-sex classes. The strength of social bonds between adult chimpanzees also influenced their use and responsiveness to gestures. Adult males used and responded to gestures made by other adult males with whom they shared strong social bonds frequently. In contrast, the strength of social bonds did not affect the frequency with which adult females gestured to each other.

The results of this study can be interpreted in the context of what we know about the behavior of chimpanzees in the wild. Adult male chimpanzees are more social than members of other age-sex classes (review in Muller and Mitani 2005). They frequently associate, remain in close spatial proximity to each other, and cooperate in several situations, including coalitions, meat sharing, and territorial boundary patrols (*ibid*.). Specific pairs of adult males maintain strong and enduring social bonds with kin and non-kin alike, sometimes for several years (Mitani 2009). The social relationships forged between males influence the acquisition and maintenance of dominance rank (Nishida 1983), which in turn have important fitness consequences (Boesch et al. 2006; Inoue et al. 2008; Wroblewski et al. 2009; Newton-Fisher et al. 2010). The behavior of adult female chimpanzees, especially those living in East Africa, differs considerably from that of adult males. Adult females are relatively asocial, and as a consequence, they interact with others infrequently (review in Muller and Mitani 2005). Adolescent male and female chimpanzees face particular social challenges. As they grow and develop over prolonged periods spanning several years, adolescent male chimpanzees struggle as they attempt to integrate themselves into the adult male social network (Pusey 1990). Consequently, they affiliate and cooperate less often than do other chimpanzees. The lives of adolescent females parallel those of adolescent males as both experience social difficulties. Unlike male chimpanzees, females disperse from their natal groups during adolescence when they are around 10 years old (Nishida and Kawanaka 1972; Pusey 1979). After joining their new communities, adolescent females form only relatively weak social bonds with resident chimpanzees (Kahlenberg et al. 2008).

Communication mediates social interactions and relationships (Marler 1976). Because chimpanzee social relationships vary markedly between members of different age-sex classes, some pairs of individuals are likely have reason to communicate more often than others, resulting in differences in the use and responsiveness to gestures. The observations presented here conform to this expectation by showing that adult males, the most gregarious chimpanzees who stand the most to gain by forging cooperative relationships with individuals of similar age and sex, selectively use and respond to gestures produced by other adult males. Importantly, this selectivity occurs above and beyond the typical high levels of gregariousness displayed between adult males, as frequencies of use and responsiveness to gestures persist after controlling for associations. Members of other age-sex classes, adult females, adolescent males, and adolescent females, rely less on social relationships, and perhaps as a result, these individuals fail to show any selectivity in their frequency of use of gestures; they communicate equally often to themselves and others and at relatively low rates.

Close examination of the types of responses given by adult males to gestures produced by other adult males and members of different age-sex classes indicates that active responses predominated over those made passively. Two hypotheses may account for this pattern. First, active responses may have been recorded frequently simply because they were more easily observed than passive responses. If this was the case, then the observed differences in active and passive responses were merely a methodological artifact. Countering this, however, is an alternative suggestion that dimmer light conditions under the forest canopy may have favored active responses over passive ones. If signalers used gestures with an individual from a distance, the dimmer conditions of

the forest environment may have made them more difficult to see. By reacting in an active manner rather than a passive one, recipients may have made it known more clearly to the signaler that they had seen the gesture.

The findings of this study bear on a current controversy regarding how chimpanzees and other apes acquire gestures during development. One hypothesis proposes that apes learn gestures individually via ontogenetic ritualization (Tomasello and Call 1997). In this process animals acquire gestures during repeated social interactions with specific individuals, who shape and alter their behavior. According to this hypothesis, gestures will be used idiosyncratically between specific pairs of individuals and depend critically on social relationships formed between specific dyads. Recently, Genty and colleagues (2009) have proposed an alternative hypothesis that suggests ape gestures undergo little modification over time. Instead, gestures appear fully formed in individuals, presumably at birth. This phylogenetic ritualization hypothesis makes no specific predictions about how gestures will be used or how individuals will respond to them. Although a phylogenetic origin of gestures does not mean that gestures will be used and responded to in an inflexible manner, it does not necessarily predict the kinds of variation in usage and responsiveness revealed in the preceding analyses. Instead, the preferential use of and responsiveness to gestures by adult males is more readily explained by ontogenetic ritualization.

Because male chimpanzees are philopatric, they spend their entire lives together during which they form long-lasting social bonds that have important fitness consequences. Over the course of their lifetimes, adult males experience repeated social and communicative interactions with one another. Such interactions, especially those that

take place between individuals who share strong social bonds, are likely to facilitate learning gestures via ontogenetic ritualization. In contrast, members of other age-sex classes will have fewer opportunities to form differentiated social relationships because of the nature of their life histories (see above). Consequently, there is no *a priori* reason to expect that adult female, adolescent male, and adolescent female chimpanzees will vary in their use of gestures, as found in this study.

Taken together, results of this study underscore the important influence that social relationships have on the communicative behavior of chimpanzees. Several questions nevertheless remain. First, longitudinal observations of how specific pairs of individuals acquire gestures will go a long way to help resolve the current debate regarding the development of gestures. Second, this study reveals how adult males vary in their responsiveness to gestures, but is there similar variation by members of different age-sex classes? Here too, these data can be used to test the alternative hypotheses for gesture acquisition, as the phylogenetic origin hypothesis does not predict individual differences in responsiveness. Third, do social relationships influence other aspects of gesturing, such as repertoire size and rates of repetition? Both of these issues are important as they bear on long-standing questions about intentionality. In sum, investigating these and other questions will furnish fertile areas for future research regarding gestural communication by our closest living relatives.

Table 3.1. Study subjects. The number of observation hours recorded of gesturing behavior and social behavior for individuals of different age-sex classes are shown.

Age-Sex Class	**Observation hours (gestures)**	**Observation hours (behavior)**
adult males	719	2,981
adolescent males	207	207
adult females	290	290
adolescent females	46	46

Figure 3.1. Sociality index of adult male chimpanzees.

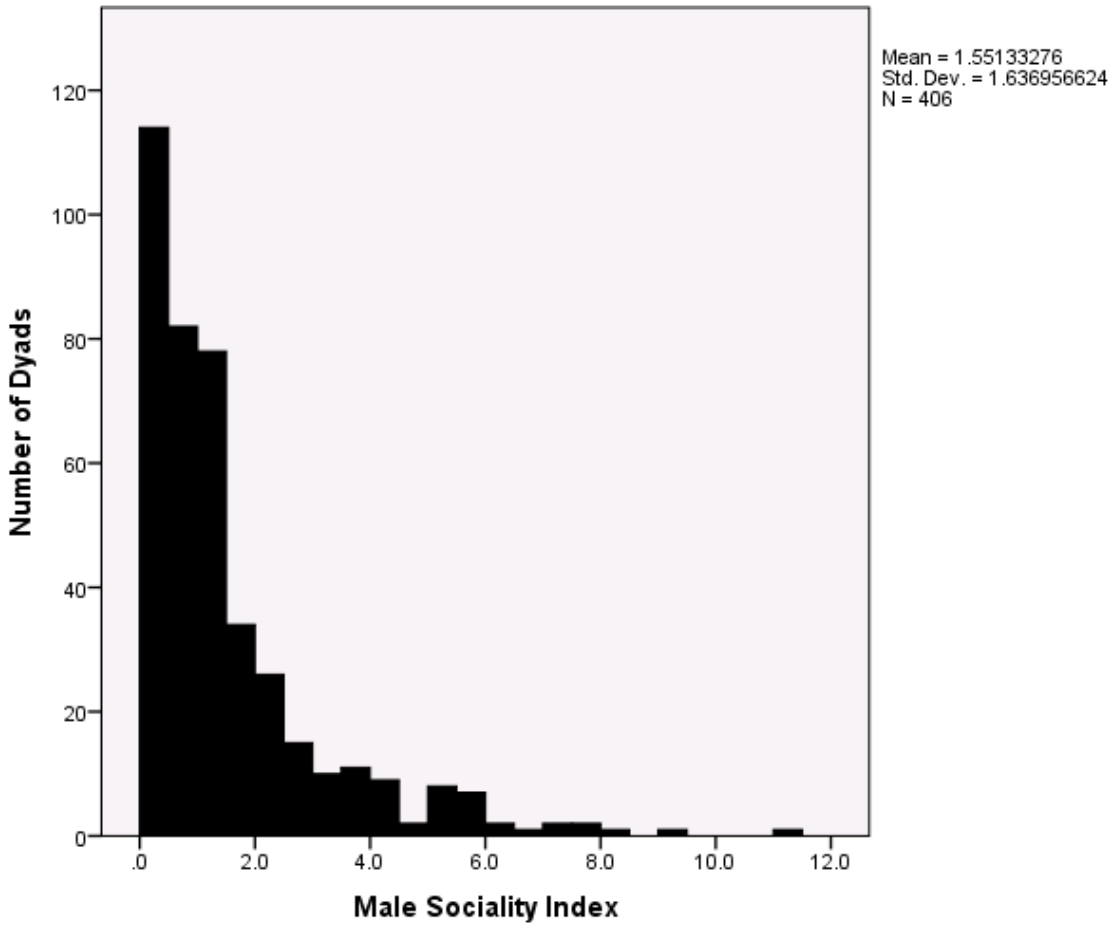


Figure 3.2. Sociality index of adult female chimpanzees.

