The Effects of Social Dynamics and Positional Behavior on Gestural Communication among African Apes

by

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ABSTRACT

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Gestures are integral components of human and non-human primate communication. In humans, children rely extensively on gesturing before speech develops (Knott 1979) and gestures remain important to communication even after the development of speech (Dunning 1971; Melinger & Levelt 2004). Gestural signaling is also central to communication in other primates, particularly African apes (Pika *et al.* 2005a). Neurological research reveals structural similarities between key language networks in the brain and manual actions in humans and non-human primates, providing evidence for an evolutionary continuity between language and bodily actions among primates (Kelly *et al.* 2002; Arbib 2005). Although much has been learned about gestural signaling in primates, an understanding of how and why gestural repertoires vary across species and what role gestures played in language evolution is incomplete.

This dissertation investigated how two factors, social dynamics (the nature of social relationships) and positional behavior (locomotor and postural behavior), shaped gestural communication within and across captive groups of western lowland gorillas (*Gorilla gorilla gorilla*), chimpanzees (*Pan troglodytes* sspp.), and bonobos (*Pan paniscus*). I conducted this research with six captive groups over the course of twenty-four months. Subjects included: 1) Two groups of western lowland gorillas at the Bronx Zoo, NY; 2) Two groups of chimpanzees at the St. Louis Zoo, MO, and Los Angeles Zoo, CA; and 3) Two groups of bonobos at the San Diego Zoo and San Diego Wild Animal Park, CA. I used a Sony Handycam to collect continuous video data of social interactions (from which I coded various aspects of gestural signaling) and 15-minute focal animal sampling (from which I coded frequencies and durations of positional behaviors).

While there was some level of inter-group variation in all species, patterns of gestural communication were accurate measures of the unique social dynamics that characterize each species. Gesturing was not restricted by the availability of the upper limbs; rather, positional behavior was often used to enhance certain gestures, particularly dominance displays. These results demonstrate that gestural signaling expresses the kind of behavioral and locomotor plasticity that could have given rise to a flexible, complex form of communication that eventually became language.

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CHAPTER 1

INTRODUCTION AND BACKGROUND

Gestures are integral components of human and non-human primate communication. The communicative value of gestures in terms of their symbolic and grammatical properties, their connection to language, and their evolutionary origins have sparked considerable controversy, yet gestures have not been studied as extensively as speech. While it is clear that children rely extensively on gestures well before speech develops (Knott 1979) and that gestures remain important to communication even after the development of speech (Dunning 1971; Melinger & Levelt 2004), the evolutionary relationship between gestures and speech remains unresolved.

Whether or not gestural signaling was the precursor to language is a hotly debated issue among linguists and anthropologists alike. Some researchers argue that gestural signaling provided the foundation for language once the shift toward bipedality in early hominins left upper limbs less suited for locomotion and more accessible for communication; controlled speech was incorporated into this system as anatomy allowed (Hewes 1973; Leroi-Gourhan 1993; Corballis 2002, 2003, 2009; Gentilucci & Corballis 2006). Others contend that language first originated from vocalizations, based heavily on research that has identified referential meaning in certain primate calls (*e.g.*, Cheney and Seyfarth 1990; Zuberbühler 2000; Seyfarth 2005). Other researchers maintain a different approach and assert that non-human primate gestures and vocalizations are entirely different systems of communication from human language and are not the basis from which language evolved (*e.g.*, Chomsky 1968; Pinker & Bloom 1990; Burling 1993; Owren & Rendall 2001).

Researchers have turned to our primate relatives for insights into the importance of gestures in primate communication and for clues about how language may have evolved in early hominins. In recent years, much has been learned about the gestural repertoires of several primate species, particularly the African apes (de Waal 1988; Tomasello *et al.* 1997; Pika *et al.* 2003, 2005a, 2005b; Liebal *et al.* 2004a; but see Liebal *et al.* 2004c, 2006; Maestripieri 2005; and Hesler & Fischer 2007 for other primates). Yet, an understanding of how and why gestural signaling varies across species and what role gestures played in language evolution is far from complete. This dissertation investigates how two factors, social dynamics (*i.e.*, group composition and the nature of social relationships) and positional behavior (locomotor and postural behavior), shape gestural communication and drive variance in gestural repertoires within and across captive groups of western lowland gorillas (*Gorilla gorilla gorilla*), chimpanzees (*Pan troglodytes* sspp.), and bonobos (*Pan paniscus*).

1.1 Gestural Communication and Language Evolution

Observe any conversation in any area of the world and it will quickly become clear that gestures are ubiquitous. The gestures themselves vary, from gesticulations used along with speech to pantomimes that represent objects or events to emblems that hold arbitrary meaning. The meaning behind gestures also varies from person to person and culture to culture (Archer 1997). Holding up two fingers in the shape of a "v," with the palm facing outward is a gesture for "peace" in the United States, but turn the hand so that the palm faces inward, and you've just insulted someone in the United Kingdom. While gestures may vary in form, meaning, and function, the common thread between them is that gestures are prevalent in all human populations, and this universality suggests that gestures are fundamental components of human communication.

The wealth of research on human gestures provides support for the notion that gestures are instrumental in communication. Children acquire gestures early in development and use them extensively before speech develops (Knott 1979; Iverson *et al.,* 2000). Even after the onset of spoken language, gestures remain important features of communication and are used in conjunction with speech into adulthood (Dunning 1971; Kendon, 1997; Melinger & Levelt, 2004). Gestures are so intimately tied to speech that even congenitally blind people gesture as often as sighted people during conversations, and people on the phone often gesture while talking even though the gestures aren't visible to their conversation partners (Iverson & Goldin-Meadow 1998).

But, gestures are not merely tools used to enhance speech. Gestures are now regarded as essential parts of language, working with speech to form an integrated system in which both modalities contribute to language production and comprehension (Kelly *et al.* 2008; Kelly *et al.* 2010). Recent studies have shown that people are better able to articulate their thoughts when using gestures, and gestures themselves can actually facilitate cognitive processes by grounding our thoughts in action (Beilock & Goldin-Meadow 2010). Specifically, Beilock and Goldin-Meadow (2010) found that, after performing physical tasks, speakers whose use of one had was restricted had a more difficult time describing the task and their second performances of the task subsequently suffered. These studies on human gestures not only provide compelling evidence for the intimate connection between speech and gestures, but also highlight the intriguing link between gestures and cognition.

Neurological evidence also sheds light on the role of gestures in shaping language evolution. In humans, Broca's area has been traditionally viewed as the speech area, but recent research reveals that this area is also active when humans perform and observe manual actions (Arbib 2005). An area homologous to this region, F5, has also been discovered in the brains of macaques. In these monkeys, F5 contains neurons dubbed "mirror neurons" that are active when macaques observe and execute facial or manual actions (Perrett *et al.* 1985; Arbib 2005). A homologue also exists in macaques for Wernicke's area, the region in humans that is involved in language comprehension. In humans and monkeys, this region is also active during facial and forearm movements (Kelly *et al.* 2002). Interestingly, primate vocalizations are not related to the F5 region, but rather the anterior cingulated cortex and other non-cortical regions (Jürgens 2002). Furthermore, Xu *et al.* (2009) found that symbolic gestures (*i.e.*, pantomimes and emblems that signify actions and stand alone without speech) are processed by the same neural system as spoken language. This suggests that the area traditionally known as the "language network," the inferior frontal and posterior temporal cortices, does not function solely as a spoken language network, but rather it is an area that processes a broader range of symbolic communication, independent of modality (Xu *et al.* 2009).

These findings have compelling implications for language evolution. Not only are these neural networks active when humans produce and comprehend spoken language, they are also active when processing gestures, suggesting that gestures were crucial to shaping human communication. Furthermore, the structural similarities between these key language areas and manual actions in both humans and non-human primates demonstrate an evolutionary continuity between language and bodily actions among primates (Kelly *et al.* 2002; Arbib 2005).

1.1.1 The Gestural Origins Theory of Human Language

The universality of gestures in human communication and the presence of homologous neurological structures relating to language production and comprehension in our primate relatives have led many to consider the role of gestures in language origins and evolution. Are gestures as important to non-human primate communication as they are to human communication? Could gestures have provided the foundation on which language was built?

One approach to answering these questions is to investigate whether human language is rooted in the vocalizations of our non-human primate ancestors, in their gestures, or in a combination of both. Although some (*e.g.*, Chomsky 1968; Pinker & Bloom 1990; Burling 1993) argue that language arose late in human evolution and is not based on the communication systems of non-human primates, decades of research demonstrate compelling links between human and non-human primate gestures and vocalizations. Many researchers of vocal signaling contend that certain non-human primate vocalizations are semantic and stem from cognitive mechanisms similar to those that underlie human language (Seyfarth *et al.* 1980, 2005; Seyfarth 2005). Others, however, argue that a more fruitful avenue for investigating precursors to human language is to explore gestural signaling.

The "gestural origins theory" of language was first introduced by Hewes (1973), and, since then, the theory has gained increasing support from other researchers (Leroi-Gourhan 1993; Corballis 2002, 2003, 2009; Copple 2003; Gentilucci & Corballis 2006). The gestural origins theory argues that the emergence of bipedality in early hominins set the stage for the upper limbs to be used for activities such as tool making and tool use, carrying objects, and manual communication. Thus, manual gestures provided the framework for language; then, more complex and controlled speech was incorporated into this system once anatomy allowed. Armstrong *et al.* (1995) argue that gestures used in human sign languages also possess properties of syntax that were originally argued by Chomsky (1968) and others to be inherent only in human speech. Arbib *et al.* (2008) propose that symbolic gestures such as pantomimes that followed syntactical rules eventually gave rise to “protosign,” which laid the groundwork for the emergence of “protolanguage” and eventually language in early hominins. Though the gesture origins theory is far from reaching wide consensus, the recent advances in cognitive neuroscience (*e.g.*, the discovery of “mirror neurons” that are active when performing or observing actions but not when vocalizing) give credence to this evolutionary scenario in which speech became incorporated into a system based originally on gestural signaling and provide evidence for continuity between gestures in human and non-human primates (Corballis 2002, 2003, 2009; Arbib 2005).

Evidence from observational and empirical studies of non-human primate gestural communication also lends support to the gestural origins theory of language. Playback studies and spectrogram analyses of primate calls have demonstrated that species such as vervet monkeys (*Cercopithecus aethiops*) and Campbell’s monkeys (*Cercopithecus campbelli*) use certain calls referentially to represent specific predators and that group members respond in different, predator-appropriate ways to these calls (Cheney & Seyfarth 1990; Zuberbühler 2000). There is also evidence that listeners can derive information about a caller (such as rank) which influences how they perceive and react to certain calls (Cheney & Seyfarth 1990; Kitchen *et al.* 2003; Seyfarth *et al.* 2005). These studies indicate some flexibility in the ways that certain primate species learn to distinguish and comprehend signals (particularly for the listener). But, there is no evidence that non-human primates invent new vocalizations (a key component of human language) and only limited evidence of flexible call production or usage in different contexts (Tomasello & Zuberbühler 2002).

While there is some evidence for flexibility in the usage of particular vocalizations for certain primate species (*e.g.*, Seyfarth *et al.* 1980; Snowdon & Hodun 1981; Mitani & Brandt 1994; Seyfarth & Cheney 1997; Ouattara *et al.* 2009), more robust evidence exists for flexibility in gestural signaling that could have given rise to language (*e.g.* Müller 2005; Pika *et al.* 2005a; Pollick & de Waal 2007; Tomasello & Call 2007; Smith 2007, 2009; Genty *et al.* 2009). Gestural communication may be more flexible than vocal communication because gestural signals are less tied to emotions (Pollick & de Waal 2007) and used commonly to communicate less “evolutionarily urgent” information than vocalizations (Pika *et al.,* 2005a, p. 43). For instance, gestures are employed most often in the context of playing, nursing, grooming, and agonism (de Waal 1988; Pika *et al.* 2003, 2005a, 2005b). These contexts are not necessarily tied to immediate survival goals, but they are undoubtedly important for navigating group life and developing and maintaining relationships with conspecifics. Vocalizations, on the other hand, are used most often during predator avoidance, group travel, foraging, and defense against aggressors. Thus, compared to vocalizations, gestures can be more easily incorporated into more social contexts, and shaped over time by repeated social interactions. Gestural signaling is also a more direct form of communication than vocal signaling in that it depends on dyadic interactions between individuals; vocalizations are typically transmitted to multiple individuals and are less reliant on the attentional states of listeners. Furthermore, apes in particular possess more precise control of their hands and fingers than their voices, which also allows for more flexible, intentional communication in the gestural modality (Preuschoft & Chivers 1993).

1.1.2 Gestural Communication Research in Apes

Scientists representing a range of disciplines from the social sciences to evolutionary biology have asserted that language is a quintessential feature of humankind (*e.g.*, Chomsky 1968; Deacon 1997; Hauser *et al.* 2002). However, despite increasing information shaping our understanding of the origins of anatomically modern humans, we are not yet clear on the suite of selection pressures favoring changes in anatomy, behavior, cognition, and genes that led to the evolution of language in *Homo sapiens*.

Although the hominin fossil record may not inform us on the presence or extent of these abilities, findings from comparative approaches involving the study of communication among non-human primates provide valuable information about which attributes of language are uniquely human and which extend farther back into our evolutionary history. Studying the communication of our closest living relatives, the African apes, increases our understanding of the contexts in which properties of language may have emerged and evolved, and offers insights into whether human language originated from vocal signals, manual gestures, or a combination of both modalities.

Previous investigations of African ape gestural communication have generally aimed to assemble clues as to how the ancestors of modern human may have communicated prior to the evolution of speech and whether certain properties of language exist in other primates. Long-term field studies of African ape behavior first uncovered the use of several communicative gestures (Schaller 1963; McGrew &

Tutin 1978; Nishida 1980; Kano 1982, 1992; Fossey 1983; Goodall 1986; Ingmanson 1996), which sparked further investigation into the importance of non-vocal signaling in these species. In the wild, chimpanzees have been observed using over a dozen distinct gestures in a variety of contexts such as play, agonism, and sex (Goodall 1986). Population-wide differences have also been identified in gestures such as *leaf-clipping displays* (Nishida 1980), and *grooming hand clasps* (McGrew & Tutin 1978) which have been instrumental in cultural interpretations of geographic variation in chimpanzee behavior (*e.g.*, de Waal 1999; Whiten *et al.* 1999; McGrew 2004). Species-specific displays, such as *chest beating*, have also been observed in wild gorillas (Schaller 1963; Fossey 1983). Early studies of captive bonobos identified many unique gestures not seen in other apes, such as frequent *genito-genital rubbing* (de Waal 1988). Since these initial observations, ethograms of gestures have been compiled for several captive and wild populations (Table 1.1) and researchers have set out to explore more explicitly the role of gestures in African ape communication.

To date, research concerning gestural communication in African apes has chiefly focused on characterizing spontaneous gestural use within species (*e.g.*, Savage-Rumbaugh *et al.* 1977; de Waal 1988; Tanner & Byrne 1996; Smith 2007, 2009; Genty *et al.* 2009; Kalan & Rainey 2009), examining the learning mechanisms involved in creating and maintaining gestures within groups (*e.g.*, Tomasello *et al.* 1997; Pika *et al.* 2003), and exploring individual capacities to learn language systems and use them to communicate with conspecifics and humans (*e.g.*, Gardner & Gardner 1969; Fouts 1973; Savage-Rumbaugh 1998). This research has revealed that African apes create new gestures regularly and many gestures are used for multiple communicative ends. Gestures are also used at different rates among different age/sex-classes. For example, subadults and juveniles tend to gesture more frequently than any other age-class (Pika *et al.* 2003, 2005a). Furthermore, African apes (particularly *Pan*) show sensitivity to audience effects when gesturing, evident in a higher prevalence of visual gestures (as opposed to tactile or auditory gestures) when recipients are oriented toward the signaler (Tanner & Byrne 1996; Hostetter *et al.* 2001; Bodamer & Gardner 2002; Pika *et al.* 2003, 2005b; Povinelli *et al.* 2003; Liebal *et al.* 2004b; Genty *et al.* 2009).

All of these studies demonstrate that gestural communication is highly variable among the African apes with regard to the types of signals and their patterns of use in each species. Yet, the extent to which factors such as ecology, locomotion, cognition, and social dynamics differentially shape gestural repertoires across the African apes has not been fully explored (Pika *et al.* 2005a). The effects of positional behavior on gestural communication, in particular, have been overlooked. To test the hypothesis that early hominins started relying on gestural communication once their upper limbs were freed from locomotion, it is important to examine how closely related non-human primates use gestures in relation to their positional behavior. In this dissertation, I set out to test the hypothesis that locomotor and postural behavior, as well as group composition and the nature of social relationships, play key roles in influencing the frequency of gestural signaling and in shaping the specific gestures used between individuals of each species.

1.1.3 Captive Studies versus Wild Studies

While it is certainly preferable to conduct behavioral research in a species' natural habitat, studying gestural communication in captivity afforded me the unique opportunity to capture very detailed accounts of subtle body movements and complex social interactions. At all study sites, I was able to observe subjects with almost continuous visibility for several hours at a time, which allowed for a high degree of accuracy not possible in a field setting. I was also able to gain a solid understanding of group dynamics because I could pinpoint changes in sexual behavior throughout the course of female reproductive cycles, witness conflicts and subsequent reconciliations, observe younger males challenging dominant males with increased frequency, and reliably record data on the same individuals every day.

Although there is potential for behavior to be altered in captivity (*e.g.*, changes in affiliative behavior or activity patterns) compared to their wild counterparts, I felt confident that the behavior of the study subjects would not be altered in a way that would adversely impact the results of this research. I took great care to select study groups with compositions similar to those observed in the wild for each species and naturalistic environments with comparable design features to reduce the likelihood of individual differences being misinterpreted as group or species differences. De Waal (1994) argues that a captive environment may not be as limiting as one might assume if we consider the “adaptive potential” of a species. De Waal (1994, p. 246) defines a species’ adaptive potential as “the entire range of conditions to which a species can adjust without compromising its health, biological functions (such as reproduction), or major parts of its natural behavioral repertoire (such as species-typical communication).” Although these captive animals were not able to transfer between groups of their own accord, the group compositions and the naturalistic environments in which the study animals lived were well within their adaptive potential, particularly given the behavioral flexibility demonstrated by long-term field studies of *Pan* (discussed in 1.2.3 and 1.2.4).

1.2 The African Apes: Social Dynamics

1.2.1 Defining and Understanding Social Dynamics

In the wild and in captivity, African apes are remarkably varied with regard to agonism, sexual behavior, dominance relationships, group size, and intra-sexual interactions (reviewed in King 2004). I use "social dynamics" as a broad term to describe the types of social relationships that exist within a species. Social dynamics can be determined by the time individuals spend in proximity, how often individuals groom, the frequency of agonistic encounters, and the stability of dominance hierarchies. Examining communicative interactions within and between age/sex-class dyads can shed light on the social dynamics of these three species and provide clues about the ways in which individuals interact and communicate information.

1.2.2 Social Dynamics of Gorillas

The majority of data available on gorilla social dynamics comes from wild studies of mountain gorillas (*Gorilla beringei beringei*) in the Virunga Mountains in East Africa (Watts 1996). Data are becoming increasingly available for eastern lowland gorillas (*Gorilla beringei graueri*) in the Kahuzi-Biéga National Park in the Democratic Republic of Congo, and western lowland gorillas (*Gorilla gorilla gorilla*) in Mbeli Bai (Parnell 2002; Breuer 2008), the Lokoué clearing in the Republic of Congo (Gatti *et al.* 2004), and the Lopé Reserve in Gabon (Tutin 1996). Data remain scant on the highly endangered cross river gorilla (*Gorilla gorilla diehli*) on the Nigeria-Cameroon border.

Data from these field sites have revealed patterns of grouping and social relationships shared by all gorilla subspecies. Gorillas typically live in groups led by a dominant silverback male with several adult females and their offspring. Females typically transfer from their natal groups, and may also transfer a second time (Watts 1990). Males may also emigrate from their natal groups as they reach sexual maturity and either join other mixed-sex breeding groups, become solitary, or form all-male bachelor groups (Robbins 1995; Gatti *et al.* 2004). In an examination of data from fourteen sites, Parnell (2002) found the typical median group size among lowland gorillas ranged from six to fourteen individuals. The most influential factor in grouping patterns seems to be male protection from inter-group aggression (Stokes *et al.* 2003).

Affiliative behavior (both within and between sexes) is not a common occurrence in adult gorillas. Stokes (2004) observed no grooming and very little affiliative behavior between adults of both sexes in over 800 hours of observation with western lowland gorillas at Mbeli Bai. When adult females do exhibit affiliative behavior, it is typically directed towards their offspring or the silverback, but rarely towards other adult females (Stokes 2004). Agonistic encounters occur with more regularity, generally between silverbacks and adult females (Stokes 2004). When conflicts occur between adult females, silverbacks often intervene via aggressive physical contact or visual displays, but serious wounding and intense aggression from males to females are rare (Watts 1992).

1.2.3 Social Dynamics of Chimpanzees

Decades of research in the field and in captivity have yielded considerable data on chimpanzee social behavior. Field data have primarily been gathered from long-term studies at the Gombe Stream National Park and the Mahale Mountains National Park in Tanzania, the Taï Forest in the Ivory Coast, the Kibale National Park and Budongo Forsest in Uganda, and Bossou, Guinea (reviewed in Mitani *et al.*

2002). This research has established that chimpanzees live in fission-fusion social systems in which a community of multiple males, females, and their dependent offspring share resources but break off into smaller parties for daily travel and foraging (Goodall 1986; Chapman & Wrangham 1993). Chapman *et al.* (1994) gathered data from various field sites and reported that average party size ranged from 2.6 to 10.1 individuals, but these parties vary dramatically in size and composition across sites and across seasons within sites.

Females typically transfer at sexual maturity, while males stay in their natal groups. Chimpanzee males are dominant to females, and male social behavior is often a function of competition between males for access to females and food resources, and for territorial defense against other groups (Baker & Smuts 1994). In captive and wild settings, males form coalitions with each other during agonistic encounters (Baker & Smuts 1994). These coalitions are often temporary alliances formed as competitive strategies enabling two individuals to out-compete a third individual. Males in the wild also travel in all-male parties that patrol the territorial borders and may cooperate to kill intruders or solitary neighboring males (Wilson & Wrangham 2003). Because males tend to associate more with other males via agonistic encounters and coalitions, interactions between males and females are rare and often take the form of dominance displays or sexual behavior.

In the wild, female chimpanzees often forage in small parties with their close kin or travel alone, so females do not spend as much time with each other as do males (Wrangham & Smuts 1980). Even in captivity, where females cannot emigrate, females tend to socialize very little with each other (but see Baker & Smuts 1994 for evidence of increased adult female affiliation in captivity), and overt dominance interactions between females tend to be rare (de Waal 1982). In captive environments, females have been known to engage in dominance displays and agonistic encounters with each other when groups are newly formed and dominance relationships are first being established (Baker & Smuts 1994). In the wild, dominant, resident females form coalitions against subordinate, immigrant females (at Gombe: Pusey 1980, Goodall 1986; at Mahale: Nishida 1989).

1.2.4 Social Dynamics of Bonobos

Information regarding bonobo social dynamics mainly comes from two field sites in the Democratic Republic of Congo: Lomako (Badrian & Badrian 1984; Thompson-Handler *et al.* 1984; White 1988) and Wamba (Kano 1992). At Lomako, bonobos exhibit a fission-fusion social system similar to chimpanzees, in which larger communities splinter into smaller daily travel parties. These parties can vary in size and composition, but they tend to be larger than chimpanzee parties and are often composed of more females than males (Chapman *et al.* 1994; Hohmann & Fruth 2002). At Wamba, however, communities remain together most of the time, rather than splitting up into smaller parties (Kano 1992). The mean size of bonobo parties reported from three field sites ranged from 5.4 to 16.9 individuals, with Wamba at the highest end of this range (Chapman *et al.* 1994).

In addition to flexibility in group size and composition, bonobos also exhibit diversity in their social relationships. As with chimpanzees, females transfer from their natal groups and may even undergo a secondary transfer (Furuichi 1989). Despite being unrelated, females interact with each other regularly, most often via sexual behavior (Hohmann *et al.* 1999; Hohmann & Fruth 2000). Interestingly, at both Lomako and Wamba, males have also been observed to disappear from their communities with frequencies similar to females, suggesting male transfer might also occur in bonobos (Hohmann & Fruth 2002). A dramatic difference between chimpanzee and bonobo social behavior is that females are often dominant to males in bonobo society, though dominance hierarchies are not always straightforward (Paoli *et al.* 2006; White & Wood 2007). Females even form coalitions with each other in agonistic encounters against males or when defending food sources against males (Kano 1992; Parish 1994). Contrary to the aggressive, sometimes fatal interactions between male chimpanzees, relationships between male bonobos are characterized by more affiliative behaviors (*e.g.*, grooming and spending time in proximity) and less intense aggressive encounters (Hohmann & Fruth 2002). These studies from wild and captive populations of bonobos paint a picture of behavioral plasticity among bonobos and suggest that bonobos are more flexible than chimpanzees and gorillas in terms of party size and composition and the nature of their dyadic interactions.