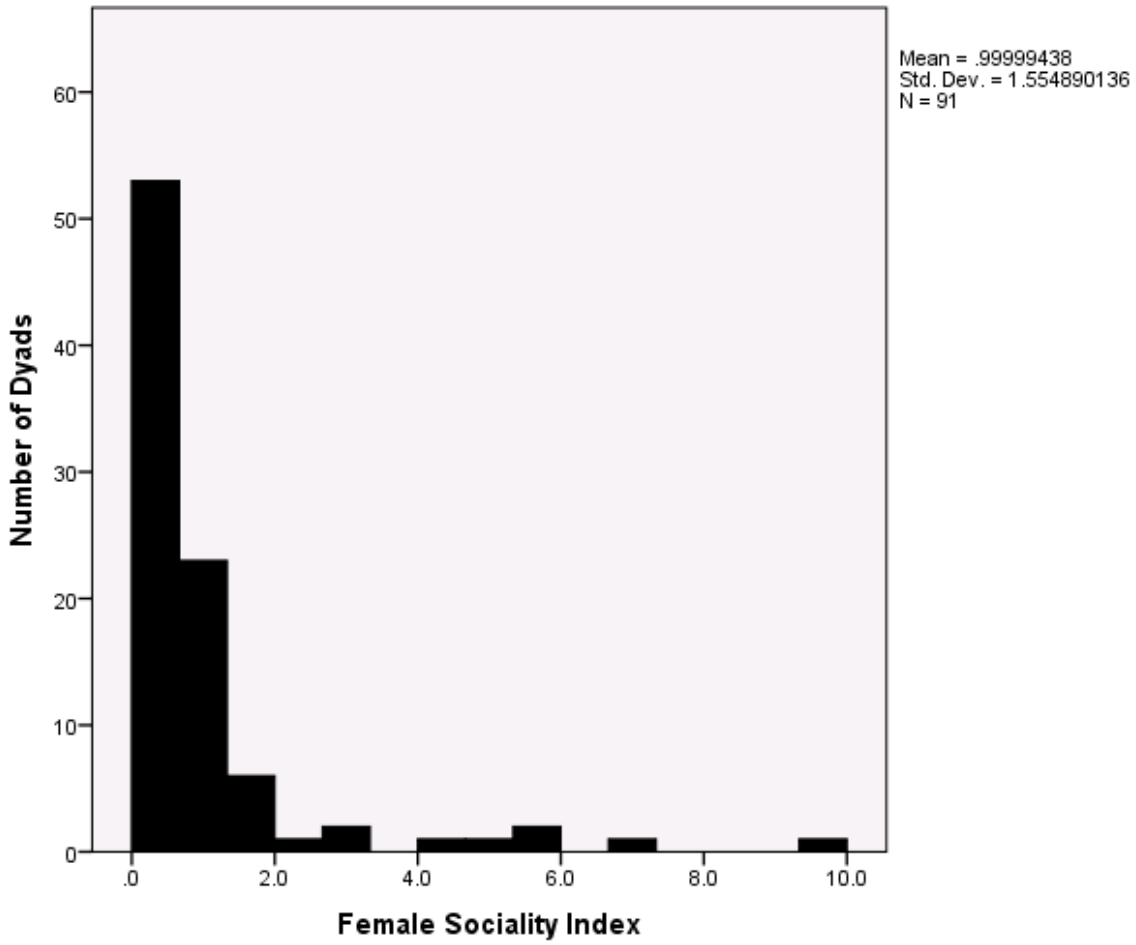


Figure 3.3. Frequency of use of gestures. Use by adult males with members of different age-sex classes. Means + 95% confidence intervals are shown

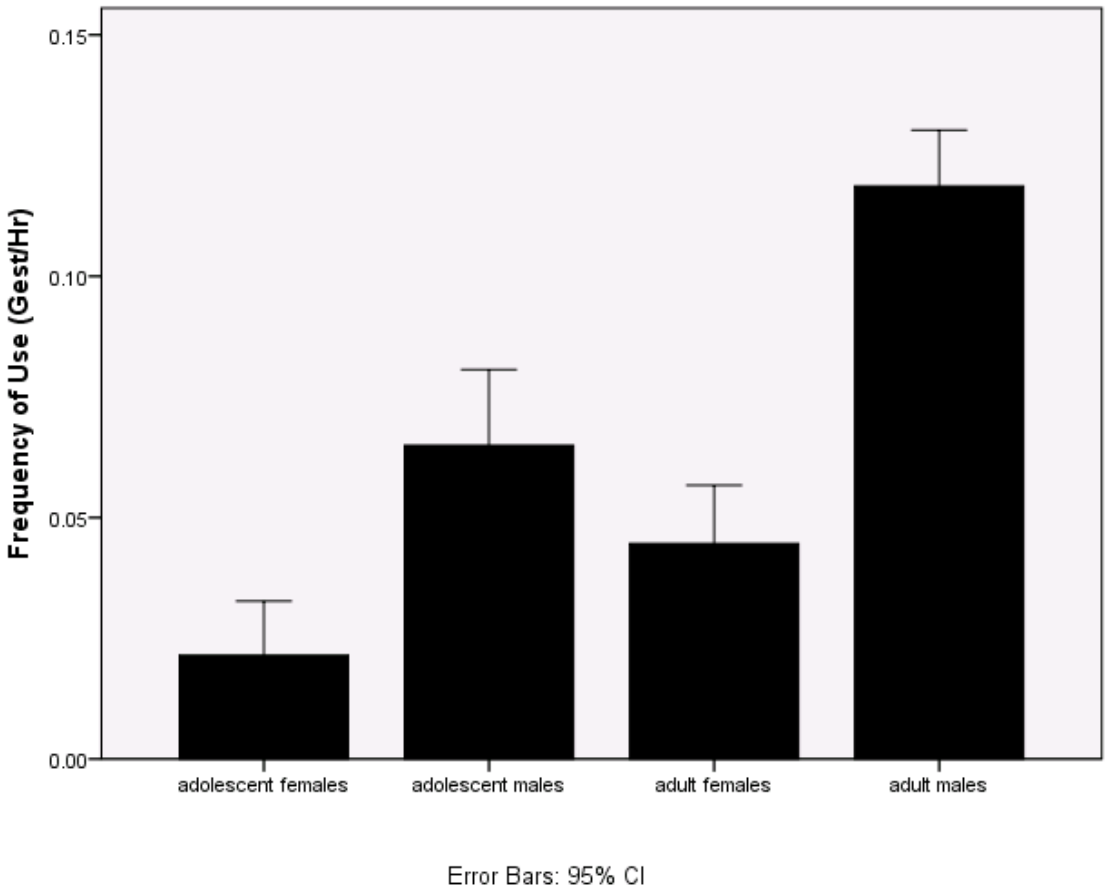


Figure 3.4. Frequency of use of gestures. Use by adult males with other adult males who possessed strong and weak social bonds with signalers. Means + 95% confidence intervals are shown

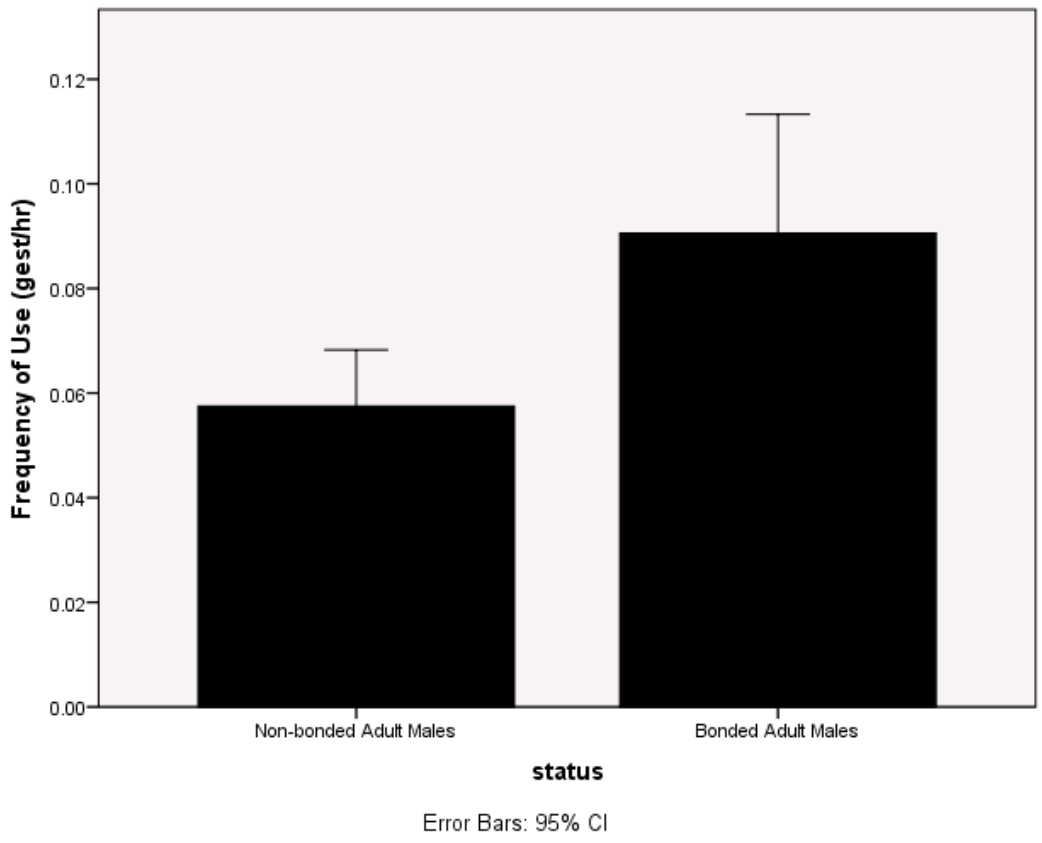


Figure 3.5. Frequency of use of gestures. Use by adult females with other adult females who possessed strong and weak social bonds with signalers. Means + 95% confidence intervals are shown.

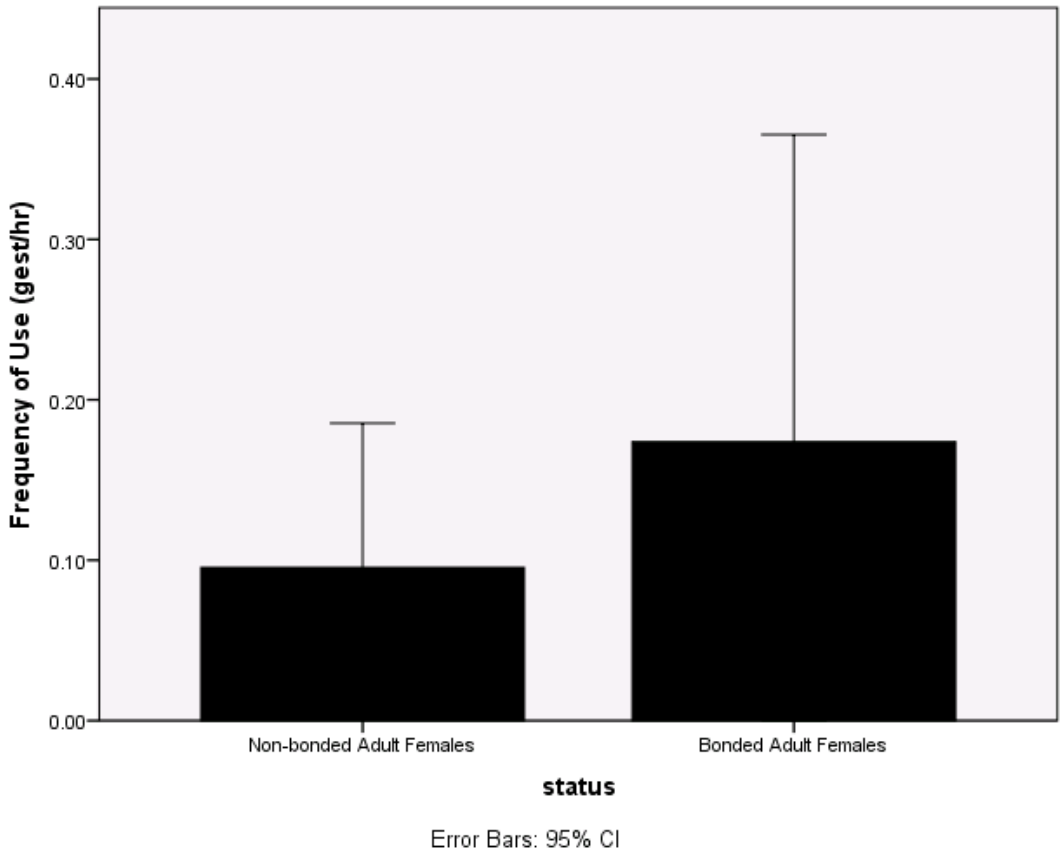


Figure 3.6. Frequency of responses to gestures by adult males. Adult male responses to members of different age-sex classes. Means + 95% confidence intervals are shown.