1.3 The African Apes: Locomotor Profiles

1.3.1 Diversity in Positional Behavior

Though all African apes are predominantly knuckle-walkers and have anatomical adaptations for suspensory locomotion, few cross-species comparisons have been done and thus no definitive answers have been reached as to exactly how African apes differ in their locomotor profiles. In particular, quantitative data are lacking with respect to terrestrial positional behavior and the degree of arboreality because researchers have been unable to consistently follow wild bonobos (Doran & Hunt 1994; Doran 1996) or gorillas (Remis 1995, 1998, 1999; Doran 1996) through dense vegetation. Doran and Hunt (1994) pooled data from various field sites for chimpanzees and mountain gorillas and reported that more than 85% of their locomotor activities were quadrupedal and 90% of their postural activities were attributed to sitting and lying. More detailed accounts of time spent in various postures or locomotion or specific positional behaviors used when terrestrial versus arboreal, however, have not been obtained due to the dearth of reliable field data for bonobos and western lowland gorillas. As a result, the relationship between positional behavior and gestural communication in the African apes has been difficult to establish. The connection between locomotion and gestural signaling must be considered when examining the evolution of non-vocal communication and exploring the variability in gestural repertoires among the African apes.

1.3.2 Locomotor Profiles of Gorillas

Unfortunately, only a handful of studies exist on the positional behavior of wild western lowland gorillas, particularly regarding terrestrial positional behavior and degrees of arboreality (Remis 1995, 1998, 1999; Doran 1996). What is clear is that gorillas spend more time on the ground and less time arboreal than the other African apes, mainly because of their large body sizes (Doran 1996; Remis 1998). This is especially so for male silverback gorillas who can weigh over twice as much as adult females (males: 170.4 kg; females: 71.5 kg, Smith & Jungers 1997).

Although extensive quantitative data are lacking, Remis (1995, 1999) has found sex differences in the ways in which adult western lowland gorillas at Bai Hokou, Central African Republic, use arboreal substrates. Overall, silverback males were less frequently arboreal than females, but increased their arboreality during the fruiting season (Remis 1995, 1999). When gorillas were arboreal, females used the peripheries of the trees more frequently when feeding in the presence of males, while males restricted their use to larger branches closest to the tree trunk (Remis 1995).

In the fruiting season of 1995 at Bai Hokou, Remis (1999) found that adult females were arboreal during 95% of the 1-minute intervals during focal samples while males were arboreal during only 58% of the samples. Doran (1996) also reported that female gorillas were observed in 43% of total arboreal sightings and males were only observed in 19% of arboreal sightings in Ndoki, Congo. These sex differences are due in part to body size differences, but group size, foraging opportunities, and dominance relationships may also influence the positional behavior of gorillas (Remis 1999).

1.3.3 Locomotor Profiles of Chimpanzees

Though not as dramatic as in gorillas, there is also sexual dimorphism in body size among chimpanzees which may influence their positional behavior. Male chimpanzees weigh on average 40-60 kg, while the mean weight for females is 32-47 kg (Morbeck & Zihlman 1989; Watts & Pusey 2002). Chimpanzees have been described as more arboreal than gorillas (Doran 1996) though quantitative measures for the duration of time spent arboreal are lacking. Furthermore, Doran (1996) examined field data from Mahale, Gombe, and the Taï forest, and found that female chimpanzees were more arboreal than males at all three sites.

Frequent arboreal bipedality has also been noted in certain populations of chimpanzees. Stanford (2008) reported 0.79 bouts of bipedality per hour in a population of chimpanzees at the Bwindi Impenetrable Forest in Uganda, a much higher rate than had been reported by Hunt (1994) for chimpanzees in Mahale (0.17 bouts/hour). These bipedal bouts were mainly postural (rather than locomotor) and used by chimpanzees when feeding on fruits in large trees (Stanford 2008). Many early accounts however, have described adult chimpanzees in the wild as less acrobatic than adult bonobos when arboreal, evident in lower levels of brachiation, arboreal leaping and diving, and bipedal locomotion (Kortland 1972; Susman *et al.* 1980).

1.3.4 Locomotor Profiles of Bonobos

While bonobos and chimpanzees are more similar in their body size than either is to gorillas, there is still significant morphological variation within the genus *Pan* (Morbeck & Zihlman 1989). In terms of body size, male bonobos weigh on average 39 kg, while the average female weight is 30 kg (Morbeck & Zihlman 1989). Bonobos also generally have longer lower limbs and lower intermembral indices than chimpanzees (Coolidge & Shea 1982; Morbeck & Zihlman 1989; Doran 1993). In Morbeck and Zihlman's (1989) comparative study of *Pan* body sizes, the mean hindlimb length of *Pan paniscus* was 540.0 mm, compared to 484.9 mm for *Pan troglodytes* at Gombe and 534.0 mm for other *Pan troglodytes* in their sample. The ways in which these morphological differences influence positional behavior have not yet been fully clarified.

Susman *et al.* (1980) reported qualitative data for the positional behavior of adult bonobos in Lomako and described them as chiefly quadrupedal but, when bonobos were arboreal, they incorporated arm-swinging, diving, leaping, and bipedal locomotion. Susman *et al.* (1980) concluded that adult bonobos have a more diverse array of arboreal locomotor behaviors than do adult chimpanzees in the wild. Doran (1993) and Doran and Hunt (1994) reported that bonobos in the wild spent more time in arboreal locomotion than chimpanzees and, when arboreal, male bonobos spent 10% of their time suspensory compared to an average of 6.5% of the time for male chimpanzees. Doran (1993) links the increased suspensory locomotion in male bonobos to their longer and narrower scapula. Videan and McGrew (2001) found that in captivity, bonobos rely on bipedality more during vigilance and when carrying objects, while chimpanzees are bipedal more during displays, but there does not appear to be species differences in the rates of bipedal locomotion or postures between the two species.

1.4 Research Questions

In this dissertation, I aimed to examine to what extent social dynamics and positional behavior influence variability in the gestural repertoires of African apes. My specific objectives included: 1) Recording gestures and the social contexts in which they are used in groups of African apes, 2) Determining whether differences in social dynamics across groups influence gestural signaling 3) Recording frequencies and durations of positional behaviors to establish locomotor profiles of African apes in captivity, and 4) Examining the effects of positional behavior on the use of upper limbs for gesturing.

1.4.1 Hypotheses and Predictions

I addressed two main questions in this research: The first question was: **1. Do the frequencies of gestural signaling and the types of gestures used differ as a function of social dynamics (*e.g.*, levels of affiliation, agonism, and sexual behavior) across species?** Within three species of *Macaca*, the types of gestures used and the frequency of gestural signaling have been shown to vary depending on the level of agonism (Maestripieri 2005). Stumptail macaques (*Macaca arctoides*), who have higher intragroup aggression and stronger group cohesion, also have a richer gestural repertoire than rhesus (*M. mulatta*) or pigtail

(*M. nemestrina*) macaques (Maestripieri 2005). I proposed that similar variation would be found in the African apes because of their diverse social dynamics.

Hypothesis: Across species, gestural signaling will differ among dyads as a function of the frequency of interactions between individuals and the nature of those interactions. The associated predictions for this hypothesis are described below and summarized in Table1.2.

Predictions for Male-Male Dyads: In gorillas, interactions between the silverback male and younger males are rare and gesturing within these dyads was expected to occur most often in the contexts of agonism or play. Within chimpanzees, strong male bonding should lead to a comparatively high frequency of male-male gestural signaling, particularly in agonistic and affiliative contexts. Bonobo males rarely interact, thus a low frequency of gesturing was expected within male-male dyads. Gestures were predicted to be used most often between bonobo males in agonistic encounters.

Predictions for Male-Female Dyads: In gorillas, affiliative male-female interactions are rare and gestures are predicted to occur mainly in the context of agonism. Within chimpanzees, male-female interactions are infrequent and gesturing was predicted to occur most frequently in sexual and agonistic contexts. In bonobos, male-female bonds have been observed to be almost as frequent as female-female bonds (Parish 1994, in captivity; Kuroda 1979, Kano 1982, at Wamba); thus, compared to chimpanzees and gorillas, a higher frequency of gesturing in bonobo male-female dyads was expected.

Predictions for Female-Female Dyads: Because female-female interactions are not common in chimpanzees and even rarer in gorillas, I predicted that the numbers of gestures used between females of these species will be fewer, relative to bonobos, and used mainly to avoid agonistic encounters or reduce social tension. Female-female affiliations are prevalent in bonobos (Hohmann *et al.* 1999; Hohmann & Fruth 2000) and, thus, I predicted a high frequency of gesturing among bonobo females, particularly in affiliative and sexual contexts.

Predictions for Sexual Context: Researchers (Kano 1992; Hohmann & Fruth 2000) have observed more frequent sexual behavior in bonobos than in chimpanzees or gorillas (but see Stanford 1998 for an alternate view), thus bonobos of all age/sex-classes were expected to use more gestures in the context of sex than chimpanzees or gorillas, and these gestures should have appeared at a relatively high frequency in the overall bonobo gestural repertoire.

Predictions for Rates of Gesturing: In all species, juveniles and infants were predicted to gesture more frequently and to use a greater number of gestures because younger individuals interact frequently with each other, especially in the context of play. A high frequency of gesturing between mothers and their offspring was also expected for all species.

The second main research question was: **2. How does positional behavior (*e.g.*, time spent in various postures and modes of locomotion) vary across species and are the ways species communicate gesturally reflected in these differences?** Few studies have been conducted on the different locomotor profiles of the African apes, and none has systematically compared positional behavior across all African apes. Studies in the wild have qualitatively described bonobos as more arboreal than chimpanzees (Susman *et al.* 1980; Doran 1993; Doran & Hunt 1994; Doran 1996), but no quantitative data exist to make solid comparisons of their overall patterns of positional behavior. This research was the first to take into account the effects of positional behavior on the availability of the upper limbs for gesturing.

Hypothesis: Locomotor profiles of African apes (which depend on environmental conditions, body size and skeletal anatomy) will dictate the availability of the upper limbs for gesturing and the frequency with which gestural communication is employed. The associated predictions for this hypothesis are described below and summarized in Table 1.2.

Predictions for Upper Limb Availability: Because of their large body size (especially males), gorillas were expected to spend more time on the ground in seated postures and less time walking bipedally than either species of *Pan*, thus freeing their upper limbs to gesture; hence, gorillas gestures should have a relatively high frequency of upper limb use. Bonobos generally have longer lower limbs than chimpanzees or gorillas (Coolidge & Shea 1982; Morbeck & Zihlman 1989; Doran 1993), which may enable them to walk bipedally more efficiently. As a result of this "liberation" (Copple 2003, p. 54) of bonobo hands, the frequency with which their upper limbs were available for gesturing was predicted to be higher than chimpanzees, whose upper limbs were expected to be occupied more often in knuckle-walking.

Predictions for Rates of Gesturing: As a result of the increased terrestriality and seated postures of gorillas (which frees their upper limbs for gesturing) and the increased bipedal locomotion of bonobos (whose upper limbs are also free to gesture), gorillas and bonobos were predicted to have greater freedom to gesture with their upper limbs, and thus they were both expected to gesture at a higher rate than chimpanzees.

1.5 Outline of Dissertation

In this dissertation, I examined how social relationships and positional behavior impacted gestural communication in three closely-related species. The information gleaned from this dissertation can be used to address the physical and social contexts under which human gesturing may have evolved, and how language may have originated. This research is also important for understanding the role of gestures in non-human primate communication compared to human communication.

In Chapter 2, I provide information on the study groups and their enclosures, as well as a description of my behavioral sampling methods. In Chapter 3, I present results for the effects of social dynamics on gestural signaling across study groups and species and discuss whether my first hypothesis was supported. In Chapter 4, I describe the locomotor profiles of the study groups and present results regarding the effects of positional behavior on gestural signaling. I then summarize my findings in relation to my second hypothesis. Finally, in Chapter 5, I review my major results and the conclusions I reached. I close by discussing the implications of this research for understanding the role of gestural signaling in shaping language evolution and the potential avenues for future research into gestures and communication.

TABLE 1.1 Examples of gestures observed among African apes from published ethograms. All existing ethograms were examined and gestures that appeared to be the same based on names and descriptions are compiled here.

Gesture	Signal Category	Species Observed
Arm On	Tactile	*Pan troglodytes*[h]
Arm Raise/Arm Up	Visual	*Pan troglodytes*[h]; *Pan paniscus*[f]
Beg	Visual	*Pan paniscus*[f]
Bipedal Swagger	Visual	*Pan troglodytes*[h]; *Pan paniscus*[f]
Bite	Tactile	*Gorilla gorilla*[j]
Body Beat	Auditory	*Gorilla gorilla*[g,j]
Body/Belly Slap	Auditory	*Gorilla gorilla*[g];*Pan troglodytes*[h]
Bow	Visual	*Gorilla gorilla*[g,j]
Charge	Visual	*Pan paniscus*[f]
Chest Beat	Auditory	*Gorilla gorilla*[a, d, g]; *Pan paniscus*[f]
Chuck Up	Visual	*Gorilla gorilla*[g]
Clap	Auditory	*Gorilla gorilla*[g,j]; *Pan troglodytes*[e,h]; *Pan paniscus*[f]
Concave Back	Visual	*Pan paniscus*[f]
Drum	Tactile	*Gorilla gorilla*[j]
Duck Face	Visual	*Pan paniscus*[f]
Embrace	Tactile	*Gorilla gorilla*[g]; *Pan troglodytes*[h]; *Pan paniscus*[f]
Finger Flex	Visual	*Pan paniscus*[f]
Foot Clap	Auditory	*Pan paniscus*[e,f]
Formal Bite	Visual/Tactile	*Gorilla gorilla*[g]; *Pan troglodytes*[i]
Funny Faces	Visual	*Pan paniscus*[f]
Gallop	Visual	*Gorilla gorilla*[g,j]; *Pan paniscus*[g]
Genital Offer	Visual	*Pan troglodytes*[i]
Genital Massage	Tactile	*Pan paniscus*[f]
Genito-Genital (GG) Rub	Tactile	*Pan paniscus*[f]
Gentle Touch	Tactile	*Pan troglodytes*[h]
Grab	Tactile	*Gorilla gorilla*[g,j]; *Pan paniscus*[i]
Grab-Pull-Push	Tactile	*Gorilla gorilla*[g,j]; *Pan paniscus*[i]
Groom	Tactile	*Pan paniscus*[f]
Grooming Hand Clasp	Tactile	*Pan troglodytes*[b]
Hand On	Tactile	*Gorilla gorilla*[g,j]
Head Bob	Visual	*Pan troglodytes*[h]; *Pan paniscus*[i]
Hunch-Over	Tactile	*Pan paniscus*[f]
Ice Skate	Visual	*Gorilla gorilla*[g,j]; *Pan paniscus*[i]
Jump	Visual	*Gorilla gorilla*[g,j]; *Pan troglodytes*[h]; *Pan paniscus*[i]
Kick	Tactile	*Pan paniscus*[i]
Lead	Tactile	*Pan troglodytes*[h]
Leaf-Clipping Display	None Given	*Pan troglodytes*[c]
Lip Lock	Tactile	*Pan troglodytes*[h]
Look At	Visual	*Pan paniscus*[i]
Long Touch	Tactile	*Gorilla gorilla*[g]
Mount	Tactile	*Pan paniscus*[f]
Mount Walk	Tactile	*Pan paniscus*[f]
Mouth Kiss	Tactile	*Pan paniscus*[f]

[a] Schaller (1963); [b] McGrew & Tutin (1978); [c] Nishida (1980); [d] Fossey (1983); [e] Ingmanson (1987); [f] de Waal (1988); [g] Pika *et al.* (2003); [h] Liebal *et al.* (2004[a]); [i] Pika *et al.* (2005b); [j] Genty *et al.* (2009)

TABLE 1.1 Examples of gestures observed among African apes from published ethograms (continued).

Gesture	Signal Category	Species Observed
Move	Visual	*Gorilla gorilla*[g]; *Pan paniscus*[i]
Offer	Visual	*Pan troglodytes*[h]
Oral Sex	Tactile	*Pan paniscus*[f]
Pat	Tactile	*Gorilla gorilla*[j];*Pan paniscus*[f]
Peer	Visual	*Gorilla gorilla*[g]; *Pan paniscus*[i]
Play Face	Visual	*Pan paniscus*[f]
Present	Visual	*Pan paniscus*[f,i]
Prod/Poke At	Tactile	*Gorilla gorilla*[g]; *Pan troglodytes*[h]
Pull	Tactile	*Gorilla gorilla*[g]; *Pan troglodytes*[h]; *Pan paniscus*[i]
Punch	Tactile	*Gorilla gorilla*[g,j]; *Pan paniscus*[e,h]
Push (Object/Body)	Tactile	*Gorilla gorilla*[g,j]; *Pan troglodytes*[h]; *Pan paniscus*[i]
Reach Arm	Visual	*Gorilla gorilla*[g,j]; *Pan troglodytes*[h]; *Pan paniscus*[f,i]
Shake (Arm/Object/Head)	Visual	*Gorilla gorilla*[g,j]; *Pan troglodytes*[h]; *Pan paniscus*[f,i]
Silent Pout	Visual	*Pan paniscus*[f]
Silent Teeth Bare	Visual	*Pan paniscus*[f]
Slap	Tactile	*Gorilla gorilla*[g,j]; *Pan paniscus*[f,i]
Slap Ground	Auditory	*Gorilla gorilla*[g,j]; *Pan troglodytes*[h]; *Pan paniscus*[f]
Somersault	Visual	*Gorilla gorilla*[g]; *Pan paniscus*[i]
Stiff Stance	Visual	*Gorilla gorilla*[g,j]
Stamp Trot	Auditory	*Pan paniscus*[f]
Stomp	Auditory	*Gorilla gorilla*[g]; *Pan troglodytes*[h]; *Pan paniscus*[f,i]
Straw Wave	Visual	*Gorilla gorilla*[g]
Tense Mouth	Visual	*Pan paniscus*[f]
Touch	Tactile	*Gorilla gorilla*[g,j];*Pan paniscus*[i]
Throw	Visual/Tactile	*Gorilla gorilla*[g]; *Pan troglodytes*[h]
Wrist-Shake	Visual	*Pan paniscus*[f]

[a] Schaller (1963); [b] McGrew & Tutin (1978); [c] Nishida (1980); [d] Fossey (1983); [e] Ingmanson (1987); [f] de Waal (1988); [g] Pika *et al.* (2003); [h] Liebal *et al.* (2004[a]); [i] Pika *et al.* (2005b); [j] Genty *et al.* (2009)

Table 1.2 Predictions for the frequency of gestural signaling based on the two main hypotheses explored in this study. Young=individuals ≤8 years old; Adult=individuals ≥9 years old.

	Gorillas	**Chimpanzees**	**Bonobos**
Among Sex Dyads	**Male-Male**: Low **Male-Female:** Low **Female-Female**: Low	**Male-Male**: High **Male-Female:** Medium **Female-Female**: Medium	**Male-Male**: Low **Male-Female:** High **Female-Female**: High
In Social Contexts	**Highest:** Agonistic **Lowest:** Affiliative	**Highest:** Affiliative/Agonistic **Lowest:** Sexual	**Highest:** Sexual **Lowest:** Agonistic
Among Age-Class Dyads	**Adult-Adult:** Low **Adult-Young:** Medium **Young-Young:** High	**Adult-Adult:** Medium **Adult-Young:** Medium **Young-Young:** High	**Adult-Adult:** Medium **Adult-Young:** Medium **Young-Young:** High
Upper Limb Availability	High (based on high frequency of sitting)	Low (based on high frequency of locomotion involving upper limbs)	High (based on high frequency of bipedality)

CHAPTER 2

STUDY DESIGN AND METHODS

2.1 Study Sites and Subjects

I conducted research with three species of African apes: Western lowland gorillas (*Gorilla gorilla gorilla*), chimpanzees (*Pan troglodytes* sspp.), and bonobos (*Pan paniscus*). Data were collected at five different captive sites over the course of twenty-four months: Intermittently from June 2005 until November 2006, and continuously from May 2007 until October 2008. My study subjects included: 1) Two groups of western lowland gorillas at the Bronx Zoo, NY (BZ): 11 individuals in Group A (BZA) and 13 individuals in Group B (BZB); 2) Two groups of chimpanzees: 11 individuals at the St. Louis Zoo, MO (SLZ) and 13 individuals at the Los Angeles Zoo, CA (LAZ); and 3) Two groups of bonobos: 8 individuals at the San Diego Zoo, CA (SDZ) and 8 individuals at the San Diego Wild Animal Park, CA (WAP). Table 2.1 shows the group compositions for each study site. I collected data on all individuals and every individual was recognizable by physical features.

In addition to selecting study groups with appropriate compositions, the enclosures themselves were an important factor in deciding upon particular study sites. Videan and McGrew (2001) found that, in captive groups of chimpanzees and bonobos, the percentages of positional behavior dedicated to locomotion and posture approximated that of their wild counterparts, suggesting that a captive environment well-equipped with climbing structures and open space is suitable for confidently examining locomotor profiles of African apes. I visited all study sites in advance (except the Los Angeles Zoo because of logistical reasons) to establish that each enclosure contained multiple arboreal substrates. These substrates varied in exact number and type, but all enclosures contained comparable combinations of trees, vines, ropes, hammocks, sway poles, or artificial beams which would allow for the expression of arboreal positional behaviors such as brachiating, climbing, and hanging. All enclosures were also equipped with ample open space and similar enrichment opportunities (in the form of browse, food items, termite mounds, and novel objects like balls and cardboard boxes), minimizing the possibility that any differences in locomotor profiles resulted from the enclosure layout or design features.

In this chapter, I describe the study subjects and sites as well as my general behavioral sampling methods and the protocol I followed when coding video data. Methods specific to analyses of the influence of social relationships and social contexts on gesture use, and the relationship between positional behavior and gesturing, are described in fuller detail in Chapters 3 and 4, respectively.

2.1.1 Gorillas at the Bronx Zoo (Group A)

The gorillas at the BZ were housed in two adjacent, outdoor enclosures totaling 4,645 m^2 within the Congo Gorilla Forest exhibit. BZA was a typical gorilla social group composed of one silverback male, four adult females, and their six juvenile and infant offspring. During the course of my data collection, one adult female died (Imani in August 2008), and three juvenile males were transferred to other facilities (Pierrepont in October 2006, Shana and Zola in September 2008). BZA's 2,601 m^2 enclosure (Figure 2.1) contained multiple natural and artificial trees, a large rock cluster, a waterfall, logs, a small wading pond, and a complex climbing structure with two large artificial trees and a network of artificial vines.

2.1.2 Gorillas at the Bronx Zoo (Group B)

The BZB group was composed of eleven females of various ages and two infant males. A silverback was introduced to the group in November 2004, but was never in the outdoor enclosure with the group during data collection, so I was unable to record any data with this silverback. From July to October 2008, several of the females were on alternating schedules in the enclosure, so not all individuals in the group were together on the same days. One juvenile female (Kioja) remained in the indoor holding area during this time and was eventually transferred to another facility. BZB's 2,044 m^2 enclosure (Figure 2.2) contained a sloping hill with natural trees and shrubs, a small artificial rock mound with a viewing window inside for public interaction, an extensive artificial tree structure, and scattered rocks and logs.

2.1.3 Chimpanzees at the St. Louis Zoo

The SLZ group was composed of three adult males, six adult females, and two juvenile females. The adult male named Hugo was the alpha male for the entire period of data collection. The SLZ enclosure (Figure 2.3) was 5,300 m^2, with a row of trees that stretched the length of the enclosure. Attached to these trees were fire hose "vines" and three small "hammocks" made out of interwoven rope and fire hose. There was a waterfall at one end of exhibit, patches of shrubs and thicker vegetation in the front of the exhibit and a rock wall that jutted up from a lower level with a small wading pond and vegetation.

2.1.4 Chimpanzees at the Los Angeles Zoo

The LAZ group consisted of two family groups totaling four adult males, six adult females, one juvenile male, and two juvenile females. The adult male named

Glenn was the alpha male for the entire period of data collection. The LAZ had two enclosures: One was a 3,530 m^2 naturalistic environment with palm trees, grassy vegetation, rocky cliffs, a rope swing, log piles, and a large waterfall (Figure 2.4). The second enclosure was a 151 m^2 "penthouse" that reached 5-7 meters high with barrels and balls, metal beams, several draped fire hoses, tire swings, and a ladder made of wood and rope. All observations occurred in the larger, naturalistic environment, which was where the group spent almost 100% of its time.