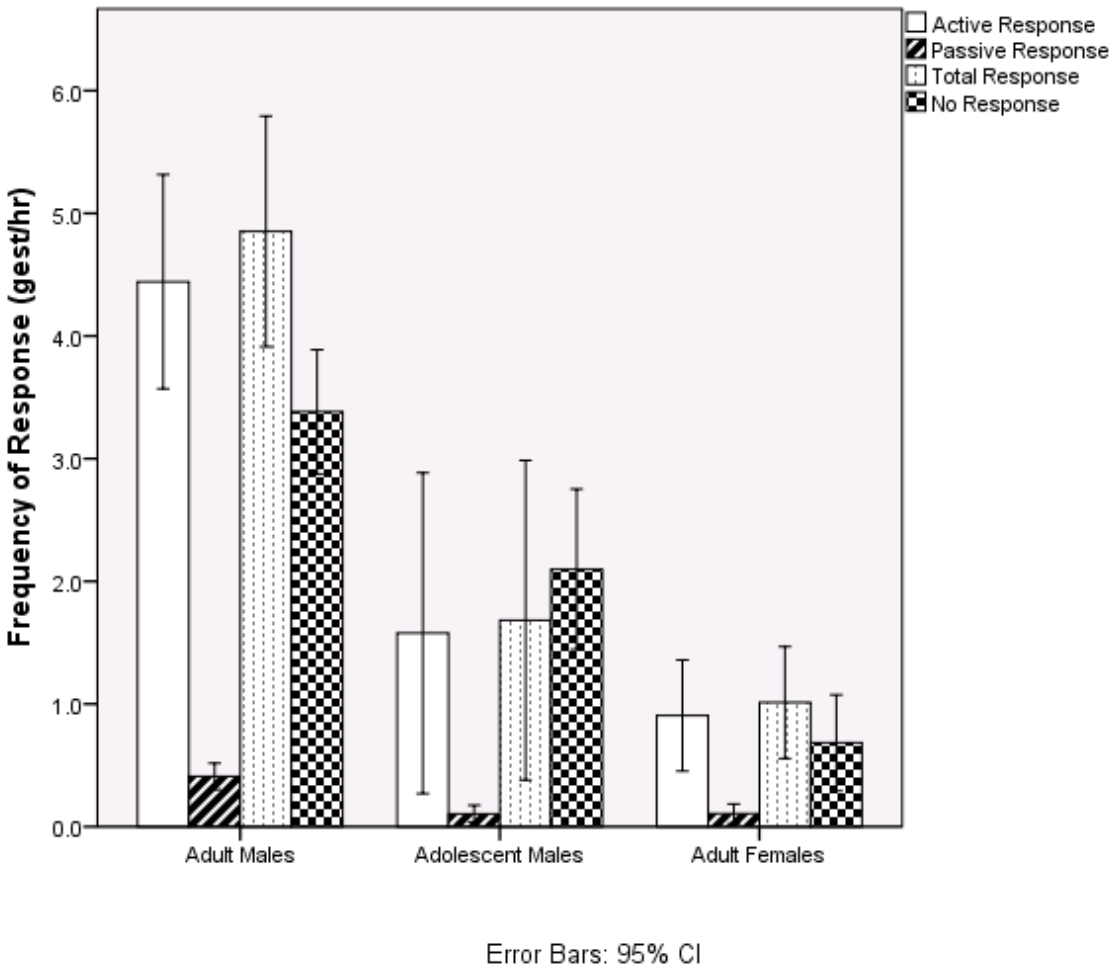
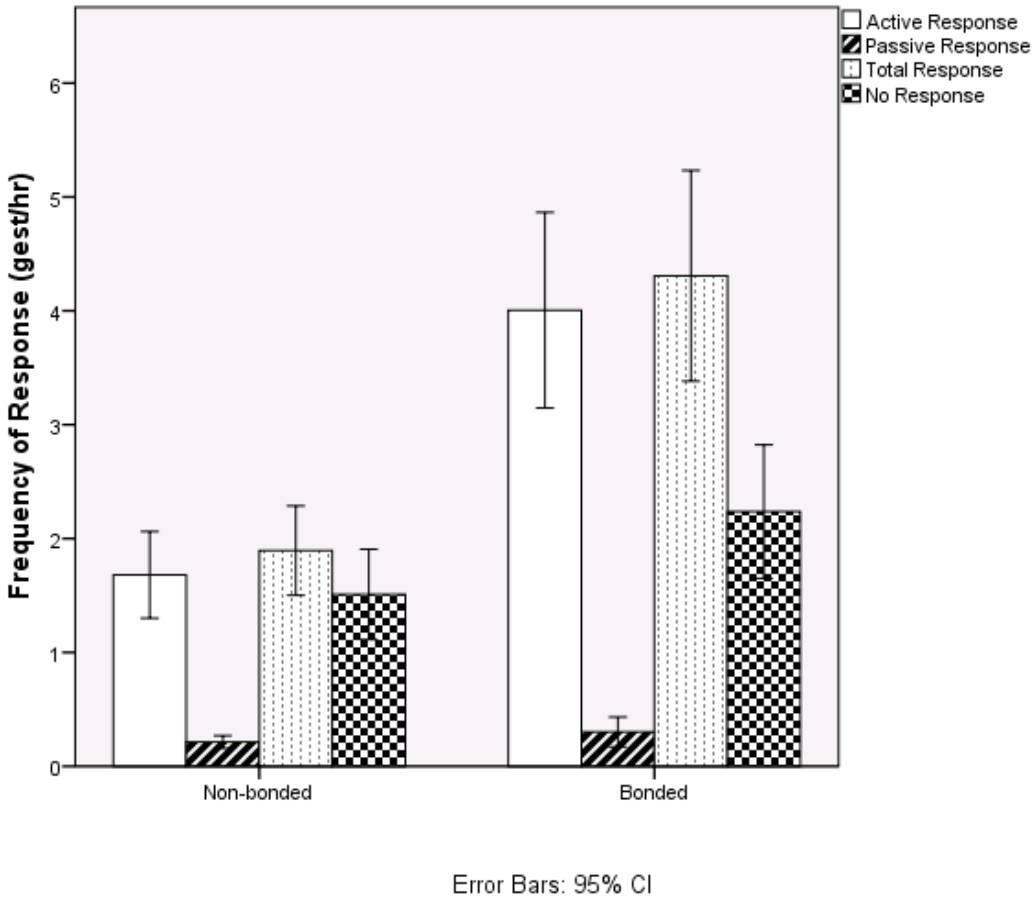


Figure 3.7. Frequency of response to gestures by adult males. Adult male responses to individuals who possessed strong and weak social bonds with respondents. Means + 95% confidence intervals are shown.



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CHAPTER IV

Gestural communication by wild chimpanzees:

Repertoire Size and Repetition Rates

ABSTRACT

Adult male chimpanzees frequently use gestures to communicate with conspecifics in their natural social and environmental settings, but few data exist regarding the number of gestures that they use and how they use them. To investigate these issues, I conducted an 18-month field study of wild chimpanzees in an unusually large community at Ngogo, Kibale National Park, Uganda. I specifically examined the number of gestures adult males used when communicating to members of different age-sex classes and how often they repeated gestures when signaling to different individuals. Results revealed that the identities of signalers and recipients affect the number of gestures that are used and how often gestures are repeated. Adult males used more gestures when they gestured to other adult males compared with when they signaled to adult females and adolescent males. Adult males also repeated gestures more often when gesturing to adult males and adolescent males compared with when they gestured to adult females. The strength of social bonds between adult males had a minimal impact on gesture repertoire size and repetition. Adult males displayed a trend to use more gestures with others with whom they formed strong bonds compared with those with whom they

maintained weaker bonds. In contrast, the strength of social bonds between adult males did not affect the rate with which they repeated gestures. These findings underscore the fact that gesturing is a communicative act involving both signalers and recipients. Understanding how gestures are used requires knowledge of both parties.

INTRODUCTION

Recently, gestural communication by our closest living relatives, the apes, has received considerable attention. Studies have shown that apes use gestures flexibly between and within contexts, with single gestures produced in multiple contexts and different gestures used in the same context (review in Tomasello and Call 2007). Additional research reveals that the types of gestures apes use vary as a function of their audience. For instance, signalers use visual gestures when potential recipients are attending to them and employ auditory gestures when recipients are looking away (Tomasello et al 1994; Pika et al. 2003, 2005; Tomasello and Call 2007). The number of gestures that apes use and their patterns of usage have been particular foci of research as these issues bear on the question of intentionality. Studies have shown that that individuals repeat gestures until they have achieved their desired response, or when this fails, they elaborate gestures by changing and using news ones (Leavens et al 2005; Leibal et al 2004; Cartmill and Byrne 2007; Hobaiter and Byrne 2011a; Roberts et al 2012). Captive chimpanzees, for example, repeat gestures if they do not achieve their goal (Leavens et al 2005). Similarly, orangutans adjust their gesturing behavior as a function of how well they are understood (Cartmill and Byrne 2007). Individuals repeat

the same gesture if they are partially understood. However, if recipients misunderstand completely, signalers do not use the same gestures but instead employ new ones (*ibid*.).

While prior studies have contributed to our understanding of how apes use gestures flexibly and intentionally, they suffer from two limitations. First, most research, to date, has been conducted in captivity. There is a paucity of data regarding how apes use gestures in their natural social and environmental settings (but see Hobaiter and Byrne 2011a,b; Roberts et al 2012). Second, gesturing behavior is a communicative act. Because communication mediates social interactions, relationships between individuals are likely to have an important impact on gestural communication. Thus far, however, no study has examined the effect of social relationships on the number of gestures apes use and how they employ them.

Chimpanzees provide a model system to investigate the influence of social relationships on gesturing behavior. Chimpanzees employ an array of gestures to communicate with conspecifics (Goodall 1968; Nishida et al. 1999; Pollick and de Waal 2007; Hobaiter and Byrne 2011). Moreover, chimpanzees form differentiated social relationships in the wild. Adult male chimpanzees in particular are quite gregarious. Specific pairs of males form strong and long-lasting social bonds that can have important fitness consequences (review in Muller and Mitani 2005). In contrast, members of other age-sex classes are less social and typically develop relatively weak bonds with others (*ibid*.). These differences in social relationships influence several aspects of chimpanzee behavior (Goodall 1986; Nishida 1990), but whether these variations affect aspects of their gestural communication remains an open question.

In this paper, I investigate gestural communication by adult males chimpanzees living in an exceptionally large community at Ngogo in the Kibale National Park, Uganda. Specifically, I examine the effects that social relationships have on repertoire size and rates of repetition. Adult male chimpanzees and their social relationships have been studied extensively at Ngogo (Mitani 2009b). In addition, the unusual size of the chimpanzee community there provides large numbers of individuals to observe, creating an ideal situation to examine the influence of social relationships on gesturing behavior.