2.1.5 Bonobos at the San Diego Zoo

The SDZ group totaled eight individuals: Three adult females, two adult males, one juvenile female, one infant female, and one orphaned infant male. The adult female named Lana was the alpha female for the entire period of data collection. The SDZ staff attempted to simulate a fission-fusion social system by varying the group composition each day and alternating the time of day during which groups were in the outdoor enclosure (*e.g.*, on Monday, individuals A, B, and C were out in the morning, then individuals B, D, and E were out in the afternoon. On Tuesday, individuals C, D, and E, were out in the morning and individuals A, B and D were out in the afternoon). For the first half of data collection, the two adult males were never in the enclosure at the same time, but the two were released together starting on April 25, 2008. The SDZ's 557 m^2 enclosure (Figure 2.5) contained one large climbing structure with a rope "hammock," several trees and logs, a cluster of artificial bamboo sway poles connected by suspended fire hoses, a waterfall, palm trees, large rocks, and a raised plateau in the center that overlooked the rest of the exhibit.

2.1.6 Bonobos at the San Diego Wild Animal Park

The WAP group consisted of eight individuals: Three adult males, three adult females, one juvenile female, and one infant female. The adult female named Loretta was the alpha female for the entire period of data collection. During data collection, the enclosure was not on view to the public. On any given day, the group was exposed only to the keeper on duty, up to four researchers, and a few safari cars filled with visitors that would drive by and stop approximately 100 meters away to view the animals for a few moments from behind a fence. The WAP's 4,800 m^2 enclosure (Figure 2.6) was a grassy island surrounded by a dry moat roughly 4 meters deep. It contained a small wading pool, small hills with tall grass, many large rocks, palm trees, artificial bamboo sway poles, a termite mound, and a climbing structure made up of a tire swing suspended in the middle of two large poles.

2.2 Data Collection and Coding Protocol

I collected data for approximately three months at each study site, with the exception of the BZ gorilla groups. I collected data on the BZ gorilla groups in several periods from 2005 to 2008. I first collected pilot data from June to August 2005; then, I collected data from September – November 2006, in May 2007, and from July – October 2008. An assistant collected data on both BZ groups for me from June to July 2007. We both alternated between groups during each day of data collection. I collected chimpanzee data from June – August 2007 (SLZ) and September – November 2007 (LAZ). I collected bonobo data from December 2007 – May 2008 (WAP) and March – June 2008 (SDZ), alternating days between sites from March to May.

The same data collection procedures were applied to all study sites. Observations were made approximately 6 days a week for roughly 5 hours a day at each study site after an initial period (2-3 days) of learning individual identities. I collected data during regular operating hours (approximately 9:30 am to 4:30 pm) in the public viewing areas at BZ, SLZ, LAZ, and SDZ. At SDZ, I was also able to collect data from two private viewing areas during feeding periods and when individuals were not visible from the public vantage points. At WAP, the enclosure was not on view to the public, so I observed the group outdoors from a grassy area surrounding the majority of the enclosure. At all sites, I collected two types of data via video recording using a Sony DCR-DVD403 Handycam and mini-DVDs: 1) *Ad libitum* gestural data when animals were within 5 m (described in detail in 2.2.2), and 2) Continuous 15-min focal animal sampling to establish locomotor profiles (described in detail in 2.2.4).

2.2.1 Defining Gestures

I followed Pika *et al.*'s (2005b) definition of a gesture as "an expressive movement of limbs or head and body postures that appears to transfer a communicative message, e.g., a request and/or a desired action/event (p. 41)." I used this definition because I was interested in gestures that could be influenced by positional behavior. Therefore, I did not consider facial expressions gestures. The challenge in identifying gestures lies in distinguishing intentional, communicative gestures from non-communicative body movements. A body movement can be recognized as a communicative gesture when the behavior or attentional state of a receiver is altered, or a particular response can be predicted reliably after the use of a certain gesture (Bodamer & Gardner 2002). For example, a play session may occur more frequently after a certain gesture is produced. Because knowledge of an animal's intention is unknown, certain criteria were used to determine whether communicative messages were being transferred:

1) *Flexibility*: If gestures are intentional, the behavior of the actor should involve some sort of goal and a degree of flexibility in the means of attaining that goal (Tomasello & Call 1997). Because gestures may be used to achieve varying goals in ever-changing social interactions, this implies that individuals will use alternative means toward the same goal or the same means toward alternative goals, and some new needs may be accommodated flexibly (Tomasello & Call 1997). For instance, extending an arm to another individual may be used to initiate grooming, as reconciliation after a conflict, or in the context of group travel when one individual directs another to follow.

2) *Audience Effects*: Sensitivity to audience effects is apparent when an actor signals differently depending on the attentional state of the recipient, shows signs of expecting a particular response from a recipient, or tries an alternative approach if the desired response is not achieved initially (Tomasello & Call 1997; Liebal *et al.* 2004b). For example, an actor may use a gesture that makes a sound, such as a *clap*, to get the attention of another individual who is not already attentive to him. If the individual is still inattentive, the actor may then use a different gesture such as a *chest beat*. Alternatively, an actor may use visual signals more frequently when the recipient is oriented towards him. Sensitivity to audience effects implies that the actor deliberately accommodates gestural signaling to the attentional state of a recipient (Tanner & Byrne 1996; Tomasello & Call 1997; Hostetter *et al.* 2001; Povinelli *et al.* 2003; Liebal *et al.* 2004b).

3) *Recipient's Response*: As Marler (1967) points out, "clues to the occurrence of communication between two animals must be found in changes in the behavior of one upon its perception of a signal from the other (p. 769)." Further evidence that gestures are intentionally communicative can be obtained by examining the subsequent responses to gestures by other individuals. For example, a recipient may approach the actor when a certain gesture is used or a play session may occur more frequently after the use of a particular gesture. Thus, the reaction of the recipient(s) can be used as an indicator of the success of a gesture as a communicative tool. However, the lack of a response can also be just as important in communication (King 2004). For example, a play request can be rebuffed, or a subordinate individual may ostensibly ignore the aggressive display of a dominant individual. Examining the recipient's response is useful for understanding the function of certain gestures, but a response is not required in order for a gesture to be identified.

Only gestures that were observed at least two times in at least two individuals were included in analyses to reduce the likelihood of coding non-communicative actions or body movements as gestures. Gestures were considered idiosyncratic if they were observed at least three times in only one individual, but these gestures were not included in analyses. Only the initial gesture was recorded, and not gestures that were produced after a social interaction was initiated. For example, if an individual used the gesture *chest beat*, the recipient responded with the gesture *grab*, and play ensued, I recorded *chest beat* as the initial gesture, *grab* as the response, and *play* as the social context that followed. Once the interaction between the actor and the recipient was underway, I did not record subsequent gestures (such as *push, pull, clap*) that were part of the play interaction since the actions were no longer communicative but were part of the interaction. A minimum of a 2-second pause must have occurred before a new gesture was recorded. For example, if the actor used a gesture to restart play after at least a two-second pause, then I regarded that as a new gesture and the interaction as distinct from the previous one.

I classified gestures into three categories: *Tactile:* Directed movements of part of an actor's body that come into physical contact with another individual's body; *Auditory:* Directed movements of part of an actor's body that generate sounds by contact with a substrate, object, or one's own body; and *Visual:* Directed movements of part of an actor's body that do not include physical contact or produce a sound.

2.2.2 Gestures and Social Dynamics

To capture gestures that initiated or attempted to initiate an interaction, I began video-recording whenever individuals were within 5 m of one another and continued until animals separated themselves beyond this distance. This 5 m threshold was based on my preliminary observations of when individuals were more likely to interact with each other. This enabled me to capture communicative events from beginning to end. The start of a communicative event was signified by one individual attempting to engage another individual with a gesture when the two individuals were not previously interacting. Rather than being stationed in one location while recording, all filming was done in multiple locations by following subjects as continuously as possible as they moved within the enclosures. Video data were then reviewed and coded to examine the aspects of social dynamics that influence gestural use, such as social context (*e.g.*, agonism, sexual, and grooming), as well as gestural signaling between sexes and age-classes.

2.2.3 Gesture Ethogram and Coding Protocol

Previous researchers have identified various gestures in captive and wild populations of African apes and created standardized definitions for these gestures in the form of gesture ethograms (Table 1.1). To consistently identify gestures, I used the gestures previously defined in published ethograms, with occasional modifications after pilot work and initial observations at each study site. As much as possible, I used the names given to gestures in the literature to remain consistent with previous studies. I established separate ethograms for each species at each study site which consisted of the gesture name, the signal type (auditory, tactile, or visual) and the operational definition of each gesture. These are compiled into one ethogram in Table 2.2.

Videos were reviewed using Intervideo WinDVD 6 software, and all gestures were coded into an Excel spreadsheet in terms of: *Actor:* Producer of the gesture; *Recipient(s):* Receiver(s) of the gesture; *Gesture:* Based on the ethogram (Table 2.2); *Context before and after gesture use:* Social context in which gesture was used such as *traveling, sexual, playing, grooming*, *agonism*, or *feeding*, and whether the context changed after gesture production (social contexts are described in detail in Chapter 3, Table 3.4); *Actor's positional behavior while gesturing:* Based on the positional behavior ethogram (Table 2.3); I quantified upper limb availability by determining whether 'one,' 'both,' or 'no' upper limbs were available at the time of gesturing, depending on the specific posture or locomotion; *Recipient's attentional state:* Direct eye contact or head oriented toward actor (*attentive*), or head oriented 90° or more away from actor (*not attentive*); *Recipient's response:* Whether the recipient responded by altering behavior or changing his or her attentional state. Responses were coded as: *Gesture*, *approach*, *move away*, *look toward*, *look away*, or *change position*. If the recipient did not respond within 4 seconds of the gesture, the response was coded as *no response*. In pilot study videos, most responses occurred within 4 seconds. All timing was determined during video review using the continuous timer on the WinDVD 6 playback toolbar.

2.2.4 Gestures and Positional Behavior

The positional behavior data I collected enabled me to establish baseline locomotor profiles for individuals (*e.g.*, time spent sitting, quadrupedal walking, climbing, and in bipedal postures) and determine how available upper limbs were for gesturing. I collected these data using 15-minute continuous focal animal sampling (Altmann 1974) via video recording. The order of focal animals sampled was chosen by matching age and sex across groups, and then using a random rotation. Animals were rarely out of view for extended periods in all study sites due to large viewing windows, outdoor viewing areas, and (in some cases) private observation platforms. If an animal was out of sight (OOS) for 1 minute or more, that focal sample was either stopped during recording or discarded during video coding, unless the OOS occurred after 8 minutes and 30 seconds, in which case the focal was more than halfway complete and it was kept for analysis. All analyses of positional behavior stemming from these focals were done after the total time spent OOS was removed. Any positional behavior must have lasted at least 2 seconds to be recorded as a behavior during coding. All timing was determined during video review using the continuous timer on the WinDVD 6 playback toolbar.

2.2.5 Positional Behavior Ethogram and Coding Protocol

I also established ethograms for various positional behaviors for each species. These are complied into one ethogram in Table 2.3. Just as with the gesture ethogram, I took postures and locomotion that had been previously defined in the literature and modified them, as needed, after pilot work and initial observations at each study site. As much as possible, I used names and definitions from published literature for more direct comparisons with available data.

Fifteen-minute focal samples were coded continuously in terms of: *Positional Behavior*: Using the ethogram in Table 2.3, I continuously recorded every posture or mode of locomotion used by the subject. The subject must have been engaged in that particular behavior for at least 2 seconds for it to be coded as a behavior; *Locomotor substrate*: The type of substrate used such as the ground, a tree, a rock, a rope, or a log; *Arboreal or Terrestrial*: Substrates that were raised off the ground such as trees, vines, and wooden beams were labeled as "arboreal." Substrates such as the ground, rocks, and logs were labeled as "terrestrial."

BZA's enclosure had a 'Tree Bridge' that connected the back of the enclosure (near the indoor holding area) to the rest of the enclosure. To travel to the major areas within BZA's enclosure, it was necessary to use the Tree Bridge, which could be crossed by quadrupedal walking. In all analyses, Tree Bridge was collapsed into the 'tree' category and labeled as an arboreal substrate because the bridge was raised off of the ground and passed over the heads of visitors.

2.3 Inter-Observer Reliability

Over the course of data coding, six undergraduate volunteers assisted me with coding the positional behaviors from the focal sample data. In total, these assistants coded 45 hours of the total 317 hours of focal data. Each assistant was trained in identifying all individuals within each group, identifying postures and locomotor behaviors from the ethogram, and classifying the specific substrates within the enclosures for each study site. Each assistant was responsible for coding data from only one study site. I was always present as assistants were coding data so that I could oversee their work. Before the assistants began coding actual data, they each coded one hour of data that I had previously coded, then I compared their data to mine to make sure the coding was consistent. All assistants were reliable to at least 98% for all positional behaviors as well as their durations.

2.4 Statistical Analyses

I assigned all individuals from all three species to the following age-classes: Infant (≤ 3 years old), Juvenile (4-8 years old), and Adult (≥ 9 years old) based on behavioral and morphological characteristics, and the accelerated age at maturity for captive apes. Most members of the "adult" class had offspring during or prior to data collection. There is a high degree of variability in age-class distinctions in the literature. For gorillas, most researchers also designate 'blackback' and 'young silverback' classes for younger males between the ages of 8 to 15 (Parnell 2002; Breuer *et al.* 2009). For chimpanzees and bonobos, some researchers distinguish a 'subadult/adolescent' class that can span from 7-14 years (*e.g.*, Goodall 1986; Videan & McGrew 2001; Pika *et al.* 2005).

In this research, the 'subadult/adolescent,' 'blackback,' and 'young silverback' distinctions were not used because small sample sizes would have prevented direct comparisons across groups and species. Because of the small sample sizes within each class and the similar patters expressed by both age-classes, I clumped infants and juveniles into a “young” age-class (0-8 years old) for analyses. Because data collection for the BZ groups spanned three years (intermittently), two individuals in BZA from the infant age-class were recruited into the juvenile class and four individuals in BZB from the juvenile class were recruited into the adult age-class for all gesture data.

Focal video data collection for BZ began in 2006, and two of the four females in BZB were nine years old at that point, so they were always classified as adults in analyses of positional behavior obtained from focal video data. When analyzing data by age-class, I classified each of those individuals by whichever class they fell in on the date the data were collected. For example, the data for the BZA male, Shana, was analyzed in the infant age-class from June to August 2005, then within the juvenile age-class for all data collected thereafter. I did not collect focal video data for one juvenile male, Pierrepont, because he was transferred to another facility before I could obtain a substantial number of focal hours. Thus, Pierrepont is not included as a BZA member in all analyses in Chapter 4.

Gestures were examined with regard to the proportion of gestures that occurred in each social context (*i.e.*, *grooming, playing, feeding, agonism*). This served to determine whether each species used gestures specifically in particular social interactions specific to their unique social dynamics (*e.g.*, female bonobos gestured most frequently to other females in the sexual context). The rates of gesturing and the types of gestures used within dyads were also analyzed in relation to sex and age-class of the actors and recipients. The durations of time (in seconds) spent in various positional behaviors were ascertained from focal sample videos and examined in relation to the total observation time per group. The number of gestures employed while in various postures and modes of locomotion was also examined to determine the most common positional behaviors of actors while they were gesturing and whether those gestures involved the upper limbs.

I used Microsoft Excel and JMP 8 (part of the SAS statistical software package) to analyze all data. I used parametric tests whenever possible and non-parametric tests when data did not meet the requirements for parametric statistics (Sokal & Rohlf 1995; Fowler *et al.* 1998). The level of significance was set at $p \leq 0.05$ for all statistical tests.

TABLE 2.1 Group compositions at each study site. Age/Sex-Classes: IM/F=Infant Male/Female, JM/F=Juvenile Male/Female, and AM/F=Adult Male/Female. Date of Birth (DOB) is listed as month/year.

2.1a. Western Lowland Gorillas (*Gorilla gorilla gorilla*):

Bronx Zoo Group A (n=11)			**Bronx Zoo Group B (n=13)**		
Name	**Age/Sex (DOB)**	**Dam/Sire**	**Name**	**Age/Sex (DOB)**	**Dam/Sire**
Zuri	AM (10/83)	Nina/Pete	Pattycake	AF (9/72)	Lulu/Kongo
Julia	AF (7/80)	Kay/Chuma	Tunko	AF (10/84)	Tanuka/Kongo
Holli	AF (11/89)	Huefanita/Kongo	Triska	AF (7/86)	Huefanita/Bendera
Tuti	AF (7/94)	Tunko/Tim	Fran	J/AF* (11/96)	Holli/Tim
Imani	AF (12/94)	Triska/Tim	Halima	J/AF* (2/97)	Huefanita/Tim
Sufi Bettine	JF (12/01)	Holli/Zuri	Layla	J/AF* (4/98)	Huefanita/Tim
Pierrepont	JM (1/01)	Julia/Zuri	Kumi	J/AF* (6/98)	Tanuka/Tim
Shana	I/JM* (9/02)	Imani/Zuri	Suki	JF (7/00)	Triska/Tim
Zola	I/JM* (11/02)	Tuti/Zuri	Kioja	JF (1/01)	Tunko/Zuri
Johari	IM (9/05)	Julia/Zuri	Nyasha	JF (2/01)	Pattycake/Zuri
Barraca	IM (2/06)	Imani/Zuri	Babatunde	IM (1/06)	Triska/Fubo
			M'domo	IM (7/06)	Fran/Fubo
			Barbara	IF (3/06)	Halima/Fubo

*These individuals were in two age-classes over the course of data collection.

2.1b. Chimpanzees (*Pan troglodytes*):

St. Louis Zoo (n=11)			**Los Angeles Zoo (n=13)**		
Name	**Age/Sex (DOB)**	**Dam/Sire**	**Name**	**Age/Sex (DOB)**	**Dam/Sire**
Smoke	AM (67? wild born)	Unknown	Shaun	AM (7/88)	Nan/Judeo
Jimiyu	AM (1/92)	Vicky/M'Chawi	Jerrard	AM (2/90)	Pandora/Judeo
Hugo	AM (5/93)	Boo/Roscoe	Glenn	AM (4/94)	Nan/Judeo
Rosebud	AF (70? wild born)	Unknown	Ripley	AM (3/96)	Pandora/Judeo
Beauty	AF (73? wild born)	Unknown	Pandora	AF (3/67)	Susie/Unknown
Mlinzi	AF (12/92)	Kibali/Keo	Nan	AF (12/79)	Bonnie/Johari
Cinder	AF (8/94)	Mollie/Smoke	Regina	AF (10/83)	Pandora/Johari
Holly	AF (3/98)	Snika/Chester	Joanna	AF (7/85)	Bonnie/Johari
Bakhari	AF (4/98)	Ruthie/Koby	Gracie	AF (1/87)	Pandora/Judeo
Utamu	JF (12/01)	Rosebud/Niger	Yoshiko	AF (7/90)	Regina/Judeo
Tammy	JF (1/02)	Unknown	Jake	JM (6/99)	Regina/Shaun
			Jean	JF (6/99)	Gracie/Shaun
			Zoe	JF (8/99)	Unknown

TABLE 2.1 Group compositions at each study site (continued).

2.1c. Bonobos (*Pan paniscus*):

San Diego Zoo (n=8)			**San Diego Wild Animal Park (n=8)**		
Name	**Age/Sex (DOB)**	**Dam/Sire**	**Name**	**Age/Sex (DOB)**	**Dam/Sire**
Yenge	AM (12/82)	Unknown	Akili	AM (2/80)	Matata/Bosondjo
Junior	AM (1/95)	Lana/Maiko	Erin	AM (12/91)	Loretta/Vernon
Lana	AF (4/79)	Linda/Kakowet	Jumanji	AM (5/96)	Marilyn-Lori/Akili
Lolita	AF (4/89)	Louise/Vernon	Loretta	AF (1/74)	Linda/Kakowet
Ikela	AF (11/91)	Louise/Akili	Connie-Lenore	AF (2/82)	Louise/Vernon
Mchumba	JF (12/00)	Lolita/Maiko	Marylin-Lori	AF (11/87)	Louise/Vernon
Makasi	IM (4/04)	Loretta/Jumanji	Muhdeblu	JF (4/01)	Marilyn-Lori/Erin
Kesi	IF (8/04)	Loretta/Yenge	Kallie	IF (3/05)	Loretta/Jumanji

TABLE 2.2 Gesture ethogram. The gestures defined in this study for all three species, listed by signal category.

TACTILE	DEFINITION
Back Pounce	*Bipedal Swagger* toward another and bends body or one arm over the other so that physical contact is made
Bite	Clamps teeth down on any part of another's body
Bite Offer	Places a body part (usually fingers, toes, or wrist) in the mouth of another
Body On	Approaches another and sits on, lies on, or presses body against the animal's body >2s
Drum	Hits another on any part of body repetitively with alternating open hands
Embrace	Wraps arm(s) and/or legs around the body of another
Genito-Genital Rub	Repeatedly moves genitals back and forth against another's genitals
Grab	Grasps any part of another's body with the whole hand; fingers are bent
Head Nuzzle	Presses and moves head back and forth against another's body
Inspect Genitals	Makes physical contact with another's genitals with face, mouth, or hands >2s
Long Touch	Gentle and sustained contact with flat hands or feet >5s
Mount Pelvic Thrust	Mounts another either from the front or back and repeatedly thrusts pelvis against the animal's body
Nibble	Opens mouth and gently kisses another animal and/or gently touches teeth against the other animal's mouth or body
Poke	Taps lightly and repetitively upon another's body with fingertips or knuckles
Pull	Grasps another forcefully with hand or foot and brings the animal closer
Push	Presses hand(s) or foot (feet) forcefully against another's body then draws hand(s) back
Slap	Approaches another quickly from a distance and hits the animal forcefully with the palm or back of hand then continues traveling
Smack	Hits another on any part of body with the palm of hand while in close contact
Take	Grabs an object from another's hand with fingers, toes, or mouth
Touch	Gentle contact with another using open hands or feet <2s
Touch Genitals	Gentle contact with another's anogenital region using hands or fingers <2s
VISUAL	**DEFINITION**
Arm Raise	Extends an arm toward another and holds it out >2s
Arm Shake	Hand is shaken loosely at wrist while arm is extended toward another
Bipedal Swagger	While in bipedal position and rocking side to side, steps in exaggerated manner with feet wide-set and one or both arms waving side to side; piloerection accompanies
Bow	Raises and lowers head and torso with arms outstretched and sometimes hands make contact with substrate below; can be accompanied by *Head Nod* or *Head Shake*
Chase	Moves quickly and suddenly towards another for >2s
Charge	Sudden and short (<2s) lunge towards another followed by either staying still or moving back to the original location
Drag	*Quadrupedal Running* while holding an object (typically a branch) in one hand and dragging it along behind
Formal Bite	Bares teeth and moves mouth towards another but does not make physical contact
Gallop	Runs quickly past another animal quadrupedally or bipedally while sometimes outstretching arm closest to the animal
Head Bang	Hits the top of own head or rubs hands from front to back of head rapidly and forcefully while in a *Crouch* posture

TABLE 2.2 Gesture ethogram (continued).

VISUAL	DEFINITION
Head Nod	Jerks head up quickly once or several times successively so that the lower face juts out
Head Shake	Shakes head repeatedly from side to side in a loose, rolling manner
Ice Skate	Pirouettes with hands on the ground or in the air as body twirls around in circles; can stay in one place or move toward another
Object Shake	Waves an object in the direction of another or when approaching another
Object Slide	*Quadrupedal Running* with object (usually flat box or paper) underneath both hands so that arms are pushing the object along while legs are moving behind
Peer	Brings face <1ft to the face of a another for >2s
Present Genitals	Raises genitals up towards another while crouching (typically female) or thrusts genitals or erection towards another by spreading legs while *Sitting* or in a *Crouch* posture (typically male)
Rock	Moves upper body side to side while *Sitting* or *Quadrupedal Standing*; sometimes accompanied by piloerection
Somersault	Body makes at least two rotations either head over feet or sideways
Staredown	Approaches another within 1m and maintains direct eye contact >2s
Swat	Waves arm or hand at another in close proximity but does not actually make physical contact
Throw	Tosses an object (such as branch or food) toward another
AUDITORY	**DEFINITION**
Body Beat	Slaps repetitively on own body (except chest) with alternating open hands or closed fists
Chest Beat	Slaps repetitively on own chest with alternating open hands or closed fists
Clap	Palms of hands come into contact with each other or palm of hand comes into contact with sole of foot in one distinct movement
Dropkick	Kicks window, rock, or metal door with both feet while hands are on the ground or other substrate; preceded by piloerection and sometimes *Bipedal Swagger* and/or *Rock*
Foot Clap	Soles of feet come into contact with each other in one distinct movement
Slap Ground	Hits substrate repetitively with alternating open hands
Stomp	Brings the sole or heel of foot suddenly and forcibly down upon a substrate

TABLE 2.3 Positional behavior ethogram. The locomotion and postures defined in this study. Modified in part from Hunt *et al.* (1996) and Morcillo *et al.* (2006).