METHODS

Study site, subjects, and behavioral observations

I conducted behavioral observations of chimpanzees at Ngogo in the Kibale National Park, Uganda, over 18 months between February 2008 to August 2009. The Ngogo study site lies close to the center of the 766 km^2 Kibale Park along the equator (00^0, 29' 53'' N; 30^0 25' 30 E) at an altitude of about 1400 m above sea level. The study area is covered with moist, evergreen forest interspersed with patches of *Pennisetum purpureum* grassland. Mean annual rainfall at Ngogo during the two-year study period was 1434 mm, with the site experiencing two dry seasons between January - February and June - July. Average maximum and minimum daily temperatures during 2008 – 2009 were 16.4 C^0 and 23.8 C^0, respectively. Struhsaker (1997) provides a detailed description of the Ngogo study site.

The Ngogo chimpanzee community is extremely large and consisted of about

170 individuals during this study. Chimpanzees at Ngogo have been observed for over 18 years, and as a result, most individuals were well habituated to human presence and relatively easy to follow. To assign age-sex classes of individuals, I used a classification system developed by Goodall (1986), who distinguished adult males (> 15 years), adult females (>14 years), and adolescent males (8 - 15 years). Using these age-sex class designations, I followed 29 adult males and collected data on the types of gestures they used and how often they repeated them with other adult males, adult females, and adolescent males. I conducted observations from 0700 to 1800 over 226 days. Focal individuals were followed for one hour, with targets selected so as to maximize the number of observation hours of each subject. I collected 719 h of focal data on adult male gesturing and social behavior. One Ugandan field assistant recorded an additional 2262 h of behavioral observations used in the analysis of social bonds.

Defining chimpanzee social bonds

To collect data on adult male social relationships, I recorded social interactions between individuals, including who associated, groomed, and maintained proximity with whom. I noted who associated with subjects at the beginning of each focal sampling session. Proximity and grooming were recorded during point samples made every 10 minutes. I assessed social relationships between adult males using these behavioral observations. I used all three behaviors to compute a composite sociality index (SI) between adult male dyads (Silk et al. 2006). Numerically this index is:

$$\frac{\frac{A_{i,j}}{A_{x,y}} + \frac{P_{i,j}}{P_{x,y}} + \frac{G_{i,j}}{G_{x,j}}}{3},$$

where $A_{i,j}$ = the frequency of association between individual i and individual j and $A_{x,y}$ = the median frequency of association between all possible (406) dyads (Silk et al 2006). The frequencies of proximity (P) and grooming (G) were also computed in the same manner.

Defining and documenting gestures

I recorded data on the types of gestures used by adult males and the number times they repeated them. I began by creating an inventory of gestures used by the Ngogo chimpanzees adapting terms employed in previous research on captive chimpanzees (Savage-Rumbaugh et al. 1977; Savage and Bakeman 1978; Tomasello et al. 1985, 1989; deWaal 1988, 1989; Pika et al. 2003, 2005; see Chapter 2). Gestures were defined as body and facial movements and postures by one individual that were directed toward another individual that resulted in a behavioral response (Plooij 1978). Three criteria differentiated gestures from non-gesturing behavior: (1) whether the signaler waited for a response, (2) whether the recipient alternated his gaze and (3) whether the signaler persisted in performing and repeating the gesture (Tomasello et al. 1985, 1989). Gestures were identified by any one of these criteria, although in practice, most fulfilled two or all three. I identified 78 gestures used by the Ngogo chimpanzees (Chapter 2 Table 2.4).

During one-hour focal observation sessions, I recorded the types of gestures used by adult males. I defined recipients of gestures as the individuals to whom the signaler directed the gesture. Recipients were classified as other adult males, adult females, and adolescent males according to the age-sex class definitions described above.

I also recorded the number of times adult males repeated gestures. I counted repeated gestures when the same gesture was: (1) used after an initial gesture; (2) given between 0 and 3 seconds after an initial gesture and (3) directed toward the same recipient. I scored the number of times individuals repeated gestures per unit time, i.e. over 60 minutes. Most gestures were repeated by chimpanzees as single actions, e.g. *arm raise*, and ended when the individual paused, and then repeated the same gesture (Tomasello et al 1985; Pika et al. 2003). However, some gestures (16.7% = 13/78 gestures), e.g. *self scratching*, were difficult to count as single gestures as they were produced rapidly over short periods of time. In these cases, I counted the entire bout as a single gesture. A bout was defined to begin with the initial use of a single gesture and to end when the signaler paused for at least 3 seconds (Tomasello et al 1985; Pika et al. 2003). For example, if more than 3 seconds passed after an individual used a rapid-fire *self-scratching* gesture, a repeated gesture bout was scored if the *same* gesture was directed toward the *same* recipient. Scoring bouts as single gestures potentially introduces bias in calculating rates of repetition by underestimating the number of repeated gestures. Because response waiting occurred after each gesturing bout, however, treating bouts as single gestures provided a behaviorally relevant way to assay the repetition of gestures.

Statistical analysis

To evaluate social bonds between adult males, I counted the number of point samples each dyad associated, were in proximity, and groomed. I then divided these values by the number of hours I observed each pair to calculate frequencies. The sociality

index (SI) measured the degree to which association, proximity, and grooming between particular dyads deviated from all other pairs in the community. High values indicated strong bonds between dyads, while low values reflected weaker bonds. Dyads with a sociality index larger than 3.19, a value equal to the mean (1.55) plus one standard deviation (1.64), were considered strongly bonded males. I considered all other dyads to be weakly bonded (SI = 0.0 – 3.0).

To assess repertoire size, I calculated the number of gesture types used by each adult male chimpanzee. I then compared the total number of gesture types used by adult males with other adult males, adolescent males, and adult females using parametric paired Student's *t* tests. I also conducted an analysis to examine whether social bonds between individuals influenced the number of gestures used by adult males. Of the 29 adult males in my sample, 17 had 3 or more strongly bonded partners, 9 males had only two partners, and 3 males had no partners. Because only 14% of dyads were strongly bonded, every adult male had substantially fewer strongly bonded partners than weakly bonded ones. Including individuals with fewer than three partners could potentially skew the results of analyses investigating the number of gestures used by males, and I excluded them as a result. For the remaining 17 individuals, I used a paired Student's *t* test to compare the number of gestures they used with strongly bonded and weakly bonded individuals.

I compared how often adult males repeated gestures with members of different age-sex classes using paired samples *t* tests. I also used a paired *t* test to examine how often adult males repeated gestures with strongly bonded males and weakly bonded

males. For all analyses, parametric tests were performed only after confirming that the data were normally distributed using a Kolmogorov-Smirnov test.

RESULTS

Adult chimpanzee social relationships

The sociality Index (SI) between adult males ranged from 0.00 to 11.06 (X + SD = 1.55 + 1.64, N = 406 dyads; Fig. 4.1). The scores, however, were strongly skewed to the left. The majority of dyads fell below 3.19, a value equal to the mean plus one standard deviation. Using this cut-off, 57 pairs (14%) formed strong bonds with each other, with the number of partners varying from 2 to 10 individuals per male.

Repertoire size

Adult males used more types of gestures with other adult males than they did with adolescent males (t_{28} = 13.24, P < 0.001; Fig. 4.2) and adult females (t_{28} = 13.10, P < 0.001; Fig. 4.2). While the age-sex class of recipients influenced repertoire size, the social bonds between signalers and recipients had only a weak effect. There was a non-significant trend for adult males to use more gestures with other adult males with whom they shared strong social bonds compared with those they employed when signaling to others with whom they shared weaker bonds (t_{16} = 1.87, P = 0.08; Fig. 4.3).

Rates of repetition

Adult males repeated gestures significantly more often when communicating with other adult males than with adult females ($t_{28} = 2.10$, $P < 0.04$; Fig. 4.4). Repetition rates did not differ, however, when adult males gestured to adult males and to adolescent males ($t_{28} = -0.24$, $P = 0.81$; Fig. 4.4). The strength of social bonds between males did not affect how often they repeated gestures with each other ($t_{16} = -0.92$, $P = 0.37$; Fig. 4.5).