LOCOMOTOR BEHAVIORS	DEFINITION
Bipedal Running	Rapid locomotion with erect upper body; feet in contact with substrate
Bipedal Running Full	*Bipedal Running* with food or object held in hand(s)
Bipedal Swaggering	Bipedal locomotion with feet wide-set and stepping in exaggerated manner, body rocking side to side; piloerection accompanies
Bipedal Walking	Slow locomotion with erect upper body; feet in contact with substrate
Bipedal Walking Full	*Bipedal Walking* with food or object held in hand(s)
Brachiating	Bimanous locomotion on an arboreal substrate, with swinging propelled by arm over arm movement
Climbing	Quadrumanous locomotion up or down substrate
Ice Skating	Pirouettes with hands on substrate or in the air as body twirls around in circles
Jumping	Feet are out of contact with substrate for >2s as body is propelled into the air then lands on substrate or another with any part of the body
Object Sliding	*Quadrupedal Running* with object (usually flat box or paper) underneath both hands so that upper limbs are pushing the object along while legs are moving behind
Quadrupedal Running	Rapid quadrupedal locomotion (knuckle-walking) with hands and feet in contact with substrate
Quadrupedal Running Full	*Quadrupedal Running* with food or object held in hand(s) or foot (feet)
Quadrupedal Walking	Slow quadrupedal locomotion (knuckle-walking) with hands and feet in contact with substrate
Quadrupedal Walking Full	*Quadrupedal Walking* with food or object held in hand(s) or foot (feet)
Sliding	Movement down smooth substrate with knees slightly bent, hands and feet remain in contact with substrate
Somersaulting	Body makes at least two rotations either head over feet or sideways
Swingsetting	Hands in contact with substrate while legs swing through arms from back to front. Once feet touch substrate, arms swing forward and entire movement repeats.
POSTURAL BEHAVIORS	**DEFINITION**
Bipedal Standing	Stationary with body in erect posture; only feet in contact with substrate
Bipedal Standing Full	*Bipedal Standing* with food or object held in hand(s)
Crouching	Body folded in half so that upper body is oriented downwards or knees bent with body in an erect posture
Hanging	Body is suspended in a vertical position while hand(s) or foot (feet) are grasped around substrate
Headstanding	*Crouch* posture but with top of head also in contact with substrate >2s
Lying Dorsally	Entire dorsum (and usually back of head) in contact with substrate
Lying Ventrally	Entire ventrum in contact with substrate

TABLE 2.3 Positional behavior ethogram (continued).

POSTURAL BEHAVIORS	DEFINITION
Lying on Side	Side of body in contact with substrate while dorsum and ventrum are not
Quadrupedal Standing	Stationary with upper body parallel to substrate and hands and feet in contact with substrate
Quadrupedal Standing Full	*Quadrupedal Standing* with food or object in hand(s) or foot (feet)
Riding	Infants or juveniles only; clinging dorsally or ventrally or sitting/standing atop dorsum of other
Sitting	Upper body in erect posture with rear in contact with substrate; legs are straight, bent, or crossed over one another

Figure 2.1 Bronx Zoo gorilla Group A enclosure. View from main public viewing area.

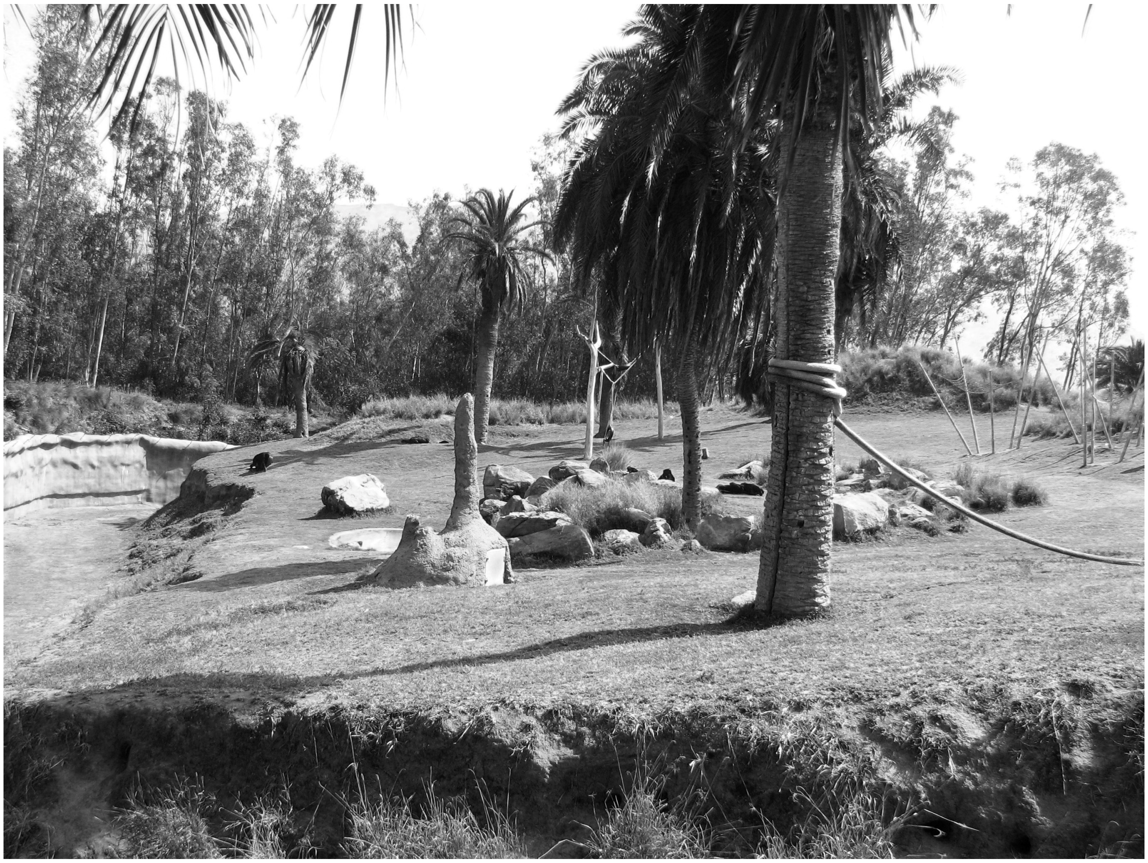
Figure 2.2 Bronx Zoo gorilla Group B enclosure. View from main public viewing area.

Figure 2.3 St. Louis Zoo chimpanzee enclosure. View from main public viewing area.

Figure 2.4 Los Angeles Zoo chimpanzee enclosure. View from main public viewing area.

Figure 2.5 San Diego Zoo bonobo enclosure. Aerial view from private viewing area.

Figure 2.6 San Diego Wild Animal Park bonobo enclosure. View from right side of enclosure.



CHAPTER 3

EFFECTS OF SOCIAL DYNAMICS ON GESTURAL SIGNALING

3.1 Introduction

The first research question I investigated was: Do the frequencies of gestural signaling and the types of gestures used differ as a function of social dynamics across species? Specifically, I hypothesized that gestural signaling would differ among dyads as a function of the frequency of interactions between individuals and the nature of those interactions (*e.g.*, affiliative, agonistic, sexual). To explore the relationship between gestural signaling and social dynamics for each species, I examined who was gesturing to whom, how frequently, and in what social contexts. Gestural signaling occurs between an actor and a recipient, so investigating signaling between dyads enabled me to construct patterns of gestural signaling between members of particular age/sex-classes in particular social contexts within a species. In this chapter, I present the results of these analyses by species and a brief discussion of these findings.

In total, I collected 536 hours of video of social behavior from which I coded several aspects of gestural signaling. I collected 200 hours of video data from Bronx Zoo (BZ) gorillas: 100 hours from BZA and 100 hours from BZB; 195 hours of video data from chimpanzees: 92 hours from the Los Angeles Zoo (LAZ) and 103 hours from the St. Louis Zoo (SLZ); and 141 hours of video data from bonobos: 80 hours from the San Diego Zoo (SDZ) and 61 hours from the San Diego Wild Animal Park (WAP). In Table 3.1, I list the different gestures recorded in this study for each group, categorized by signal type (tactile, visual, and auditory). Definitions for each gesture can be found in the gesture ethogram in Chapter 2 (Table 2.2). Thirty-five of the 49 gestures I observed in these three species were also recorded in previous studies (see Chapter 1, Table 1.1 for a list of the 69 total gestures from published ethograms), while the remaining 14 were not identified in previous research (see Table 3.1). Six of the gestures that were observed elsewhere but not in this research were facial expressions, which were not examined in this dissertation.

3.2 Effects of Social Dynamics on Gorilla Gestural Signaling

3.2.1 Gestural Repertoire and Rates of Gesturing

BZA gorillas used more gestures and gestured more frequently than BZB gorillas, though both groups were within the range of variation observed across chimpanzee and bonobo groups. BZA gorillas used 32 distinct gestures: 16 tactile, 12 visual, and 4 auditory (Table 3.1). Over the course of 100 observation hours, BZA gorillas gestured 1,767 times (17.7 gestures/hour). The average number of different gestures used by each individual in BZA was 19.6 gestures. No individual used all 32 different gestures. BZB gorillas used 24 distinct gestures: 15 tactile, 5 visual, and 4 auditory (Table 3.1). Over the course of 100 observation hours, BZB gorillas gestured 696 times (7.0 gestures/hr). The average number of different gestures used by each individual in BZB was 12.2 gestures. No individual used all 24 different gestures. The number of times gorillas in both groups used each gesture is presented in Figure 3.1. There were no idiosyncratic gestures (gestures used by only one individual more than three times) in either gorilla group.

The median number of gestures used per individual in BZA was 121.0 gestures (with a range of 17 to 315). As predicted, young gorillas in BZA gestured significantly more than adults (Figure 3.2): Adults in BZA used an average of 52.6 gestures while young individuals used an average of 188.0 gestures (one-way ANOVA, df=1, Fisher

F-value=6.869, p=0.024). The median number of gestures used by BZB gorillas was 47.0 gestures per individual (with a range of 4 to 147). When examining gesturing by age-class in BZB, young individuals also gestured significantly more than adults (Figure 3.2): Adults gestured an average of 13.5 times, while the mean number of gestures for young gorillas was 61.5 (one-way ANOVA, df=1, Fisher F-value=9.332, p=0.009).

3.2.2 Audience Effects

All gorillas used tactile, visual, and auditory gestures significantly more when recipients were attentive to them compared to when recipients were not attentive (Figure 3.3). I performed three χ^2 tests (one for each signal type) to determine whether these differences represented deviations from expected proportions, and significance values were $p<0.001$ (df=1) for each test. For tactile gestures, n=1,262 gestures when attentive, n=435 when not attentive ($\chi^2=403.0$). For visual gestures, n=384 gestures when attentive, n=49 when not attentive ($\chi^2=259.2$). For auditory gestures, n=217 gestures when attentive, n=116 when not attentive ($\chi^2=30.6$).

Audience effects were evident when groups were examined separately as well. For BZA: 74.8% of tactile gestures (n=936), 87.2% of visual gestures (n=231), and 66.1% of auditory gestures (n=166) were used when recipients were attentive rather than not attentive. For BZB: 73.1% of tactile (n=326), 91.1% of visual (n=153), 62.2% of auditory gestures (n=51) were used when recipients were attentive rather than not attentive.

When responses to individual gestures were examined, there was not one response that occurred more frequently than others, rather recipients responded in several ways to each gesture. Thus, I examined the recipient’s response to each signal type to determine whether tactile, visual, and auditory gestures received different types of responses from recipients. Responses were categorized as: *Approach* (including chase, move toward, and follow), *change position*, *gesture*, *look away*, *look toward, move away,* or *no response*. As Figure 3.4 shows, the most frequent response to tactile gestures was to *gesture* in return (47.3%, n=804), the most frequent responses to visual gestures were *no response* (35.2%, n=149) and *move away* (34.5%, n=146), and the most frequent response to auditory gestures was *no response* (52.1%, n=163). Finally, the most frequent response to a combination of gestures (*gesture combos*) was to *gesture* in return (55.2%, n=16).

3.2.3 Gesturing Within Dyads

To address how gestural signaling was affected by social dynamics, I also examined to whom individuals gestured most often. I predicted that gesturing would occur at lower frequencies between adults and higher frequencies between mother and offspring dyads. BZA and BZB shared the same pattern of signaling between age-classes, thus I combined data from both groups for this analysis. As predicted, there was less gesturing within adult dyads. As Table 3.2 shows, adult gorillas gestured significantly more to young gorillas than to other adults (Z-test for two proportions: $Z=8.697$, $p<0.05$). Young gorillas, however gestured significantly more to other young gorillas than to adults (Z-test for two proportions: $Z=17.183$, $p<0.05$).

Gestural signaling was also examined by what sex adult actors gestured to most frequently (Table 3.3). I restricted this analysis only to BZA since no adult male was present in BZB and, therefore, no opportunity existed for gesturing between adult males and other individuals. Adult females (n=7) gestured significantly more to group males than to group females (Z-test for two proportions: $Z=6.206$, $p<0.05$).

Out of the 168 gestures produced by adult females in BZA, only two of them were directed to the silverback, while the remaining 166 gestures were directed to their male offspring. There was no significant difference in the number of times the silverback (n=1) gestured to group females (n=14 gestures) compared to group males (n=9 gestures) or multiple recipients of mixed sex (n=9 gestures; Z-test for two proportions: Z=0.33, p□0.05). Although the sample of adult males is limited to only one silverback, it is worth noting that he showed the same pattern as adult male chimpanzees and bonobos of gesturing most frequently to females rather than to the young males present. Juveniles and infants were not included as actors because of small sample sizes.

To obtain a more complete understanding of how gorilla social dynamics influence gestural signaling, I also examined which individuals were most favored as frequent gesture recipients. I counted the total number of gestures each individual directed to each recipient to determine whether patterns could be detected at the group or species levels. As predicted, the most frequent gesture recipients for all BZA adult females were their offspring. For instance, among adult females in BZA, 85.7% of Julia's, gestures (n=35) were directed to her offspring, Pierrepont and Johari, and 71.1% of Imani's gestures (n=121) were directed to her offspring, Shana and Barraca. While the silverback gestured to females most often, his juvenile son, Pierrepont, (18.8%, n=6) and the alpha female, Holli (15.6%, n=5) received gestures from him more frequently than any other recipients. Young individuals also gestured to their mothers more frequently than they gestured to any other group members, though juveniles, in particular, also gestured frequently to other young members of the group.

Gestural signaling among members of BZB showed a slightly different pattern. Nursing mothers in the group (n=3) did gesture frequently to their offspring, which supported my prediction. But, two of them gestured slightly more frequently to other females in the group than to their offspring, though differences were not significant. For example, the adult female, Halima, gestured most often to two other females in the group (20.7% to Layla and 17.1% to Fran), and to her infant in 14.6% of her total 82 gestures. Two of the three infants gestured more frequently to other infants than to their mothers. For example, the infant Babatunde gestured 53 times to the other two infants (57.6% of his total gestures), but only gestured to his mother 4 times (4.3% of his 92 gestures).

3.2.4 Social Contexts

I identified fourteen different social contexts (described in Table 3.4) that could be generalized across the three study species. I examined the number of gestures produced in each of these contexts as well as the social context that followed the production of gestures to test my prediction that gestural signaling in gorillas would occur most frequently in the contexts of *agonism* and *playing*. The most frequent social contexts in which gestures were produced are presented for both groups in Figure 3.5. Gorillas in both groups gestured most often when they were *near recipient* (<2 m) but not interacting (BZA: 46.0%, n=812 gestures; BZB: 47.3%, n=329 gestures). I also examined the social contexts that immediately followed the production of gestures by comparing the social contexts that occurred after the production of tactile, visual, and auditory gestures (Figure 3.6). Tactile gestures produced by gorillas most frequently led to *playing* (33.0%, n=561). Visual gestures were most frequently followed by *feeding* and the actor being *near recipient* (25.1%, n=106 for each), and the most frequent context after an auditory gesture was produced was *near recipient* (52.7%, n=165). Finally, actors were *playing* with recipients most frequently after *gesture combos* (37.9%, n=11). Contrary to my prediction, gestural signaling occurred at very low frequencies in the context of *agonism* (<1%) in both groups of gorillas.

Just as recipients' responses were varied, the same was true for the contexts that each gesture elicited. Each gesture resulted in an average of 5.9 different social contexts. Nine gestures led to one particular context in more than 50% of cases (all other gestures led to a variety of contexts). *Playing* was the most frequent context (>50% of counts) following the production of several gestures: *Bite* (76.3%, n=76 counts), *chase* (67.2%, n=76 counts), *drum* (50.0%, n=24 counts), and *somersault* (66.7%, n=12 counts). *Nursing* occurred after *formal bite* in 50% of cases (n=8), while *near recipient* was the most common context after *long touch* (53.1%, n=64 counts) and *slap ground* (66.0%, n=106 counts). *Feeding* was the most frequent context after both *peer* (59.6%, n=146) and *take* (65.2%, n=66).

3.3 Effects of Social Dynamics on Chimpanzee Gestural Signaling

3.3.1 Gestural Repertoire and Rates of Gesturing

Chimpanzees in SLZ and LAZ were very similar in the types of gestures they used, but there was considerable inter-group variation in the frequency of gestural signaling. SLZ chimpanzees used 28 distinct gestures: 16 tactile, 11 visual, and 1 auditory (Table 3.1). Over the course of 92 observation hours, SLZ chimpanzees gestured 1,336 times (14.5 gestures/hr). The average number of different gesture types used by each individual in SLZ was 13.8 gestures. No individual used all 28 different gestures. LAZ chimpanzees used 27 distinct gestures: 16 tactile, 10 visual, and 1 auditory (Table 3.1). Over the course of 104 observation hours, LAZ chimpanzees gestured 705 times (6.8 gestures/hr). The average number of different gesture types used by each individual in LAZ was 15.8 gestures. No individual used all 27 different gestures. The number of times chimpanzees in both groups used each gesture is presented in Figure 3.7.

There was one idiosyncratic gesture observed in SLZ (*spit water*), which was used three times by the juvenile female, Tammy. Tammy filled her mouth with water from a spigot in the enclosure and sprayed it at another juvenile female to initiate play. Because this gesture was idiosyncratic, it was not included in analyses. Another gesture, *rock*, was not idiosyncratic for SLZ chimpanzees, but it was used in a manner that was unique to SLZ chimpanzees. Two adult females (Holly and Bakhari) rocked side to side to initiate a stereotypical locomotor behavior called "training," in which both females held on to each other and stepped in synchrony in an exaggerated manner. This usage of the *rock* gesture varied from that of the LAZ group, whose members (almost exclusively males) used it during dominance displays.

The median number of gestures used per individual in SLZ was 76.0 gestures (with a range of 30 to 476). As predicted, SLZ chimpanzees shared the same pattern as gorillas of young individuals gesturing significantly more than adults (Figure 3.2). On average, adults in SLZ used 77.7 gestures, and young chimpanzees used 318.5 gestures (one-way ANOVA, df=1, Fisher F-value=11.939, p=0.007). There were no young males in SLZ.

LAZ chimpanzees gestured much less: The median number of gestures used per individual was 45.0 gestures (with a range of 23 to 174). Contrary to my prediction, young chimpanzees did not gesture significantly more than adults in LAZ

(Figure 3.2): On average, adults in LAZ used 57.6 gestures, while young chimpanzees used 43.0 gestures (one-way ANOVA, df=1, Fisher F-value=0.290, p=0.601).

3.3.2 Audience Effects

All chimpanzees used tactile, visual, and auditory gestures significantly more when recipients were attentive to them compared to when recipients were not attentive (Figure 3.3). For tactile gestures, n=927 gestures when attentive, n=460 when not attentive (χ^2=157.2, p< 0.001, df=1); for visual gestures, n=605 gestures when attentive, n=33 when not attentive (χ^2=512.8, p< 0.001, df=1); for auditory gestures, n=14 gestures when attentive, n=2 when not attentive (χ^2=30.6, p=0.003, df=1).

Audience effects were just as strong when groups were examined separately. For SLZ: 66.9% of tactile gestures (n=616), 93.7% of visual gestures (n=374), and 100% of auditory gestures (n=6) were used when recipients were attentive. For LAZ: 67.3% of tactile (n=311), 96.7% of visual (n=231), and 80.0% of auditory gestures (n=8) were used when recipients were attentive.

As with gorillas, when responses to individual gestures were examined, there was no one specific response to most gestures, rather recipients responded in several ways to each gesture. Thus, I examined the responses to each signal type to determine whether tactile, visual, and auditory gestures received different types of responses from recipients. Responses were categorized in the same way as with gorillas but *grooming* was also observed as a response for chimpanzees. As Figure 3.8 shows, the most frequent responses to auditory gestures was *no response* (40.0%, n=6) whereas *gesture* in return was the most frequent response to tactile gestures (27.2%, n=370), visual gestures (33.3%, n=206), and *gesture combos* (31.3%, n=15).

3.3.3 Gesturing Within Dyads

To address how gestures were affected by social dynamics, I also examined to whom individuals gestured most often. I predicted that gesturing would occur most frequently between young individuals then to a lesser degree between adults and within adult-young dyads. SLZ and LAZ shared the same pattern of signaling between age-classes, thus I combined data for both groups for this analysis. Contrary to my prediction, young chimpanzees gestured significantly more to adult chimpanzees than to other young individuals (Table 3.2; Z-test for two proportions: Z=5.306, $p<0.05$). As expected, adult chimpanzees gestured significantly more frequently to other adults than to young chimpanzees (Table 3.2; Z-test for two proportions: Z=10.727, $p<0.05$).

Gestural signaling was also examined by what sex adult actors gestured to most frequently (Table 3.3). Among adults, I predicted that there would be a higher frequency of gesturing between males compared to male-female and female-female dyads because bonds between adult males would be stronger. For this analysis, data from SLZ and LAZ were not combined because the adult females demonstrated different patterns of gesturing. Neither group of chimpanzees supported my prediction that there would be a higher frequency of gesturing within adult male dyads. In SLZ, adult females (n=6) gestured significantly more to females than to group males (Table 3.3; Z-test for two proportions: Z=14.267, $p<0.05$). Adult males in SLZ (n=3) gestured significantly more to group females than to group males (Z-test for two proportions: Z=7.996, $p<0.05$). In LAZ, adult females demonstrated the opposite pattern of SLZ females: Adult females (n=6) gestured significantly more to group males than to group females (Z-test for two proportions: Z=3.762, $p<0.05$). As in SLZ, adult males in LAZ (n=4) gestured significantly more to group females than to group males (Z-test for two proportions: Z=5.915, $p<0.05$). Juveniles and infants were not included as actors because of small sample sizes.

As in BZA, there was very little gestural signaling between the alpha male and other group members in SLZ. In SLZ, the alpha male (Hugo) used a total of 32 gestures. Those gestures were dispersed throughout the group, but the greatest proportion to a single individual was to an older female named Beauty (27.7%, n=9 gestures). Hugo received more gestures from the two juvenile females than from any other group members (n=19 gestures). There was only one mother-offspring pair in SLZ (Rosebud and her daughter, Utamu) and predictably, they were each other's favored gesturing partner. Rosebud gestured to Utamu almost exclusively (96.3%, n=26 gestures) while Utamu gestured to Rosebud more frequently than she did to any other group member (35.3%, n=171 gestures). Juvenile females also gestured frequently to each other: 74.5% of Tammy's gestures were directed to Utamu (n=114) and 28.5% of Utamu's gestures were directed to Tammy (n=138 gestures).

In LAZ, there was more gesturing between the alpha male (Glenn) and other group members than in SLZ. Glenn used a total of 174 gestures, and these were dispersed throughout the group. Glenn gestured to all group members at least once, and all group members gestured to him at least once. Glenn also gestured frequently to the entire group (15.5%, n=27 gestures) in the form of dominance displays and to one adult female, Gracie (12.1%, n=21 gestures). Interestingly, Glenn's mother, Nan, gestured to her adult son more than she did any other group member (41.4% of her total gestures, n=12 gestures). There were no nursing mothers with dependent offspring in LAZ.