DISCUSSION

Results presented in this paper shed light on how chimpanzees use gestures in the wild. Specifically, they reveal that the identities of signalers and recipients affect the number of gestures that are used and how often gestures are repeated. Adult males used more gestures when they signaled to other adult males than they did when signaling to adult females and adolescent males. Adult males also repeated gestures more often when communicating to adult males and adolescent males compared with when they communicated to adult females. The strength of social bonds between adult males had a minimal impact on gesture repertoire size and repetition. Adult males showed a trend to use more gestures with others with whom they formed strong bonds compared with those with whom they maintained weaker bonds. In contrast, the strength of social bonds between adult males did not affect the rate with which they repeated gestures.

Prior research investigating the number of gestures that apes use and the number of times they repeat them have addressed the issue of intentionality, with most studies

conducted in captivity. Here observations reveal that chimpanzees alter the kinds of gestures they use as a function of the attentional states of recipients (Tomasello et al 1994), exhibit response waiting after signalers gesture (*ibid*.), and repeat the same gesture if they have not achieved their goal (Leavens and Hopkins 1998; Leavens et al 2005). Fewer studies have investigated chimpanzee gestural communication in the wild. In this context, recent research on the Sonso community of chimpanzees in the Budongo Forest Reserve, Uganda, furnish data to compare with my findings. At Budongo, juvenile and sub-adult chimpanzees use more gestures than do adults (Hobaiter and Byrne 2011a). Similarly, young chimpanzees showed a tendency to use different gestures repeatedly during rapid-fire sequences, while adults used gestures singly (Hobaiter and Byrne 2011b).

At first blush, the results from Budongo appear to differ dramatically from those documented at Ngogo, where individual adult males display the largest repertoires of gestures and repeat them often when communicating to other adult males. Presently, it is impossible to resolve these differences because of two empirical and methodological reasons. Empirically, I did not collect observations of gesturing behavior by juvenile chimpanzees, so it remains unclear whether young chimpanzees possess larger repertoires than do adults at Ngogo. Methodologically, results from this study highlight the fact that gesturing is a communicative act that involves both signalers and recipients. The number of gestures used and patterns of usage clearly vary as a function of who gestures to whom. For example, adult males employ many more gestures when communicating to other adult males than they do when signaling to adult females. Observations in the former context provide a very different picture regarding repertoire size than those

derived from the latter situation. Prior studies at Budongo do not differentiate signalers gesturing in distinct contexts, and as a consequence, the differences between studies may be more apparent than real. Additional research at Budongo and Ngogo will be required to address this issue.

What accounts for the variation in repertoire size and use of gestures by chimpanzees at Ngogo? I propose two factors that may explain why adult males use a large number of gestures with other adult males. First, life history characteristics may play an important role. Male chimpanzees are philopatric; they are born, live, and die within the same community. In contrast, females disperse from their natal groups during adolescence when they are around 10 years old (Nishida and Kawanaka 1972; Pusey 1979). Like adult females, adolescent males begin to socialize with adult males later in life as they attempt to integrate themselves into the adult male social network (Pusey 1990). One prominent hypothesis suggests that chimpanzees learn gestures via ontogenetic ritualization (Tomasello et al 1994). In this process, individuals acquire gestures through repeated social interactions with specific individuals. Because of the sex bias in dispersal, prolonged period of male development during which young males spend scant time with adult males, and fission-fusion nature of chimpanzee society where all individuals are not together all of the time (Nishida 1968), adult males will have fewer experiences with adult females and adolescent males than they do with other adult males. As a consequence, adult males may have less time to develop and refine their gestural repertoires with adult females and adolescent males than they do with other adult males with whom they have spent their entire lives.

Variations in social relationships between members of different age-sex classes provide the basis for a second hypothesis to explain the observed differences in repertoire size reported here. Adult male chimpanzees are much more social than are adult females and adolescent male (review in Muller and Mitani 2005). Adult male chimpanzees engage in a variety of cooperative behaviors, including coalitions, meat sharing, and territorial boundary patrols (Mitani 2009a). Such behavior yields tangible benefits with regard to mating success (Duffy et al. 2007), maintenance of dominance rank (Nishida et al. 1992), warding off neighboring males (Wilson and Wrangham 2003; Mitani and Watts 2005), defending females (Williams et al. 2004), and increasing the size of the communal territory (Mitani et al. 2010). To obtain these proximate and ultimate benefits, adult male chimpanzees have greater need to communicate with each other than they do with members of other age-sex classes, resulting in the larger array of gestures employed between them. It would interesting to compare the frequency of use and response of gestures between cooperative endeavors of hunting/patrolling and times of other affiliation.

Why do adult males repeat gestures often with other adult males and with individuals with whom they share strong social bonds? Adult males form strong and enduring bonds as they cooperate with each other to obtain important social and fitness benefits (Mitani 2009b). Because communication mediates these social relationships, adult males are quite likely to form and maintain these bonds with others via the repeated use of gestures. As adolescent males become integrated into the social network, adult males begin to forge new relationships with them and repeating gestures with them may be a conduit to achieve this goal. Adult males, who interact and cooperate with adult

females relatively infrequently, will have less need to communicate with them. In the process, gestures will be repeated less often during exchanges between them.

Taken together results of this study underscore the importance of analyzing gestural communication as an exchange involving two individuals, both signalers and recipients. Without knowledge of both parties and their social relationships, it is difficult, if not impossible, to understand how often gestures are employed and patterns of usage.

Figure 4.1. Sociality indexes of adult males chimpanzees.

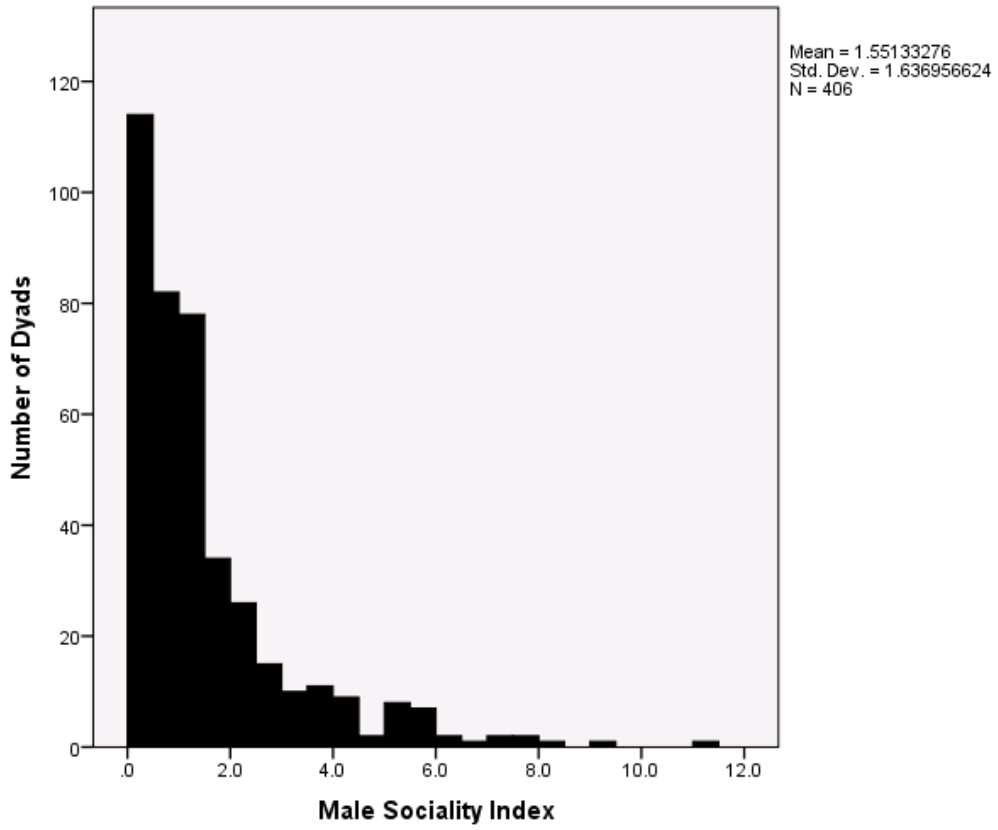


Figure 4.2. Repertoire size of adult male chimpanzees. Box plots of the number of gestures adult males used with members of different age-sex classes are shown.