3.3.4 Social Contexts

I identified fourteen different social contexts (described in Table 3.4) that could be generalized across the three study species. I examined the number of gestures produced in each of these contexts as well as the social contexts that followed the production of a gesture. I predicted that chimpanzees would gesture most frequently in sexual, agonistic, and affiliative (*i.e.*, *grooming, playing,* and *near recipient*) contexts. The most frequent social contexts in which gestures were produced are presented for both groups in Figure 3.9. Chimpanzees in both groups gestured most often when they were *near recipient* (<2 m) but not interacting (SLZ: 50.9%, n=680 gestures; LAZ: 33.0%, n=233 gestures). The two groups were very similar, but one key difference is that 10.0% of LAZ chimpanzee gestures occurred in the context of *agonism*, while less than 1.0% of SLZ gestures occurred in this context.

I also examined the social context that immediately followed the production of a gesture by comparing the social contexts that occurred after the production of tactile, visual, and auditory gestures (Figure 3.10). *Traveling* was the most frequent social context after the production of tactile (25.1%, n=347) and visual (22.3%, n=139) gestures. Actors were *alone* (>2 m from any others) most frequently after auditory gestures were produced (40.0%, n=6), and finally, actors were *traveling* most frequently after *gesture combos* (33.3%, n=7).

Just as recipients' responses were varied, the same was true for the contexts that each gesture elicited. Each gesture resulted in an average of 7.3 different social contexts. Four gestures led to one particular context in more than 50% of cases (all other gestures led to a variety of contexts). Actors were most frequently *alone* (>2 m from any others) after a *dropkick* gesture (60.0%, n=6 counts). *Feeding* was the most frequent context following *peer* (55.0%, n=131 counts). *Traveling* was the most frequent context following *rock* (51.5%, n=68 counts). Finally, *playing* was the most frequent context following *swat* (57.1%, n=28 counts).

3.4 Effects of Social Dynamics on Bonobo Gestural Signaling

3.4.1. Gestural Repertoire and Rates of Gesturing

There was considerable variation in the frequency of gestural signaling between bonobos at SDZ and WAP. SDZ bonobos used 27 distinct gestures: 15 tactile, 9 visual, and 3 auditory (Table 3.1). Over the course of 80 observation hours, SDZ bonobos gestured 1,249 times (15.6 gestures/hr). The average number of different gestures used by each individual in SDZ was 16.4 gestures. No individual used all 27 different gestures. Two idiosyncratic gestures were used by young bonobos: The visual gesture *swat* (used by the juvenile female Mchumba) and the tactile gesture *drum* (used by the infant female Kesi). While these gestures were not used by other bonobos, they were observed in both gorilla groups and in SLZ chimpanzees. Because these gestures were idiosyncratic to those individuals, they were not included in analyses.

WAP bonobos used 33 distinct gestures: 19 tactile, 10 visual, and 4 auditory (Table 3.1). Over the course of 61 observation hours, WAP bonobos gestured 2,237 times (36.1 gestures/hr). The average number of different gestures used by each individual in WAP was 19.9 gestures. No individual used all 33 different gestures. There were no idiosyncratic gestures present in this group. The number of times bonobos in both groups used each gesture is presented in Figure 3.11.

Bonobos used more gestures per individual than any other study species. The median number of gestures per individual in SDZ was 104.0 gestures (with a range of 45 to 545). Contrary to my prediction, there was no significant difference between the frequency of gesturing in adults and young in SDZ: On average, adults in SDZ used 94.4 gestures and young bonobos used 259.0 gestures (Figure 3.2; one-way ANOVA, df=1, Fisher F-value=2.354, p=0.176). Though, one infant female gestured much more than the rest of the group (n=545 gestures). WAP bonobos gestured more than all other study groups: A median of 193 gestures per individual (with a range of 100 to 954). As predicted, young bonobos in WAP gestured significantly more than adults: On average, adults in WAP used 170.5 gestures, and young bonobos used 607.0 gestures (Figure 3.2; one-way ANOVA, df=1, Fisher F-value=6.274, p=0.041). One infant female in WAP also gestured at an unusually high frequency (n=954 gestures), more than all BZ gorillas or all LAZ chimpanzees combined.

3.4.2 Audience Effects

All bonobos used tactile, visual, and auditory gestures significantly more when recipients were attentive to them compared to when recipients were not attentive (Figure 3.3). For tactile gestures: n=1,956 gestures when attentive, n=604 when not attentive (χ^2=714.0); for visual gestures: n=624 gestures when attentive, n=15 when not attentive (χ^2=580.4); for auditory gestures: n=273 gestures when attentive, n=14 when not attentive (χ^2=233.7). For all three χ^2 tests, significance values were $p< 0.001$ (df=1).

Audience effects remained strong when groups were examined separately. For SDZ: 78.6% of tactile gestures (n=723), 98.8 % of visual gestures (n=248), and 97.4

% of auditory gestures (n=76) were used when recipients were attentive. For WAP: 75.2% of tactile gestures (n=1,233), 96.9% of visual gestures (n=376), and 94.3% of auditory gestures (n=197) were used when recipients were attentive.

As with gorillas and chimpanzees, when responses to individual gestures were examined, there was no one particular response to most gestures, rather recipients responded in several ways to each gesture. Thus, I examined the recipient's response to each signal type to determine whether tactile, visual, and auditory gestures received different types of responses from recipients. Responses were categorized the same as for chimpanzees, but *share food* was also observed as a response by bonobos. As Figure 3.12 shows, the most frequent response to a tactile gesture was to *gesture* in return (34.8%, n=892), the most frequent response to a visual gesture was to *move away* (43.1%, n=273), the most frequent response to an auditory gesture was *no response* (96.5%, n=275). Finally, the most frequent response to a *gesture combo* was to *approach* (37.5%, n=3).

3.4.3 Gesturing Within Dyads

To address how gestures were affected by social dynamics, I also examined to whom individuals gestured most often. SDZ and WAP shared the same pattern of signaling between age-classes, thus I combined their data for this analysis. As Table 3.2 shows, contrary to predictions, adults gestured almost equally to other adults and to young bonobos (Z-test for two proportions: $Z=1.457$, $p>0.05$). However, young bonobos gestured significantly more to adults than to other young bonobos (Table 3.2; Z-test for two proportions: $Z=18.863$, $p<0.05$).

I also predicted that gestural signaling among adults would occur at lower frequencies between males and at higher frequencies within male-female and female-female dyads. I restricted the SDZ bonobo data set in this analysis because of the fission-fusion group management system employed by SDZ keepers (described fully in Chapter 2, section 2.1.5). From March 14 – April 24, 2008, the two adult males were never in the outdoor enclosure at the same time. Following group management changes, the two males were regularly together in the outdoor enclosure from April 25 – June 3, 2008. Therefore, for this analysis, I used the subset of data collected after April 25 (n=31 hours) so that adult males had the opportunity to gesture to each other. These data were combined with all data from WAP because adult actors demonstrated the same patterns of gesturing. My predictions regarding gesturing within sex dyads were supported (Table 3.3): Adult females (n=6) gestured comparably to group females and group males (Z-test for two proportions: $Z=1.135$, p□0.05). Adult males (n=5), however, followed the same pattern of gorilla and chimpanzee adult males and gestured significantly more to group females than to group males (Z-test for two proportions: $Z=11.053$, $p<0.05$). Juveniles and infants were not included as actors because of small sample sizes.

I also examined actors individually to determine favored gesture partners within the groups. As observed in BZA, BZB, and SLZ, there was a pattern of frequent mother-offspring gesturing in both bonobo groups. The alpha females in SDZ and WAP were both mothers of dependent offspring during the study period. Lana, the alpha female at SDZ, gestured 156 times, and she directed more of these gestures to her infant daughter, Kesi (36.5%, n=57 gestures) than to any other single recipient. In turn, Kesi gestured most often to Lana (48.6% of her total gestures, n=265 gestures) than to any other single recipient. Both adult males gestured more frequently to the juvenile female (Mchumba) than to any other single recipient:

45.6% (n=47 gestures) of Junior's gestures and 29.9% (n=26 gestures) of Yenge's gestures were directed to Mchumba.

Loretta, the alpha female at WAP, gestured 216 times. She gestured most frequently to her offspring, her adult male son, Erin (28.7%, n=62 gestures), and her infant daughter, Kallie (28.2%, n=61 gestures). All group members gestured directly to Loretta, but Kallie gestured to her the most often (51.5% of her total 954 gestures). Adult males in WAP also gestured more frequently to young females than to any other recipients: 35.6% (n=48 gestures) of Akili's gestures, 34.0% (n=34 gestures) of Erin's gestures, and 47.2% (n=116 gestures) of Jumanji's gestures were directed to young females.

3.4.4 Social Contexts

I examined the number of gestures produced in each of the fourteen different social contexts I identified (Table 3.4), as well as the social context that followed the production of a gesture. I predicted that bonobos would gesture most frequently in the *sexual* context and least frequently in the context of *agonism*. However, these predictions were not supported in either group. The most frequent social contexts in which gestures were produced are presented for both groups in Figure 3.13. Bonobos in both groups gestured most often when they were within 2 m of the recipient (*near recipient*) but not interacting (SDZ: 55.1%, n=688 gestures; WAP: 40.6%, n=908 gestures).

I also examined the social contexts that immediately followed the production of gestures by comparing the social contexts that occurred after the production of tactile, visual, and auditory gestures (Figure 3.14). *Playing* was the most frequent social context after the production of tactile (23.4%, n=598) and visual (19.9%, n=126) gestures. Actors were *grooming* most frequently after auditory gestures were produced (97.9%, n=279). The auditory gestures *clap* (n=120 counts) and *foot clap* (n=114 counts) were used to either initiate *grooming* or occurred while grooming was underway, and the context did not change after their production. Finally, actors were *near recipient* (<2 m) most frequently after *gesture combos* (37.5%, n=3). Bonobos did not gesture as frequently as expected in the *sexual* context, but gestures did lead to a *sexual* context more frequently than in gorillas or chimpanzees, particularly for visual gestures. Both bonobo groups also used gestures that could be described as "sexual" more frequently than gorillas or chimpanzees: *Present genitals*, *touch genitals, inspect genitals, genito-genital rub,* and *mount pelvic thrust* (see Figure 3.11 for exact numbers).

Just as recipients' responses were varied, the same was true for the number of different contexts that each gesture elicited. Each gesture resulted in an average of 6.9 different contexts. Fifteen gestures led to a particular context in more than 50% of cases (all other gestures led to a variety of contexts). Several gestures led to *play* most frequently: *Bite* (87.2%, n=47 counts), *bow* (50.0%, n=10 counts), *head nuzzle* (52.9%, n=17 counts), *head shake* (64.7%, n=17 counts), and *somersault* (84.3%, n=19 counts). Many gestures were also most frequently followed by *grooming*: *Clap* (97.5%, n=120 counts), *foot clap* (99.1%, n=114), *slap ground* (89.5%, n=19 counts), and *stomp* (100%, n=31 counts). *Feeding* was the most frequent context following *peer* (66.0%, n=100 counts) and *take* (51.2%, n=86 counts). A *sexual* context was the most frequent context following the production of *genito-genital rub* (66.7%, n=6 counts) and *present genitals* (51.7%, n=60 counts). These gestures, while considered sexual in nature, were also used to initiate play or other social interactions. Actors were most frequently *alone* (>2 m from any others) after an *object slide* gesture

(55.7%, n=106 counts), but *near recipient* (<2 m) after *long touch* (54.3%, n=24 counts).

3.5 Chapter Summary and Conclusions

I hypothesized that, across species, gestural signaling would differ among dyads as a function of the frequency of interactions between individuals and the nature of those interactions. Certain aspects of the distinctive social dynamics that characterize each species were visible in their patterns of gestural signaling. But, inter-group variation suggests that gestural signaling is flexible and susceptible to differences in group composition and the particular relationships between group members.

Across the three study species, there was substantial overlap in tactile gestures (12 were shared by all three species). But, only one visual gesture and no auditory gestures were shared by all species (even within chimpanzee and bonobo groups). Thus, tactile gestures appeared to be the most flexible and universal of the signal types, while particular visual and auditory gestures were more specific to each taxon. Gorillas were the most uniform of the three species, sharing 24 gestures between the study groups.

All individuals in all study groups used tactile, visual, and auditory gestures more frequently when recipients were attentive rather than not attentive. Audience effects were particularly strong for visual gestures (such as *arm raise*, *chase*, or *object shake*), evident in the low percentage of visual gestures used when recipients were not attentive to the actor (Figure 3.3). Responses to specific gestures were varied and few gestures actually elicited a uniform response within a species or across species. The same was true for social contexts that immediately followed gestures. Across species, the only two gestures that were reliably followed by the same contexts were *bite* (led to *play* most often) and *peer* (led to *feeding* most often). This indicates that the majority of gestures have multiple functions and, therefore, variable responses across groups and species.

Contrary to my predictions regarding rates of gesturing, there was considerable variation within species, so no consistent patterns could be identified with respect to how frequently each species gestured. However, within each species, several patterns were apparent in terms of frequent gesture partners and gestural signaling within age-classes. In four of the six study groups, young individuals gestured significantly more frequently than adults (Figure 3.2). The two exceptions were LAZ chimpanzees and SDZ bonobos. The LAZ group was the only group that did not contain mothers with nursing infants, and gestures between mothers and infant offspring accounted for a large percentage of gestures in all other groups. The youngest members of LAZ were eight years old, while all other groups contained infants and younger juveniles. LAZ chimpanzees may have conformed to predictions if there were younger members in the group, particularly dependent offspring. Among SDZ young individuals, the infant female gestured much more frequently than anyone else, but otherwise individuals of all age-classes were very similar in the number of gestures they used. WAP bonobos were also fairly uniform in the number of gestures produced by each individual, but the high frequency of gesturing by the infant female drove up the average for the young age-class. The higher frequency of adult gesturing observed in bonobos is representative of the frequent interactions between bonobos of all age/sex-classes.

Across all three species, adult males gestured more frequently to group females than to males or to multiple individuals of mixed sex (Table 3.3). These females were more often young females rather than adult females, except in the case of the silverback, who gestured more frequently to adult females (n=10 gestures) than to the juvenile female (n=3 gestures) in BZA. This finding was not surprising since males (particularly chimpanzee and bonobo males) are highly attuned to the reproductive statuses of females, which leads to male-initiated contact between sexes.

The frequency of gesturing signaling was clearly high between mothers and their dependent offspring in all three species. But, there was variation across groups with respect to other frequent recipients of adult female gestures. SLZ adult females gestured most often to females and LAZ adult females gestured most often to males. This difference was due to in large part to two particular adult females in SLZ. As mentioned in 3.3.1, Holly and Bakhari demonstrated a unique rocking behavior and subsequent ‘training’ locomotion. This behavior was typically initiated by Holly and it led to an unusually high frequency of gesturing between these two adult females. Holly directed 80.0% of her 175 gestures to Bakhari, and Bakhari directed 62.1% of her 145 gestures to Holly. An additional factor influencing the patterns of gestural signaling among adult females in SLZ was that there were no young males present in that group, and young males were the frequent recipients of adult female gestures in LAZ. Interactions between adult females in both groups were hardly ever agonistic. Only one gesture occurred in the context of *agonism* by an adult female in LAZ, and this was the reconciliatory visual gesture *arm raise* used between two adult females when other group members were in conflict. On two occasions in SLZ, gestures between adult females led to direct agonism between them. In the wild, females typically transfer from their natal groups, so steady interaction with the same females throughout their lives is not common. However, female chimpanzees in captivity have been shown to associate more with each other in affiliative contexts and even form coalitions with each other (Baker & Smuts 1994; de Waal 1994). This female-female affiliation has also been observed in at least one population of wild chimpanzees at Taï Forest, Ivory Coast, presumably in response to high predation rates by leopards (Boesch 1991).

As predicted, adult female gorillas communicated very little with the silverback, and gestural signaling between the alpha male or female and the rest of the group was much more frequent in the chimpanzee and bonobo groups. This pattern of gestural signaling among gorillas would appear to accurately reflect the nature of the relationships between the silverback and the adult females, which is characterized by very little direct interaction (Stokes 2004). Chimpanzees and bonobos, on the other hand, have more regular interactions between the sexes and between the alpha of the group and the rest of the group members. These differences in social dynamics were reflected in gestural signaling within dyads among my study groups.

In both gorilla groups, there was very little gesturing in the *grooming* context compared to chimpanzee and bonobo groups. Again, this seems an accurate reflection of the low degree of this type of affiliative behavior among gorillas. The only group that gestured frequently in the context of *agonism* was the chimpanzee group at LAZ; hence, the high frequency of gesturing in the context of *agonism* that I predicted for gorillas was not supported. LAZ chimpanzees used a large proportion of gestures such as *back pounce* and *bipedal swagger* that were used frequently during agonistic encounters or dominance displays, but these gestures were used in a much smaller proportion in SLZ (Figure 3.7). Perhaps the low degree of agonism in SLZ was due to the more “hands-off” approach to dominance and the particular temperament of the alpha male in that group. An alpha male chimpanzee who is subdued and solitary (such as in SLZ) creates a different tone in the group and a different way of interacting than an alpha male who is more volatile and constantly asserting his status within the group (such as in LAZ). Differences between the leadership styles of the two alpha males were seemingly reflected in patterns of gestural signaling within each group.

Also contrary to my predictions, there was less gesturing in the *sexual* context within both bonobo groups. But, *genito-genital rub*, *present genitals*, *mount pelvic thrust* and other similar gestures were used frequently in both groups and the *sexual* context occurred more frequently than any other context after the use of *genito-genital rub* and *present genitals*. It is unclear why the sexual behavior in these bonobo groups was lower than that reported elsewhere (Kano 1992; Hohmann & Fruth 2000). But, while gesturing in the *sexual* context did not occur as frequently as expected, bonobos did use more gestures in the *sexual* context than gorillas or chimpanzees.

How often individuals communicate with each other and the nature of that communication can depend on the number of young individuals in the group, the presence of dependent offspring, and even the particular personalities and leadership styles of dominant individuals. Many of my predictions regarding the frequency of gestural signaling across certain dyads and within certain social contexts were supported in all three species. However, some predictions (such as adult female gesturing in chimpanzees) were not supported. Nonetheless, it appears that general patterns of gestural signaling can be used as measures of the social dynamics of a species, but the frequency of gestural signaling among certain individuals and within particular social contexts can stray from these patterns because of specific relationships within a group, particularly within a behaviorally flexible genus like *Pan*.

Table 3.1 Gestures recorded by study group. Shaded rows signify gestures shared by all study groups. Gestures marked with * are those not recorded in previous studies.

		Gorillas		Chimpanzees		Bonobos	
		BZA	**BZB**	**SLZ**	**LAZ**	**SDZ**	**WAP**
Tactile:	Back Pounce*			✓	✓	✓	✓
	Bite	✓	✓	✓	✓	✓	✓
	Bite Offer*				✓		
	Body On	✓	✓	✓	✓	✓	✓
	Drum	✓	✓				
	Embrace	✓	✓	✓	✓	✓	✓
	Genito-Genital Rub						✓
	Grab	✓	✓	✓	✓	✓	✓
	Head Nuzzle*	✓	✓	✓	✓	✓	✓
	Inspect Genitals*			✓	✓		✓
	Long Touch	✓	✓	✓	✓	✓	✓
	Mount Pelvic Thrust	✓					✓
	Nibble	✓	✓		✓		✓
	Poke			✓		✓	✓
	Pull	✓	✓	✓	✓	✓	✓
	Push	✓	✓	✓	✓	✓	✓
	Slap	✓	✓	✓		✓	✓
	Smack*	✓	✓	✓	✓	✓	✓
	Take*	✓	✓	✓	✓	✓	✓
	Touch	✓	✓	✓	✓	✓	✓
	Touch Genitals	✓	✓	✓	✓	✓	✓
Visual:	Arm Raise	✓		✓	✓	✓	✓
	Arm Shake				✓		
	Bipedal Swagger			✓	✓		
	Bow			✓	✓	✓	✓
	Chase*	✓	✓	✓		✓	✓
	Charge	✓			✓	✓	✓
	Formal Bite	✓					
	Gallop	✓	✓				
	Head Bang*	✓					
	Head Nod*			✓	✓		
	Head Shake						✓
	Ice Skate	✓					
	Object Shake	✓	✓	✓	✓		✓
	Object Slide*					✓	✓
	Peer	✓	✓	✓	✓	✓	✓
	Present Genitals			✓	✓	✓	✓
	Rock*			✓	✓		
	Somersault	✓				✓	✓
	Staredown*	✓					
	Swat*	✓	✓	✓			
	Throw			✓			
Auditory:	Body Beat	✓	✓				
	Chest Beat	✓	✓				
	Clap	✓	✓			✓	✓
	Dropkick*				✓		
	Foot Clap					✓	✓
	Slap Ground	✓	✓				✓
	Stomp			✓		✓	✓

Table 3.2 Gestural signaling between age-classes. Percentage of gestures used by age-class.

	Gorillas	Chimpanzees	Bonobos
Adult to Adult	18.4%*	64.2%*	45.8%
Adult to Young	75.7%*	30.7%*	49.5%
Adult to Mixed Ages	5.9%	5.1%	4.7%
Young to Young	68.9%*	39.5%*	26.4%*
Young to Adult	27.4%*	59.7%*	73.4%*
Young to Mixed Ages	3.7%	0.8%	0.2%

*Z-test for proportions, $p<0.05$ (tests comparing Adult-Adult to Adult-Young and Young-Young to Young-Adult in each species).
Total adult gestures: Gorillas n=358, chimpanzees n=1,281, bonobos n=1,495.
Total young gestures: Gorillas n=2,106, chimpanzees n=760, bonobos n=1,991.
Gorillas: Adult n=11; Young n=18.
Chimpanzees: Adult n=19; Young n=5.
Bonobos: Adult n=11; Young n=5.

Table 3.3 Gestural signaling between sexes. Percentage of gestures used by adult actors only.

	Gorillas	Chimpanzees		Bonobos
	BZA	**SLZ**	**LAZ**	**SDZ+WAP**
Female to Female	25.5%*	92.0%*	37.2%*	50.3%
Female to Male	72.7%*	7.3%*	62.8%*	45.0%
Female to Both Sexes	1.7%	0.8%	0%	4.7%
Male to Male	28.1%	5.1%*	23.1%*	17.8%*
Male to Female	43.8%	93.3%*	62.9%*	76.2%*
Male to Both Sexes	28.1%	1.5%	13.9%	6.0%

*Z-test for proportions, $p<0.05$ (tests comparing Female-Female to Female-Male and Male-Male to Male-Female in each group).
Total adult female gestures: Gorillas n=231, chimpanzees n=749, bonobos n=622.
Total adult male gestures: Gorillas n=32, chimpanzees n=532, bonobos n=584.
Gorillas: Females n=5; males n=6 (BZA).
Chimpanzees: Females n=8; males n=3 (SLZ); Females n=8; males n=5 (LAZ).
Bonobos: Females n=6; males=5 (SDZ+WAP).

Table 3.4 Social contexts defined for all study groups. Social contexts are from the perspective of the actor and the recipient (*i.e.*, if the actor and recipient are grooming, the social context is *grooming*, but if the recipient is grooming with others, the context is *others grooming*).

SOCIAL CONTEXT	DESCRIPTION
Agonism	Any group members are displaying, piloerecting, vocalizing, or otherwise visibly agitated
Alone	Actor is not within 2 m of any other individuals
Embracing	Actor and recipient are hugging each other for >5 s
Feeding	When keepers are tossing out food or when food is actively being eaten by the actor or recipient
Grooming	Actor is engaged in grooming with the recipient
Near Others	Within 2 m of another group member, but not the recipient
Near Recipient	Within 2 m of the recipient
Nursing	Actor is the nursing mother or the infant actively nursing
Others Grooming	The recipient is engaged in grooming with others
Others Playing	The recipient is actively playing with others
Playing	Active playing between the actor and recipient
Riding	Actor or recipient is clinging to the dorsum or ventrum of another
Sexual	Sex, genital inspection, genito-genital rubbing, or mounting by actor or recipient
Traveling	Actor actively moving alone, or chasing/following/riding on the recipient

Figure 3.1a Distribution of gorilla gestures. Definitions of all gestures are in Table 3.1. *Gesture combos*=When two or more gestures were used in quick (<2 s) succession. Total gestures at BZA=1,767.

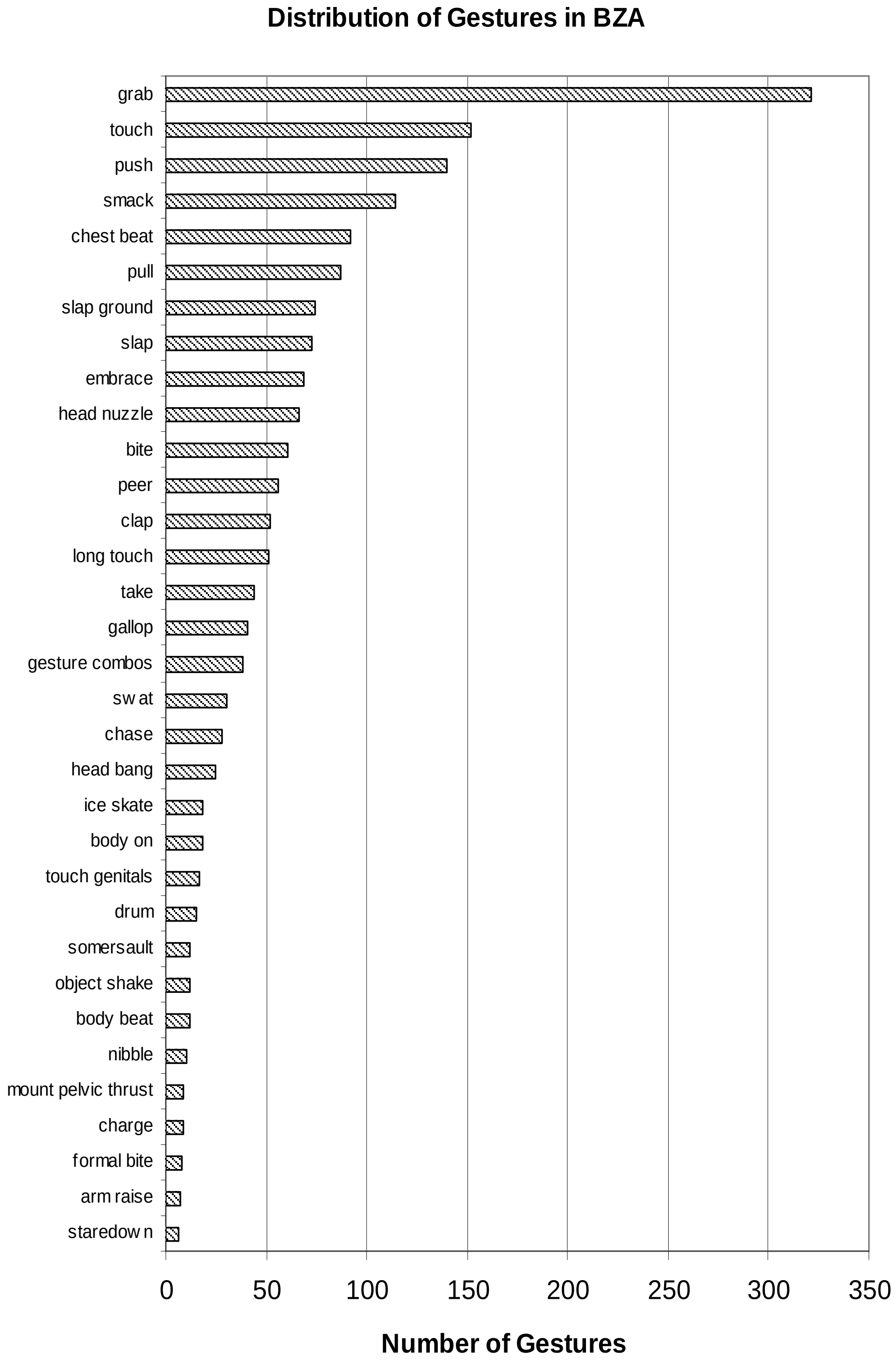


Figure 3.1b Distribution of gorilla gestures (continued). Total gestures at BZB=696.

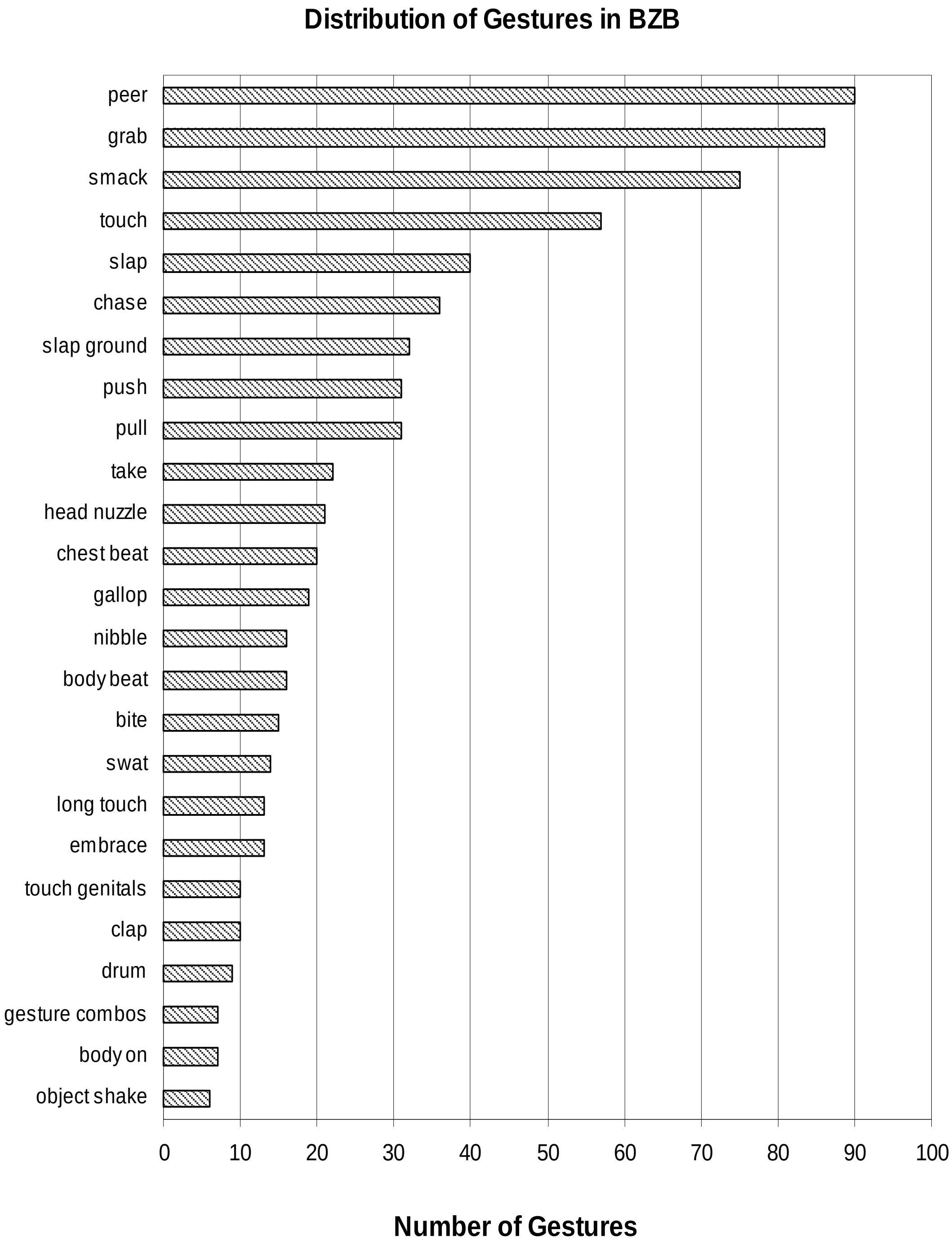
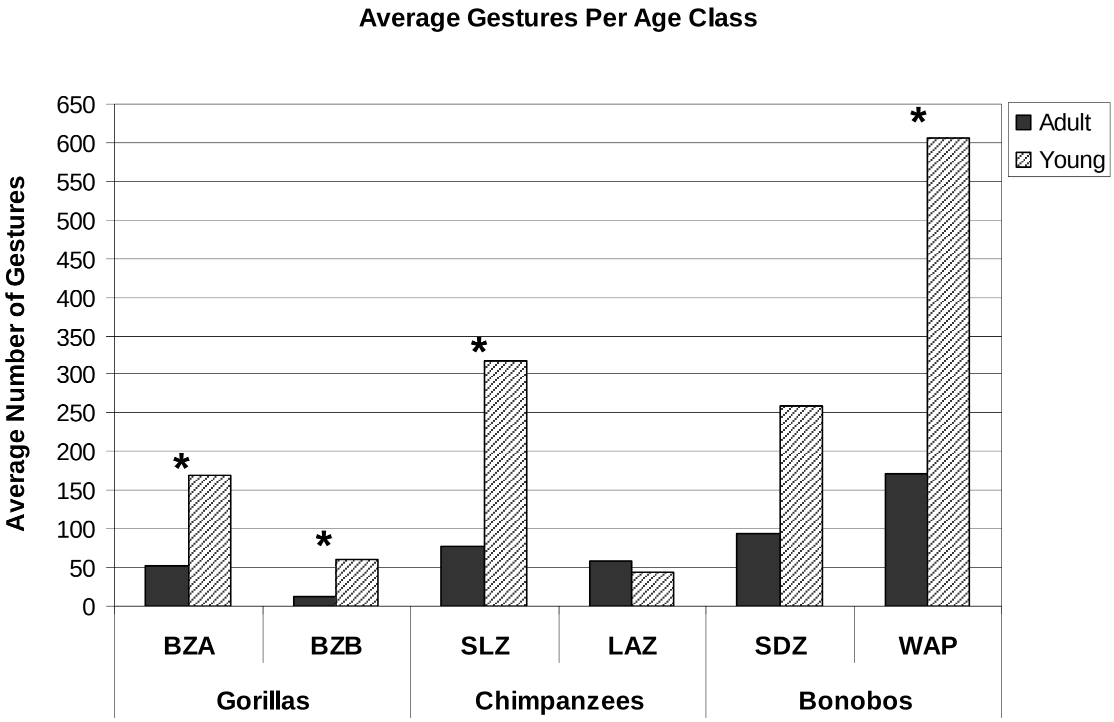
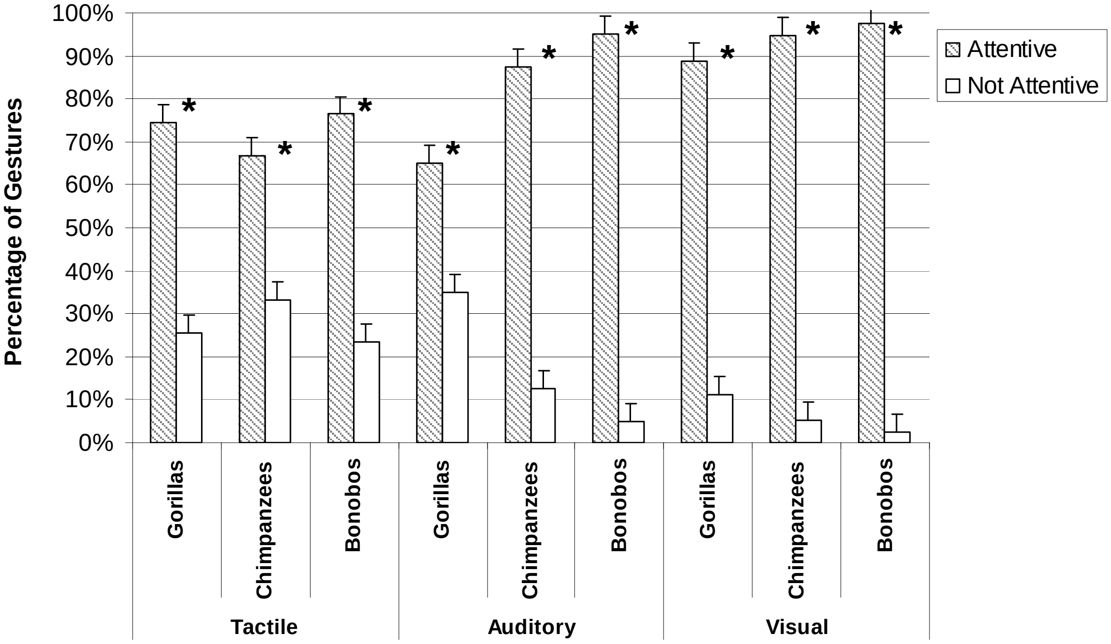


Figure 3.2 Average number of gestures produced by age-class. Young=Individuals ≤8 years old; Adult=Individuals ≥9 years old. Four females in BZB were included in both age-classes.



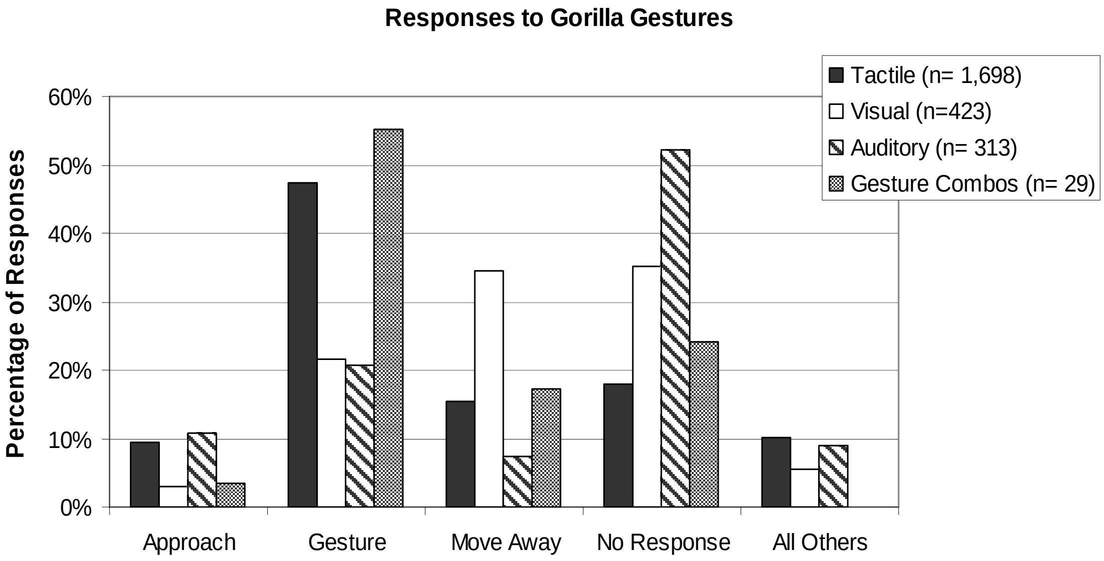
* p<0.05
BZA: Adult n=5, Young n=8; BZB: Adult n=6, Young n=10.
SLZ: Adult n=9, Young n=2; LAZ: Adult n=10, Young n=3.
SDZ: Adult n=5, Young n=3; WAP: Adult n=6, Young n=10.

Figure 3.3 Audience effects by species and signal type. Groups are combined for each species. Attentive=Direct eye contact or head oriented <90° toward actor; Not Attentive=Head oriented 90° or more away from actor.



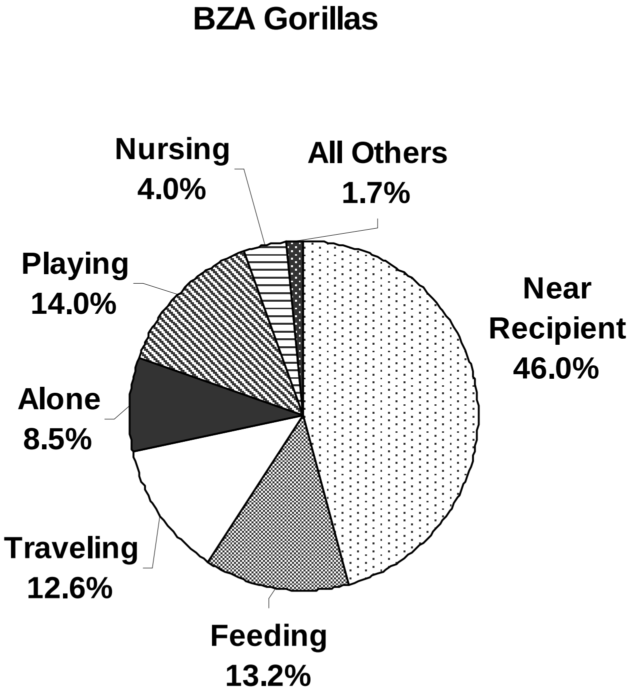
* $p<0.05$

Figure 3.4 Recipient responses to gorilla gestures. *All Others*=All responses that occurred <10% after a gesture was produced.



Total Responses: *Approach*=207, *Gesture*=977, *Move Away*=433, *No Response*=623, *All Others*=223.

Figure 3.5 Social contexts in which gestures were used most frequently in gorillas. The social contexts prior to gesture production. *All Others*=Social contexts in which gestures occurred less than 3%.



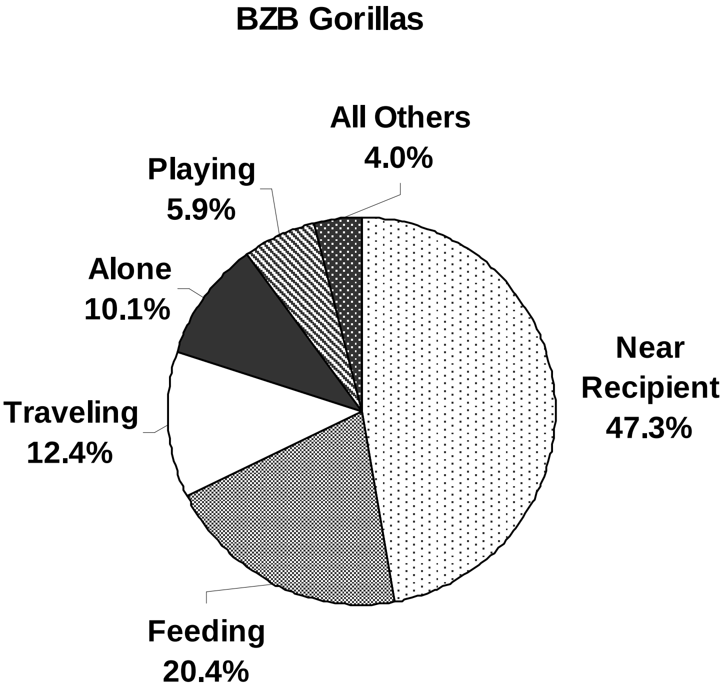


Figure 3.6 Social contexts following gorilla gestures. The social context that occurred after each signal type was produced for both groups. *All Others*=Contexts that followed gestures <5% of the total number of gestures.

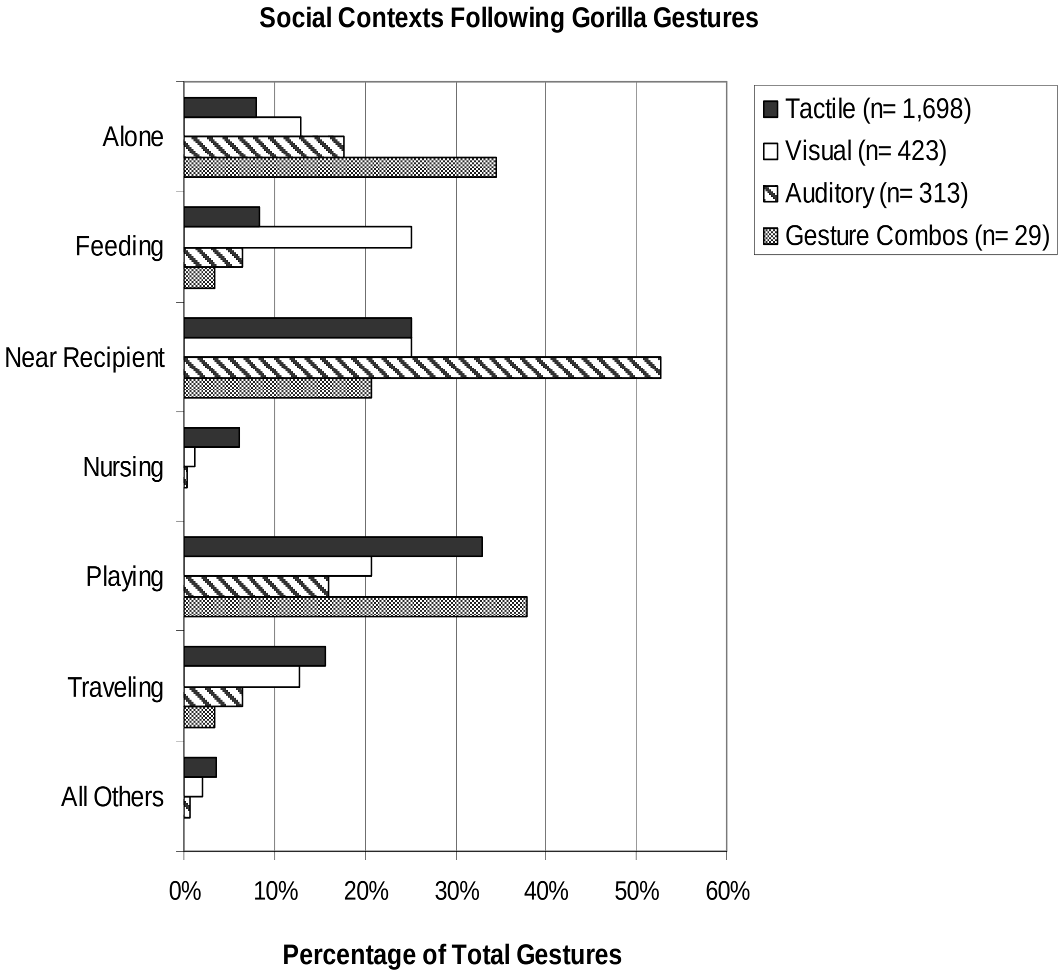


Figure 3.7a Distribution of chimpanzee gestures. Definitions of all gestures are in Table 3.1. *Gesture combos*=When two or more gestures were used in quick (<2 s) succession. Total gestures at SLZ=1,336.

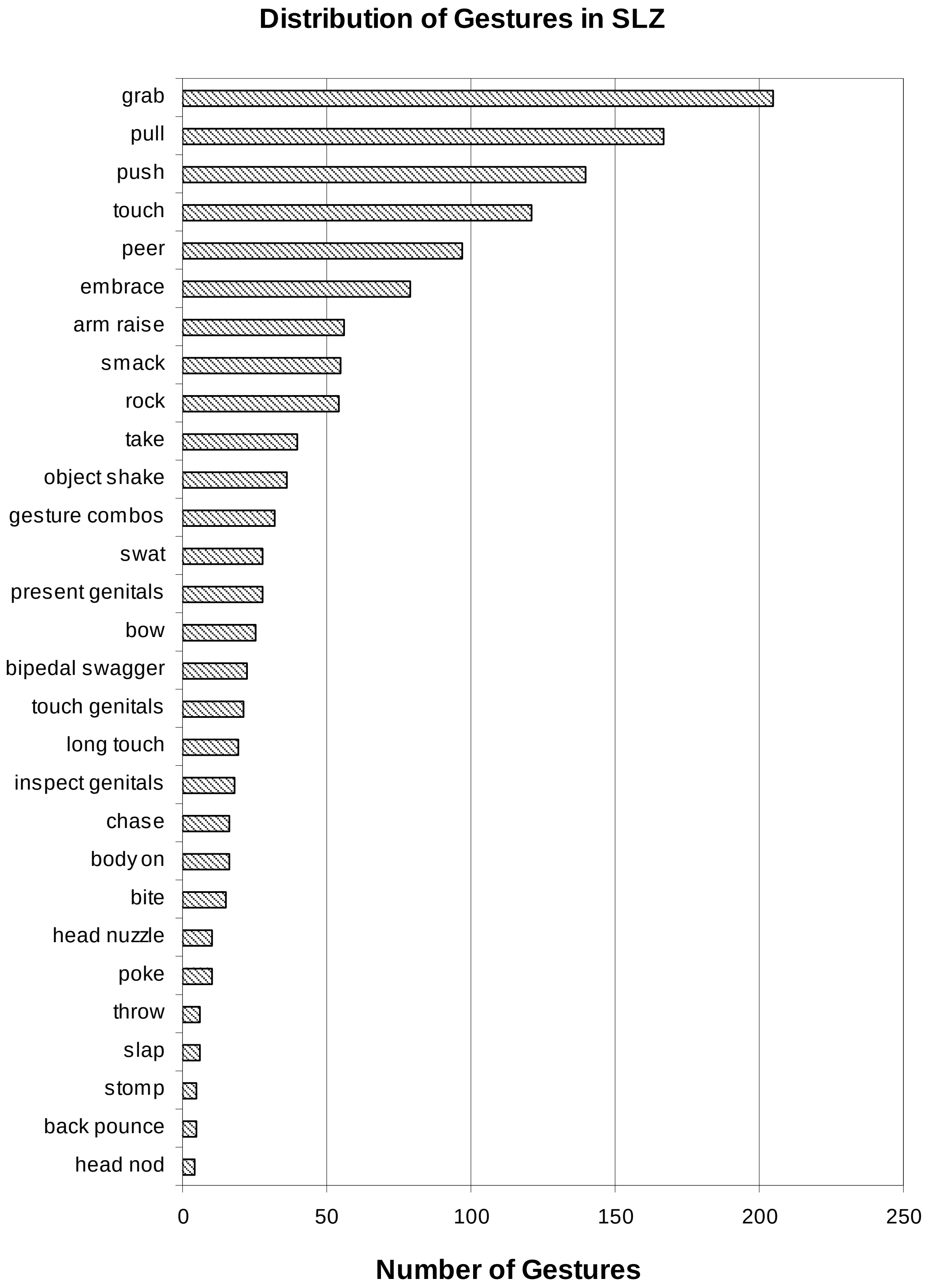


Figure 3.7b Distribution of chimpanzee gestures (continued). Total gestures at LAZ=705.