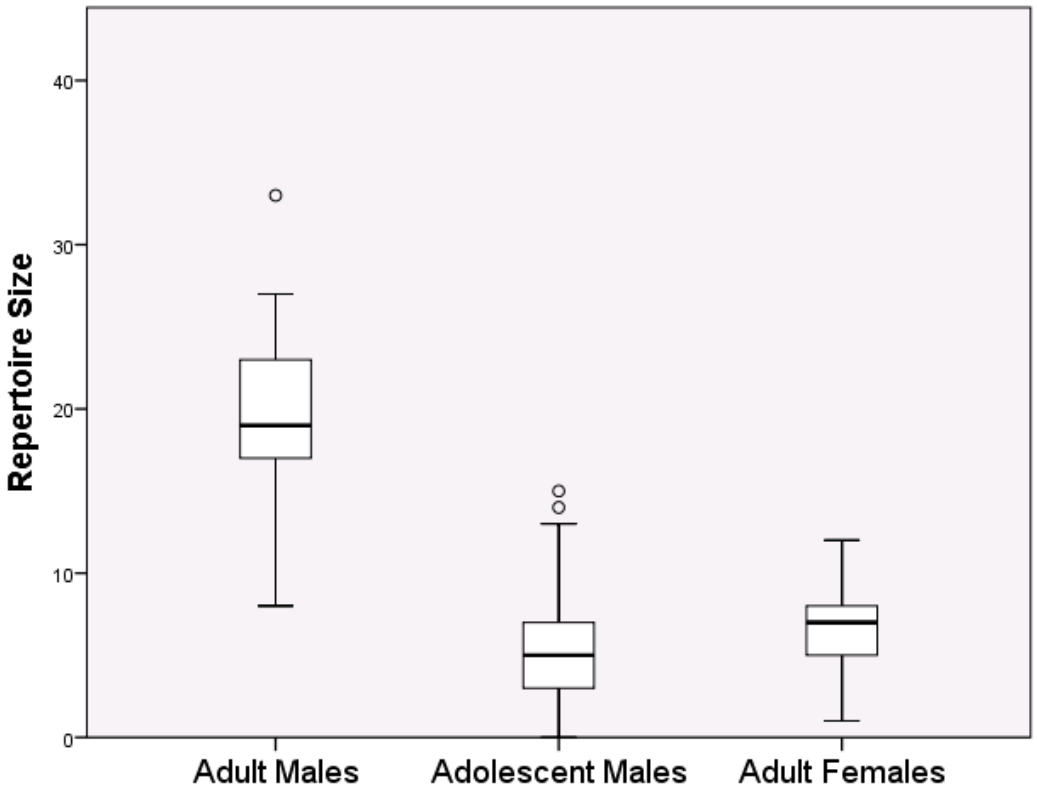


Figure 4.3 Repertoire size of adult male chimpanzees. Box plots of the number of gestures adult males used with other adult males who shared weak and strong social bonds are shown.

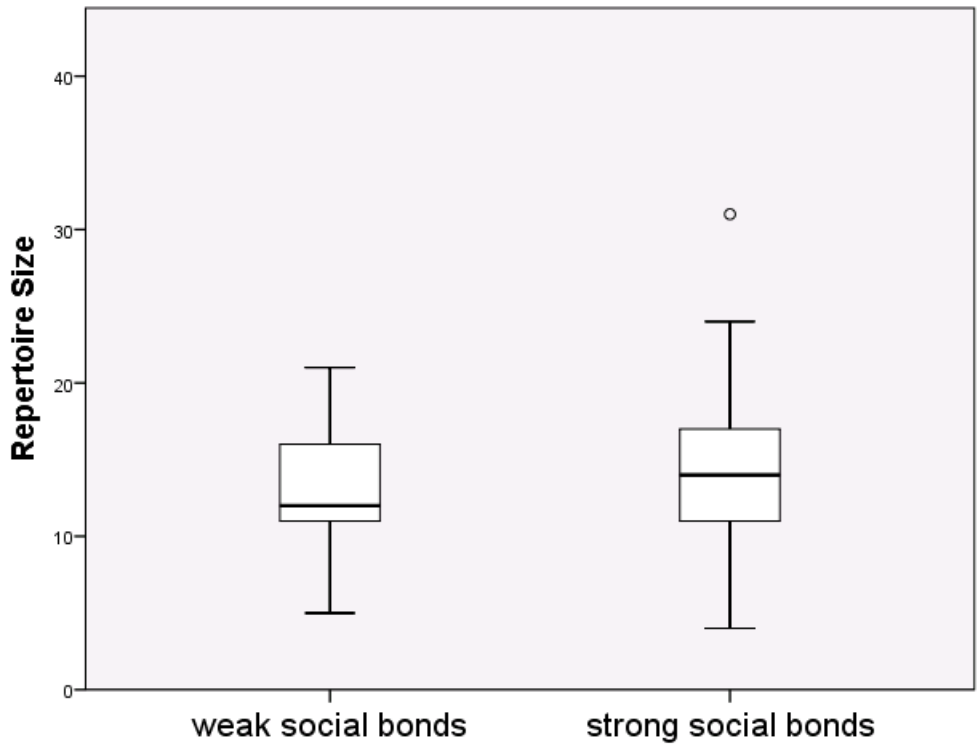


Figure 4.4. Repetition rates by adult male chimpanzees. The number of times adult males repeated gestures when communicating with members of different age-sex classes are shown. Means + 1 SE are displayed.

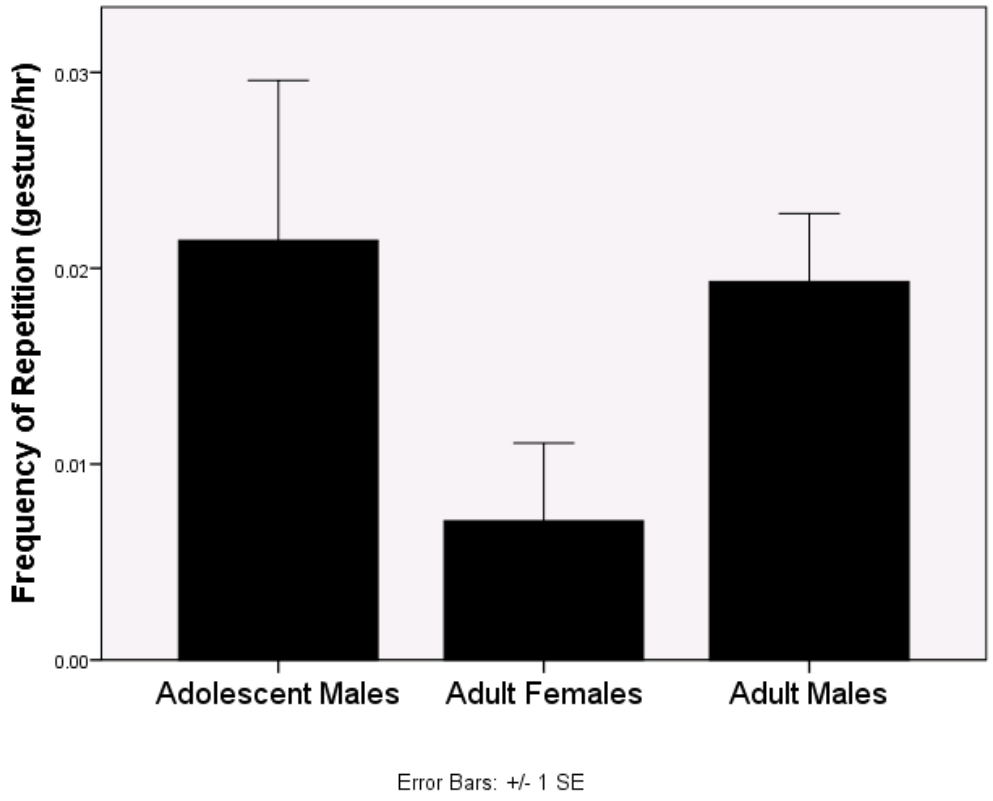
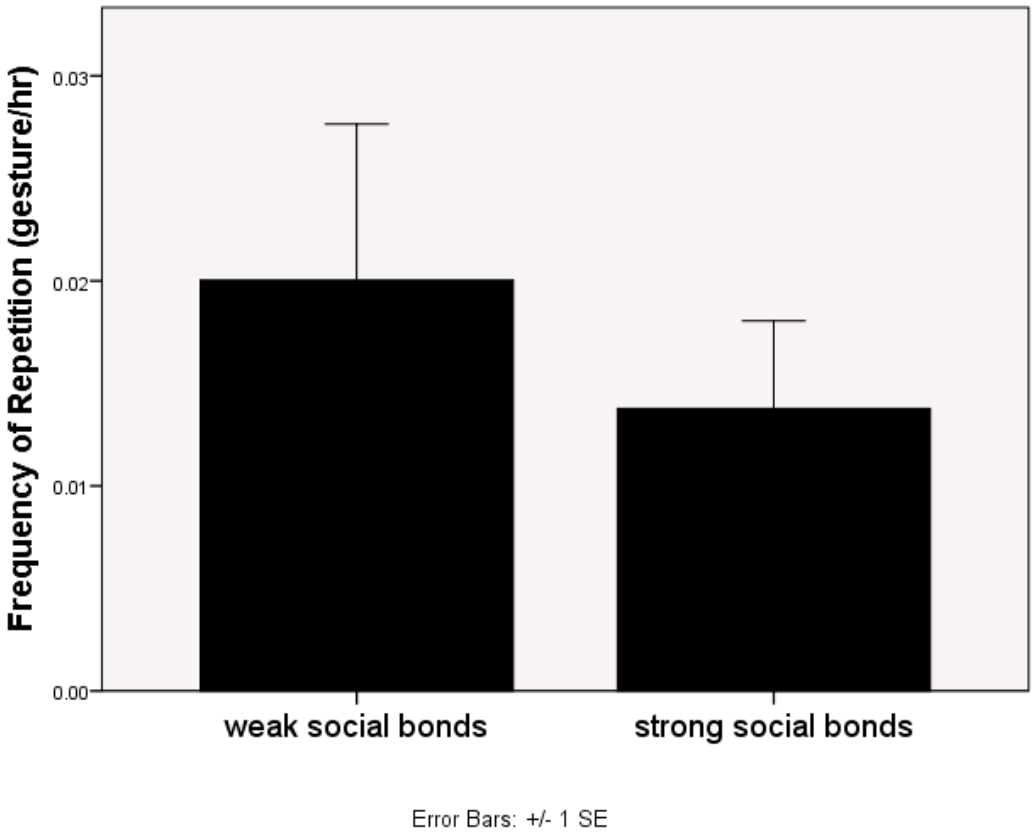