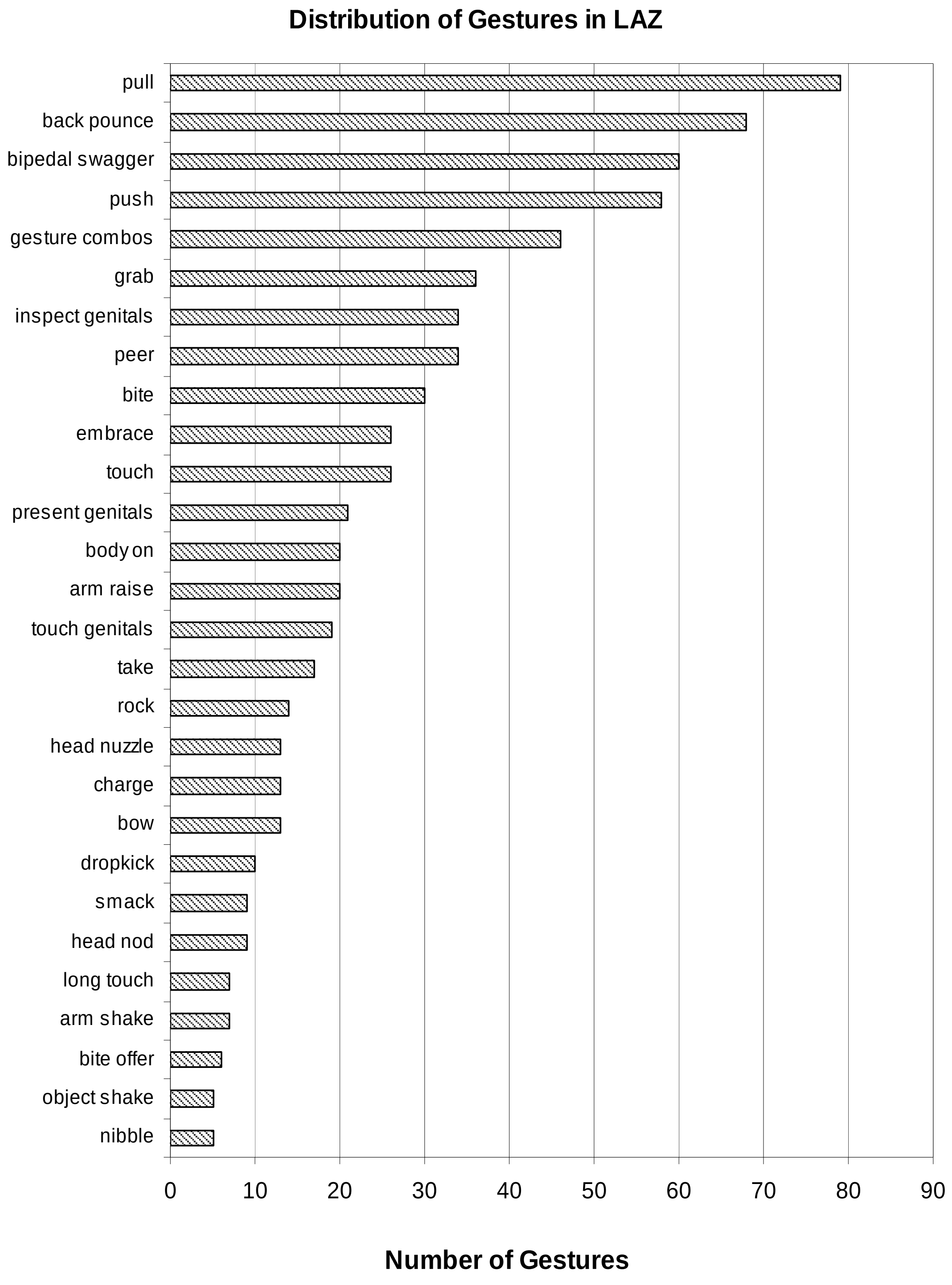
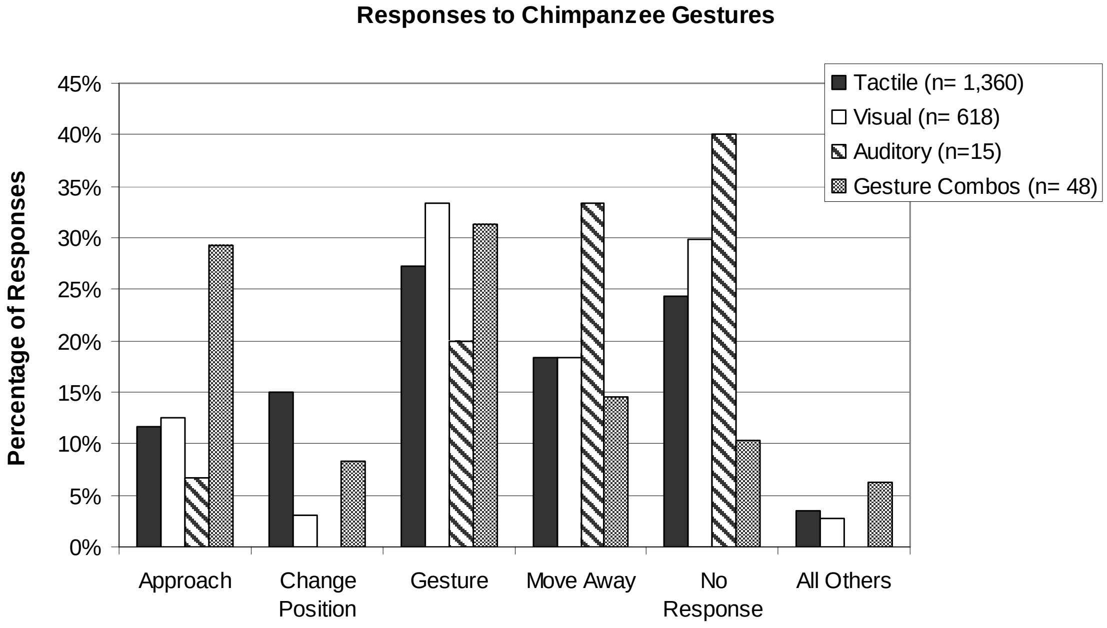
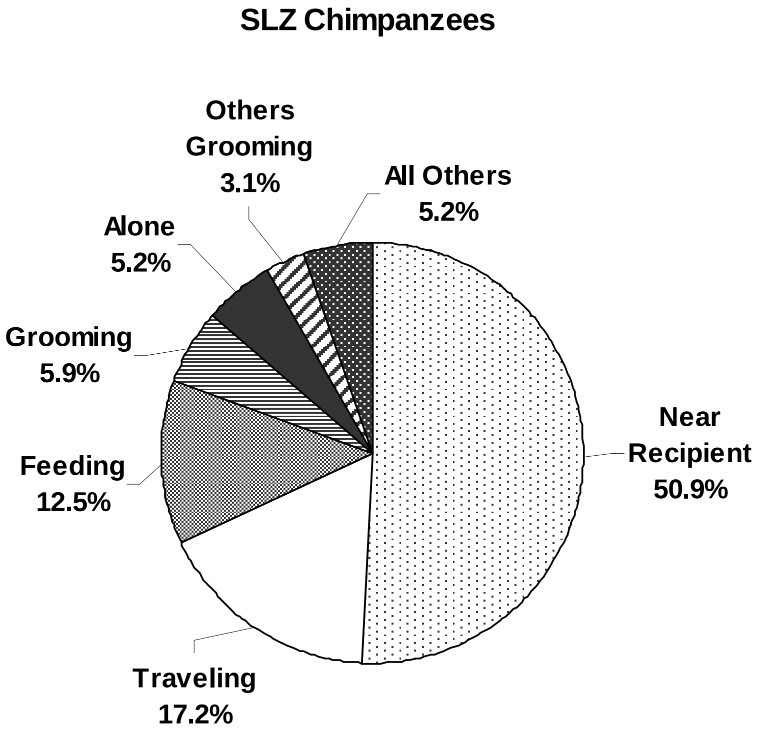


Figure 3.8 Recipient responses to chimpanzee gestures. *All Others*=All responses that occurred in <10% after a gesture was produced.



Total Responses: *Approach*=251, *Change Position*=227, *Gesture*=594, *Move Away*=375, *No Response*=527, *All Others*=67.

Figure 3.9 Social contexts in which gestures were used most frequently in chimpanzees. *All Others*=Social contexts in which gestures occurred less than 3%.



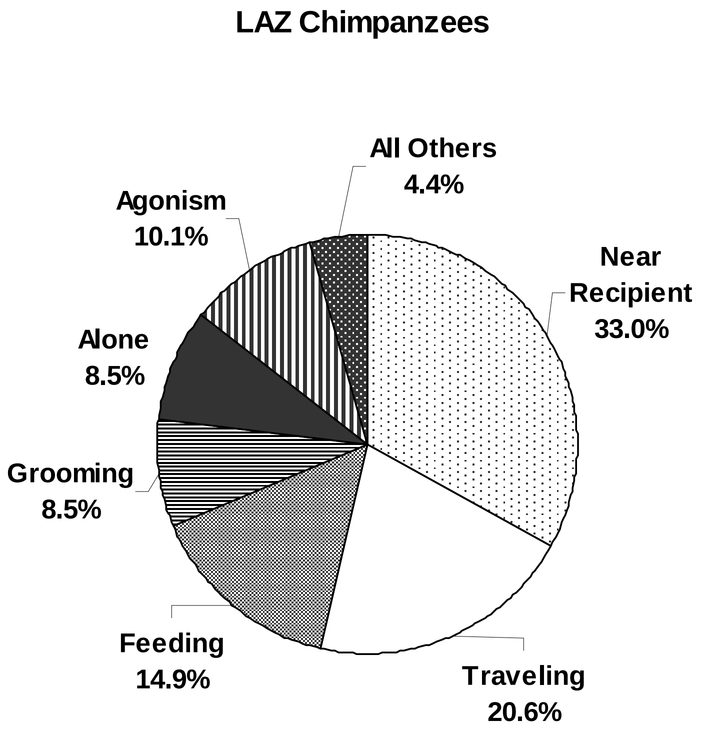


Figure 3.10 Social contexts following chimpanzee gestures. The social context that occurred after each signal type was produced for both groups. *All Others*=Contexts that followed gestures <5% of the total number of gestures.

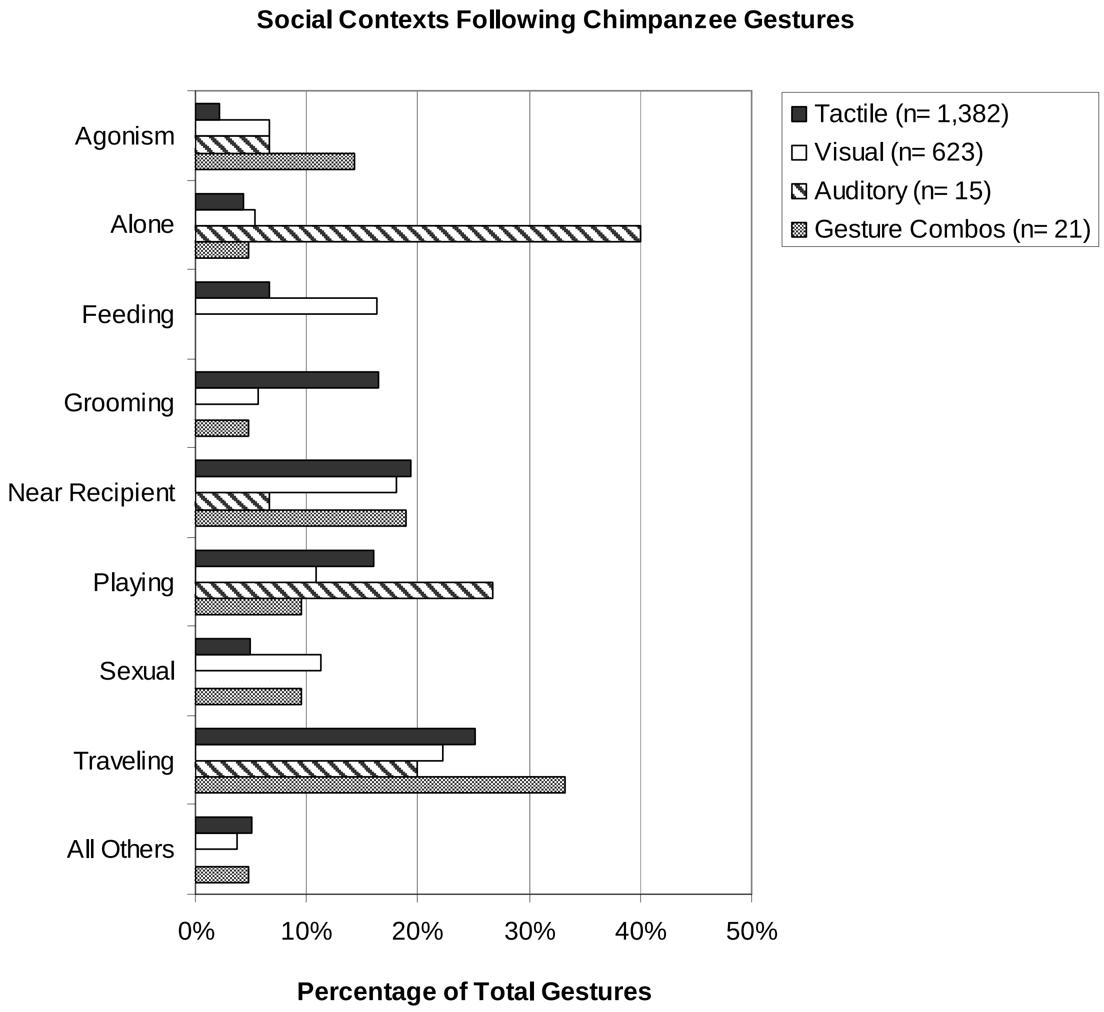


Figure 3.11a Distribution of bonobo gestures. Definitions of all gestures are in Table 3.1. *Gesture combos*=When two or more gestures were used in quick (<2 s) succession. Total gestures from SDZ=1,249.

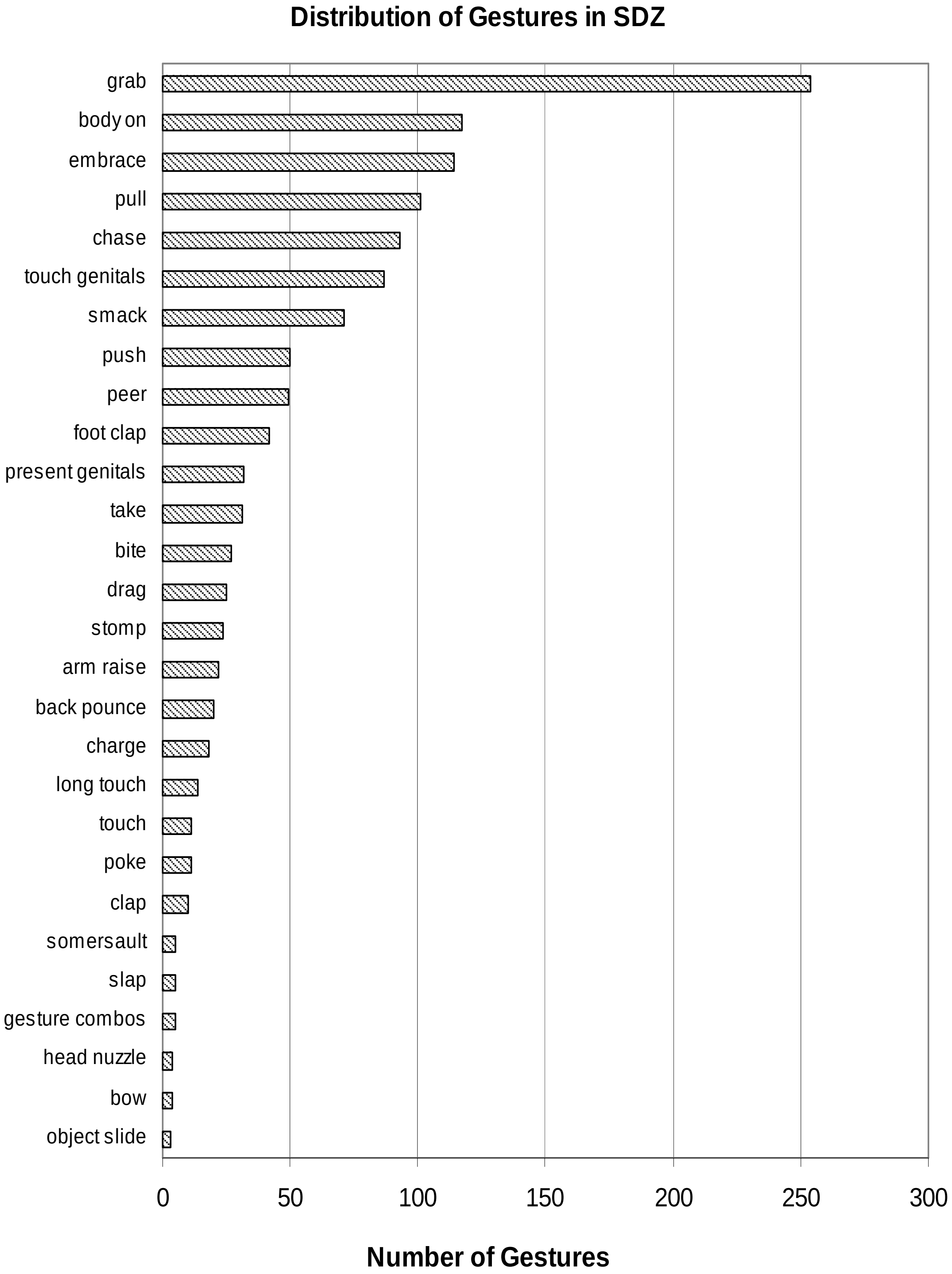


Figure 3.11b Distribution of bonobo gestures (continued). Total gestures from WAP=2,237.

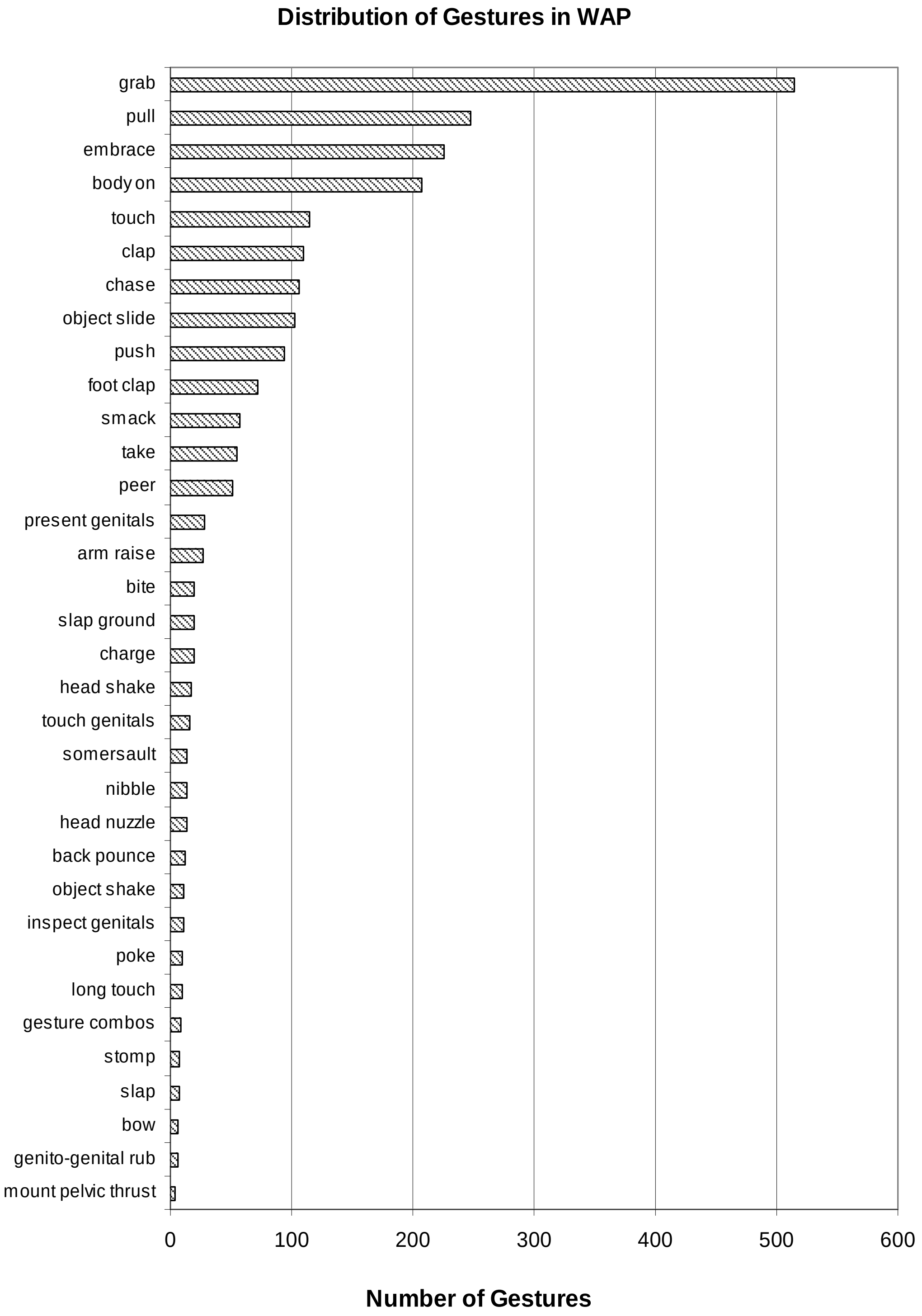
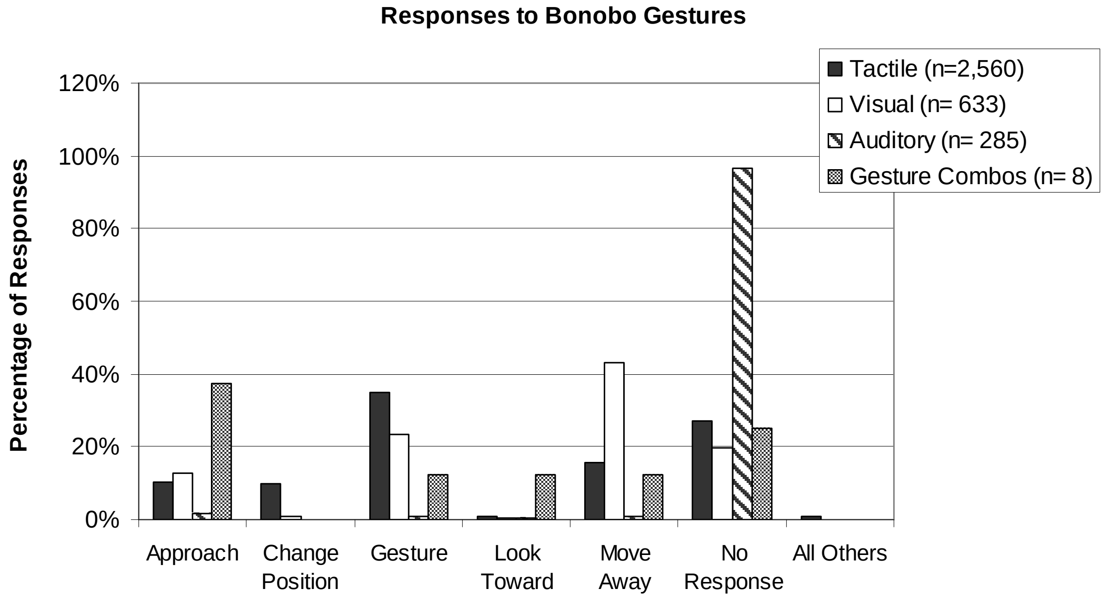
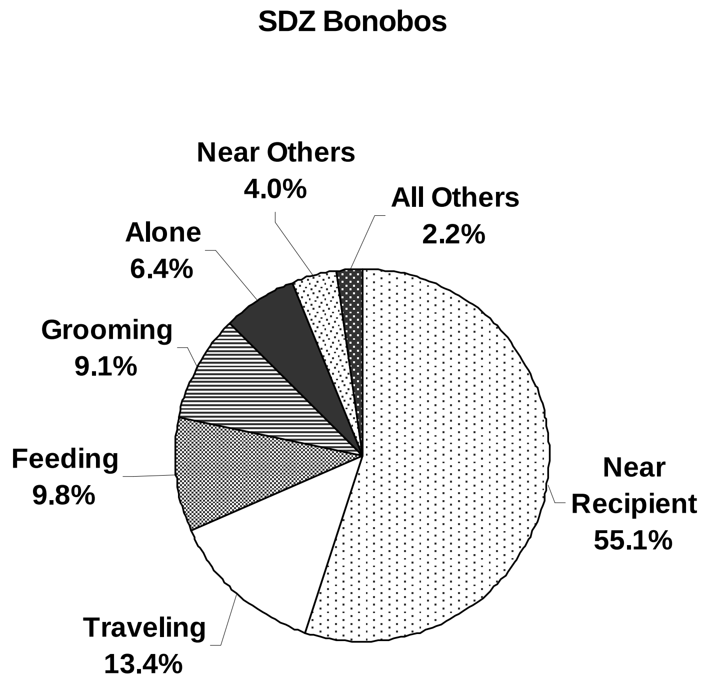


Figure 3.12 Recipient responses to bonobo gestures. *All Others*=All responses that occurred in <10% after a gesture was produced.