Figure 4.5. Repetition rates by adult male chimpanzees. The number of times adult males repeated gestures when communicating with other adult males who shared weak and strong social bonds are shown. Means + 1 SE are displayed.



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CHAPTER V

Conclusion

In this thesis, I addressed several questions. What kinds of gestures do chimpanzees use? Do they use them flexibly in different contexts? Is there variation in the number of gestures employed by chimpanzees across study sites? Do chimpanzees living in different areas use gestures in different ways? Do social relationships influence the use of and responsiveness to gestures? To answer these questions, I conducted a systematic field study of gestural communication by chimpanzees living at Ngogo in the Kibale National Park, Uganda.

Repertoire size, behavioral contexts, and comparisons among groups

The Ngogo chimpanzees produced 78 gestures in six behavioral contexts. Gestures took 3 different forms, with signalers gesturing to others via sight, sound, or touch. Visual and tactile gestures were produced more frequently than auditory gestures. Visual and tactile gestures were also employed flexibly in multiple contexts more often than they were used in only one situation. These results suggest that the Ngogo chimpanzees use gestures flexibly. Doing so may permit individuals to communicate successfully as they navigate their complex social environments.

My results conform to findings made in prior research, where chimpanzees have been shown to use gestures in a flexible and intentional manner in captivity (Tomasello 2007; Pollick and deWaal 2007). Taken together, these findings bear on the issue of the evolution of human language. One hypothesis is that our prehuman ancestors initially used gestures before gaining the abilities to produce and learn language (Hewes 1973; Hockett 1978; Burling 1993; Armstrong et al. 1995). Results from this thesis suggest that if wild chimpanzees use gestures flexibly in their natural environmental settings, then our early hominin ancestors also had the ability to do so. This shift toward a more flexible and intentional means of communication could have provided the foundation for the evolution of language.

Apart from these evolutionary speculations, my findings are relevant to a current controversy regarding how apes acquire gestures. One hypothesis invokes an important role for the genetic basis of gesturing (Genty et al 2009), while another places importance on the social nature of individuals (Tomasello and Call 1997). Results presented here support both hypotheses to some degree. Comparisons with other studies revealed that wild chimpanzees in three other communities produced a similar number of gestures as those by the Ngogo chimpanzees. This stunning similarity in the number of gestures produced by chimpanzees living in disparate areas is mirrored in another finding; chimpanzees across study populations also use the same kinds of gestures. Together, these observations are consistent with the hypothesis that chimpanzees acquire gestures through a process of phylogenetic ritualization (Genty et al 2009). If gestures are hard-wired, and to an extent, genetically predetermined, then there should be a high degree of

similarity in the numbers and kinds of gestures produced by chimpanzees in different populations.

Social relationships influence gestural communication

Additional results from this thesis support an alternative hypothesis; gesture acquisition is influenced by, if not dependent upon, social interactions among individuals. These considerations lead to the second major question addressed in this thesis. Do social relationships among chimpanzees influence their gestural communication? Specifically, does variation in social relationships affect who signals and responds to whom? The extraordinary size of the Ngogo chimpanzee community provided large samples of individuals and an ideal situation to address this question.

The findings presented here indicate that, as is the case with other aspects of chimpanzee behavior, social relationships have a large and pervasive effect on gestural communication. Because chimpanzee social relationships vary markedly between members of different age-sex classes, some pairs of individuals communicated more often than others, resulting in differences in the use and responsiveness to gestures. Adult males used and responded to gestures with each other more often than they did with adolescents or females. Additional analysis revealed that adult males used and responded to gestures frequently with adult males with whom they formed strong bonds compared with others with whom they shared weaker bonds. In contrast, adult females did not alter their gesturing behavior between bonded and non-bonded individuals. These results are consistent with an alternative hypothesis that proposes chimpanzees acquire gestures

through a process ontogenetic ritualization (Tomasello and Call 1997). In this process, individuals acquire gestures during repeated social interactions with specific individuals, who shape and alter their behavior. Currently, there is no clear resolution to the problem of how chimpanzees and other apes develop and acquire gestures. A definitive answer to the question must await longitudinal studies of known individuals, preferably in the wild where individuals are exposed to a full range of social partners and ecological conditions.

One significant finding of this thesis bears special comment. My results underscore the fact that gesturing is a communicative act involving both signalers and recipients. Understanding any communicative act, such as gesturing behavior, requires knowledge of both parties. For example, the number of gestures utilized by adult males varies markedly as a function of the identity of recipients. In addition, the manner with which adult males use gestures also changes depending on the recipients, with gestures repeated often to other adult and adolescent males. It should not be surprising that these observations can be interpreted within the context of what we know about male chimpanzee social relationships. Adult males display nonrandom patterns of affiliation and cooperation with other individuals, and these interactions have long-term fitness effects (Mitani 2009). To obtain these fitness benefits, adult male chimpanzees have strong motivation to forge bonds with one another. Using gestures to communicate is one proximate means that they can employ to achieve this goal.

Directions for future research

While this thesis provides novel data on the gestural communication of wild chimpanzees, my findings generate several questions that will require further study. For instance, longitudinal observations of specific individuals will go a long way to help resolve current debates regarding gesture acquisition. The role that mothers play when communicating with their infants will be of special interest in this regard and will shed additional light on the role that learning plays, if any, in the development of gesturing behavior. Examining whether particular dyads use idiosyncratic gestures would furnish an additional way to test the ontogenetic ritualization hypothesis. Alternatively, more comparative data would permit a more thorough examination of the similarities and differences between the gestural repertoires of chimpanzees at different sites, and furnish a means to evaluate the phylogenetic ritualization hypothesis. One major finding of this thesis points to the importance of social relationships in shaping gesturing behavior. Because male chimpanzee social relationships change over time, it would be of interest to track these changing relationships and evaluate the effects of such changes on the communication patterns of partners. Similarly, to what extent do social relationships influence the use of and responsiveness to gestures among members of other age-sex classes such as adolescent males and females, who experience quite different social worlds? Finally, further studies using similar methodological approaches can be used to address how all of the species of apes use and respond to gestures in the wild. Data on wild orangutans and gibbons, mountain gorillas, and bonobos would broaden the scope of gesture research to address phylogenetic similarities and differences between species. Investigating these and other questions provide fertile areas for future research regarding how our closest living relatives use gestures to communicate.

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