Total Responses: *Approach*=355, *Change Position*=261, *Gesture*=1,042, *Look Toward*=24, *Move Away*=680, *No Response*=1,099, *All Others*=25.

Figure 3.13 Social contexts in which gestures were used most frequently for bonobos. *All Others*=Social contexts in which gestures occurred less than 3%.


SDZ Bonobos

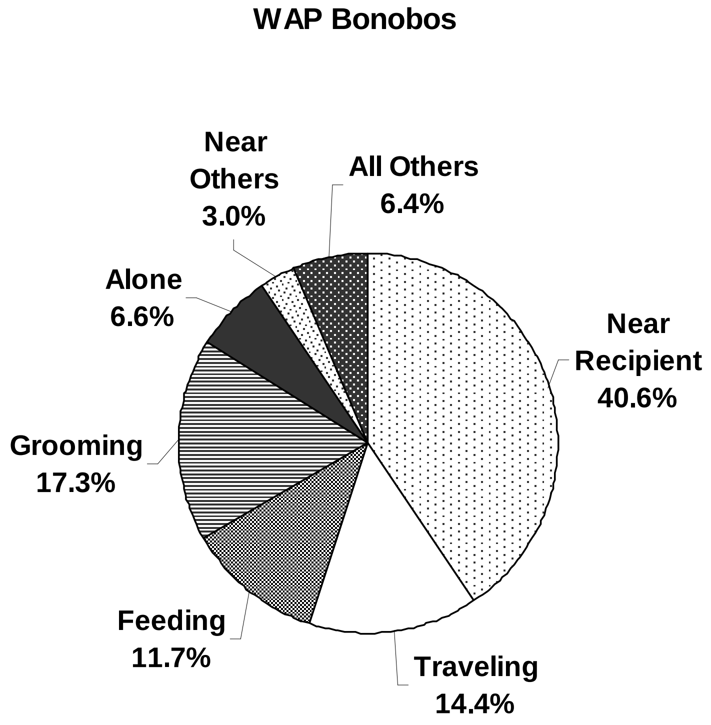
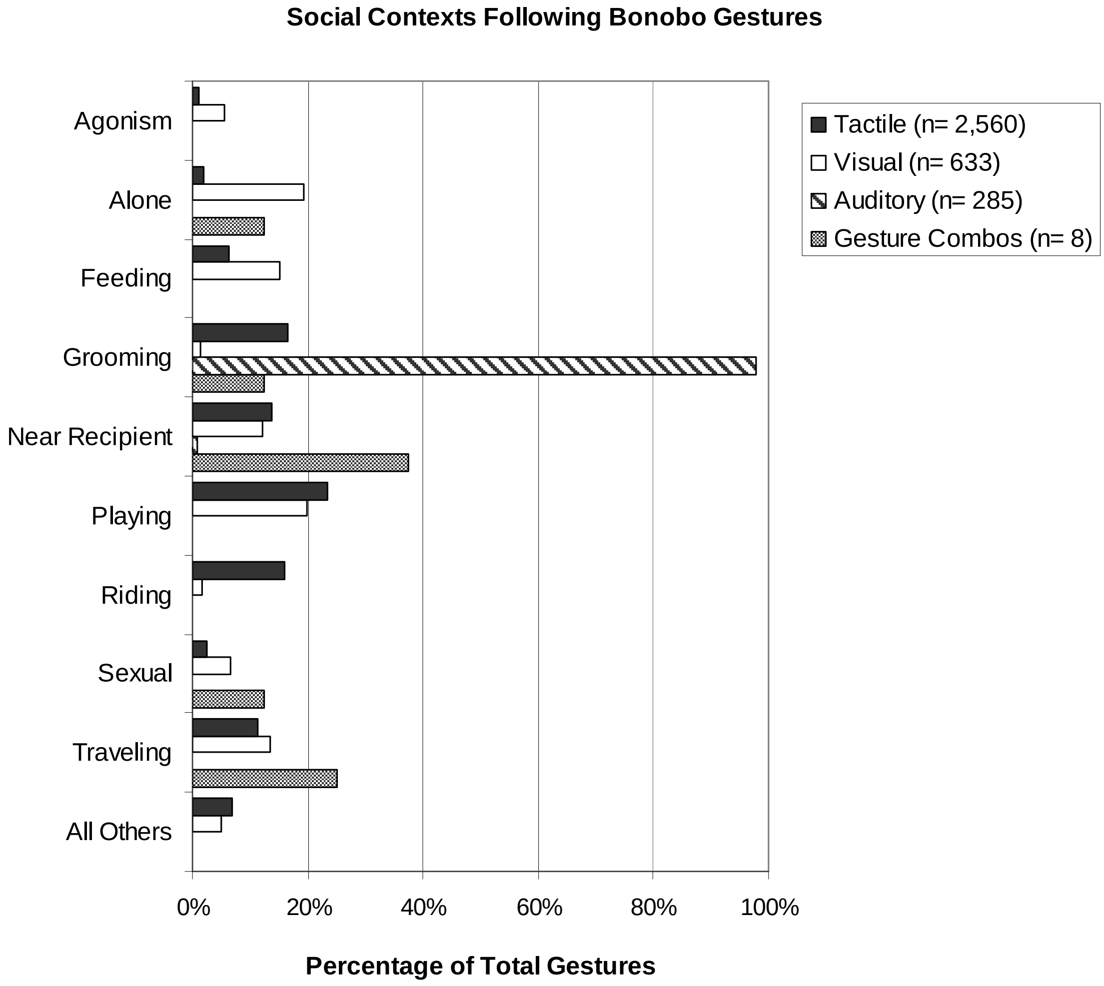

WAP Bonobos

Figure 3.14 Social contexts following bonobo gestures. The social context that occurred after each signal type was produced for both groups. *All Others*=Contexts that followed gestures <5% of the total number of gestures.



CHAPTER 4

EFFECTS OF POSITIONAL BEHAVIOR ON GESTURAL SIGNALING

4.1 Introduction

The second research question I investigated was: How does positional behavior (postures and modes of locomotion) vary across African apes and are the ways these species communicate with manual gestures reflected in these differences? To explore the relationship between gestural signaling and positional behavior, I examined the proportions of time spent in various positional behaviors, the frequencies of these behaviors, and the degree of arboreality versus terrestriality. Then, I examined the particular posture or mode of locomotion actors used at the time of gesturing to determine whether upper limb availability influenced gestural signaling. In this chapter, I present the results of these analyses by species.

In total, I collected 317 hours of 15-minute focal sample video from which I continuously coded all positional behaviors. I collected 113 hours of video data from Bronx Zoo (BZ) gorillas: 56 hours from BZA (an average of 5.6 hrs per individual) and 57 hours from BZB (an average of 5.8 hrs per individual). I collected 146 hours of video data from chimpanzees: 61 hours from SLZ (an average of 5.5 hrs per individual) and 85 hours from LAZ (an average of 6.5 hrs per individual). Finally, I collected 58 hours of video data from bonobos: 27 hours for SDZ (an average of 3.3 hrs per individual) and 31 hours for WAP (an average of 3.9 hrs per individual). The different positional behaviors recorded in this study for each group are listed in Table 4.1. Definitions for these behaviors can be found in the positional behavior ethogram in Chapter 2 (Table 2.3).

4.2 Effects of Positional Behavior on Gorilla Gestural Signaling

4.2.1 Gorilla Locomotor Profile

To understand how positional behavior may influence gestural signaling in gorillas, I recorded postures and modes of locomotion used by all members of both gorilla groups. This enabled me to establish an overall locomotor profile for gorillas. Both gorilla groups used remarkably similar positional behaviors in similar proportions, therefore, I present results with the groups combined. In both groups, there were age-class differences in the proportions of time spent in various postures and modes of locomotion, so data are presented separately for adults and young gorillas.

In both groups, all gorillas engaged in postural behaviors more than locomotor behaviors (n=5,658 min in postural behaviors, n=634 min in locomotor behaviors). Overall, gorillas spent 59.0% of their time *sitting*, 20.1% *lying*, 8.9% *quadrupedal standing*, 1.3% *crouching*, and 1.2% *climbing*. All other positional behaviors made up less than 1% of the total focal sampling time.

When time was divided by postures and locomotion, the three most prominent postures for gorillas of all age/sex-classes were *sitting*, *lying*, and *quadrupedal standing* (Figure 4.1). Young gorillas also incorporated *crouching* and *bipedal standing* into their repertoires, which were common postures during play (Figure 4.1). When I examined the total counts of each posture rather than the total durations of each, these three behaviors remained the most used postural behaviors, but *quadrupedal standing* was used slightly more frequently than *sitting* (*quadrupedal standing*: n=2,725 counts or 39.5%; *sitting*: n=2,520 counts or 36.5% of 6,906 posture counts).

The two most prominent modes of locomotion for gorillas were *quadrupedal walking* (*i.e.,* knuckle-walking) and *climbing*, though they were used in differing proportions by adults and young (Figure 4.2). Young gorillas relied less on *quadrupedal walking*, and they also incorporated more *quadrupedal running* and *bipedal walking* into to their locomotor repertoires than adults. When I examined the total counts of each mode of locomotion, these three behaviors remained the most used locomotor behaviors (BZ combined: For *quadrupedal walking*, n=4,153 counts or 76.7% of 5,412 locomotion counts; for *climbing*, n=548 counts or 10.1%). In both groups, young gorillas were *climbing* much more frequently than adults: In BZA, young gorillas were responsible for 74.0% (n=230 counts) and adult gorillas were responsible for 26.0% (n=81 counts) of total *climbing* counts. In BZB, young gorillas were responsible for 83.5% (n=198 counts) and adult gorillas were responsible for 16.5% (n=39 counts) of total *climbing* counts.

4.2.2 Arboreality versus Terrestriality

To establish a complete picture of gorilla locomotor profiles for these study groups, I also examined the proportions of time spent arboreally and terrestrially, as well as what positional behaviors were employed while on arboreal and terrestrial substrates. The proportions of time spent on arboreal and terrestrial substrates for both groups were very similar, with substantially more time spent terrestrially than arboreally. BZA gorillas were arboreal for 18.3% (n=565 min) of their focal time and terrestrial for 81.7% (n=2,518 min) of their total 3,083 min of focal sampling time. BZB gorillas were arboreal for 14.1% (n=452 min) of their focal time and terrestrial for 85.9% (n=2,756 min) of their total 3,208 min of focal sampling time. However, within each group, there were age-class differences in arboreality and terrestriality

(Table 4.2). In both groups, young individuals were significantly more arboreal than terrestrial (χ^2=40.960, p<0.0001, df=1 for BZA and BZB), as were adults (χ^2=38.440, p<0.0001, df=1 for BZA adults and χ^2=60.840, p<0.0001, df=1 for BZB adults). When the adult male was removed from BZA data, the adult females in BZA were significantly more arboreal than adult females in BZB (average arboreal counts for BZA adult females=50.8, average arboreal counts for BZA adult females=23.8; χ^2=9.720, p<0.002, df=1). The silverback (in BZA) was arboreal for a total of 1 min 30 sec (12 of 314 total counts).

Figure 4.3 shows the percentage of time gorillas spent in various postures when they were arboreal compared to when they were terrestrial. BZA and BZB are combined because they demonstrated clear similarities in the proportion of time devoted to the different positional behaviors. Gorillas relied on the same postures whether they were arboreal or terrestrial (Figure 4.3). The posture that was used in the highest percentage of time was *sitting* (66.0%, n=616 min when arboreal; 64.9%, n=1782 min when terrestrial), followed by *lying* (28.1%, n=262 min when arboreal; 23.3%, n=640 min when terrestrial). *Quadrupedal standing*, *hanging*, and *crouching* were also used in smaller percentages on arboreal and terrestrial substrates. *Climbing* was the main mode of locomotion used by gorillas when on arboreal substrates (74.5%, n=64 min), but gorillas engaged mostly in *quadrupedal walking* when in terrestrial locomotion (89.4%, n=490 min; Figure 4.4). *Sliding* was used only by BZA gorillas while coming down a smooth arboreal substrate, particularly the Tree Bridge (2.1%, n=2 min).

4.2.3 Positional Behavior While Gesturing

All gestures were categorized by those that required at least one upper limb, both upper limbs, or no upper limbs to determine if positional behavior influenced the use of certain manual gestures (Table 4.3). I predicted that gorillas would be *sitting* more often than the other species, and therefore they would take advantage of the availability of their upper limbs to gesture more frequently with them. Gestures were indeed produced most often by gorillas when they were *sitting* (25.6%, n=630 gestures), followed by *quadrupedal standing* (14.1%, n=347 gestures), *quadrupedal running* (12.6%, n=310 gestures), *bipedal standing* (12.4%, n=305 gestures), *quadrupedal walking* (11.9%, n=294 gestures), *lying* (6.6%, n=163 gestures), and *crouching* (5.7%, n=141 gestures; Figure 4.5). Gorillas gestured in all other positional behaviors less than 5.0% of the cases in which gestures were produced. Gorillas also used gestures that required the use of one or both upper limbs in high frequencies (Table 4.3): The five most frequent gestures used by BZA gorillas were *grab*, *touch*, *push*, *smack*, and *chest beat*; the five most frequent gestures used by BZB gorillas were *peer*, *grab*, *smack, touch*, and *slap*. All of these gestures except *peer* also required the use of at least one limb. Gorillas gestured frequently in positional behaviors that were used less than 1.0% of their total focal sampling time (*e.g., quadrupedal running*, *bipedal standing*, and *quadrupedal walking*). An example of a frequent gesture used in an infrequent positional behavior is the characteristic gorilla gesture, *chest beat*. This gesture was used 112 times and 74.1% (n=83) of those times, the actor was in some form of bipedal posture or locomotion. Only in 22.3% (n=25) of the times when gorillas used the *chest beat* gesture were the actors *sitting*.

Interestingly, gorillas also gestured frequently in positional behaviors in which no upper limbs were free to gesture (*e.g.*, when *quadrupedal running* or *quadrupedal walking;* Figure 4.5). In these cases, the locomotion was actually part of the gesture itself. Several gestures, by definition, involved a locomotor or postural component. For example, *gallop* required *quadrupedal* or *bipedal running*, and *slap* requires *quadrupedal running* toward a recipient from >2 m. The most frequent gestures used when gorillas were *bipedal running* were *slap* (25.5%) and *gallop* (14.9% of 47 total gestures), and both of these gestures required the use of at least one upper limb. The most frequently used bipedal positional behavior was *bipedal standing* (BZA n=162 counts, BZB n=90 counts), followed by *bipedal walking* (BZA n=93 counts, BZB n=83 counts); however, the average duration of a bipedal bout (posture or locomotion) for both BZA and BZB was only 6 seconds. Both gorilla groups also used bipedal locomotion while carrying objects (*bipedal walking full*): BZA n=27 counts, BZB n=37 counts).

4.3 Effects of Positional Behavior on Chimpanzee Gestural Signaling

4.3.1 Chimpanzee Locomotor Profile

To understand how positional behavior may influence gestural signaling in chimpanzees, I recorded postures and modes of locomotion used by all members of both chimpanzee groups. This enabled me to establish an overall locomotor profile for chimpanzees. Both chimpanzee groups used similar positional behaviors in similar proportions, therefore I present results with the groups combined. As in gorillas, there were age-class differences in the proportions of time spent in various postures and modes of locomotion, so data are presented separately for adults and young chimpanzees.

In both groups, all chimpanzees engaged in postural behaviors more than locomotor behaviors (n=7,552 min in postural behaviors, n=724 min in locomotor behaviors). Overall, chimpanzees spent 58.9% of their time *sitting*, 29.9% *lying*, 7.4% *quadrupedal walking*, and 2.5% *quadrupedal standing*. All other positional behaviors made up less than 1.0% of the total focal sampling time. When time was divided by postures and locomotion, the three most prominent postures for chimpanzees were *sitting*, *lying*, and *quadrupedal standing*, just as in gorillas (Figure 4.6). When I examined the frequency of each posture, these three behaviors remained the most used postural behaviors, but *quadrupedal standing* was used more frequently than *lying* by LAZ chimpanzees (for *quadrupedal standing*: n=668 counts or 28.7% of 2,328 LAZ posture counts; for *lying*: n=394 counts or 16.9%).

While the proportions of time spent in certain postures were similar in both young and adult chimpanzees, the two age-classes varied in the modes of locomotion each used (Figure 4.7). The most prominent modes of locomotion for adult chimpanzees in both groups were *quadrupedal walking*, *climbing*, and *bipedal walking*. The most prominent modes of locomotion for young chimpanzees in both groups were *quadrupedal walking*, *climbing*, *quadrupedal running*, and *brachiating* (Figure 4.7), though the two groups varied in the proportion of time spent in each. When young chimpanzees in SLZ were in locomotion, they devoted 30.6% (n=20 min) of their time to *climbing*, while LAZ young individuals only devoted 7.6% (n=6 min) of their time *climbing*. Young chimpanzees in SLZ engaged in *brachiating* 4.7% (n=3 min) of their time spent in locomotion, while young chimpanzees in LAZ only spent 0.2% (n=8 sec) of their time in locomotion *brachiating*. When I examined the total counts of each mode of locomotion in addition to the time spent in each mode of locomotion, the top three behaviors remained the most used locomotor behaviors but *bipedal walking* was used more frequently than *brachiating* in both groups (for *bipedal walking*: n=97 counts or 2.0% of 4,831 total locomotion counts; for *brachiating*: n=48 counts or 1.0%). Counts of *bipedal walking* included *bipedal walking full* (carrying an object) and *bipedal swaggering*.

4.3.2 Arboreality versus Terrestriality

To establish a complete picture of chimpanzee locomotor profiles for these study groups, I also examined the proportions of time spent arboreally and terrestrially, as well as what positional behaviors were employed while on arboreal and terrestrial substrates. SLZ chimpanzees spent a much greater proportion of their time arboreal than LAZ chimpanzees. In fact, SLZ chimpanzees spent the greatest proportion of time arboreal out of all study groups. SLZ chimpanzees were arboreal for 20.3% (n=744 min) of their focal time and terrestrial for 79.7% (n=2,916 min) of their total 3,659 min of focal sampling time. LAZ chimpanzees were arboreal for 4.6% (n=212 min) of their focal time and terrestrial for 95.4% (n=4,405 min) of their total 4,617 min of focal sampling time. The higher proportion of time spent arboreal in SLZ was due, in part, to the increased arboreality of young individuals in the group.

When examined by age-class, young individuals were significantly more arboreal than terrestrial in both groups (Table 4.4): $\chi^2=9.000$, $p<0.0027$, df=1 for SLZ young and $\chi^2=60.840$, $p<0.0001$, df=1 for LAZ young. Young chimpanzees in SLZ (n=2) were the most arboreal of any age-class from any group (34.9%, n=231 min). Adults in both groups were also significantly more arboreal (Table 4.4):

$\chi^2=43.560$, $p<0.0001$, df=1 for SLZ adults and $\chi^2=92.160$, $p<0.0001$, df=1 for LAZ adults.

Figure 4.8 shows the percentage of time chimpanzees spent in various postures when they were arboreal as compared to when they were terrestrial. SLZ and LAZ are combined because they demonstrated clear similarities in the percentages of time devoted to the different positional behaviors. Both groups relied on the same postures whether they were arboreal or terrestrial (Figure 4.8). The posture that was used in the largest percentage of time whether chimpanzees were arboreal or terrestrial was *sitting* (63.0%, n=562 min when arboreal; 64.7%, n=4,310 min when terrestrial) followed by *lying* (33.3%, n=297 min when arboreal; 31.8%, n=2,119 min when terrestrial). *Quadrupedal standing* and *hanging* were also used in smaller percentages on arboreal and terrestrial substrates (Figure 4.8).

Chimpanzee groups were similar in terms of the postures they used when arboreal and terrestrial, but there was group variation with regard to arboreal locomotion. Thus, data from SLZ and LAZ are presented separately in Figure 4.9. Chimpanzees at SLZ relied heavily on *climbing* (86.4%, n=48 min) when in arboreal locomotion, while chimpanzees at LAZ only used *climbing* 60.8% (n=5 min) of the time when in arboreal locomotion. LAZ chimpanzees used more *quadrupedal walking* when on arboreal substrates than SLZ chimpanzees (LAZ: 35.1%, n=3 min; SLZ: 5.8%, n=3 min), and SLZ chimpanzees used more *brachiating* than LAZ chimpanzees (SLZ: 6.9%, n=4 min, LAZ=1.6%, n=1 min). Chimpanzee groups were more similar in terms of terrestrial locomotion. Both groups used *quadrupedal walking* the majority of the time (SLZ: 91.7%, n=301 min; LAZ: 91.8%, n=305 min), and both groups engaged in *climbing*, *bipedal walking*, and *quadrupedal running* to smaller degrees as well (Figure 4.9).

4.3.3 Positional Behavior While Gesturing

All gestures were categorized by those that required at least one upper limb, both upper limbs, or no upper limbs to determine if positional behavior influenced the use of certain gestures (Table 4.3). I predicted that chimpanzees would be engaged in locomotion more often than the other species, and therefore their upper limbs would not be as free to gesture. Thus, chimpanzees were expected to use fewer gestures involving the upper limbs. However, this prediction was not supported. The five most frequent gestures used by SLZ chimpanzees were almost identical to those used by gorillas: *Grab*, *pull*, *push*, *touch*, and *peer*. All of these gestures except *peer* required the use of at least one limb. The five most frequent gestures used by LAZ chimpanzees were *pull*, *back pounce*, *bipedal swagger*, *push*, and *gesture combos* (multiple gestures used simultaneously). All of these gestures required the use of one or both upper limbs, particularly *bipedal swagger*.

Figure 4.10 shows the most frequent positional behaviors used by chimpanzees during gestural signaling: Chimpanzees gestured most often when they were *sitting* (35.5%), followed by *quadrupedal standing* (17.0%), *bipedal walking* (10.7%), *quadrupedal walking* (10.5%), and *lying* (5.5%). *Bipedal walking* included *bipedal walking full* and *bipedal swaggering*. Chimpanzees gestured in all other positional behaviors less than 5.0% of the cases in which gestures were produced. Chimpanzees exhibited a pattern similar to that of gorillas, with one key exception: The higher frequency of gesturing while *bipedal walking*. Interestingly, chimpanzees were not always gesturing with their upper limbs while *bipedal walking*. Rather, the bipedal locomotion itself doubled as a gesture. A characteristic chimpanzee gesture is *bipedal swagger*, in which chimpanzees (generally adult males) use bipedal locomotion as part of a dominance display. *Bipedal swagger* accounted for 74.3% of the gestures produced while *bipedal walking*. During *bipedal swagger*, the upper limbs were either waved back and forth or used to shake or throw objects.

4.4 Effects of Positional Behavior on Bonobo Gestural Signaling

4.4.1 Bonobo Locomotor Profile

To understand how positional behavior may influence gestural signaling in bonobos, I recorded postures and modes of locomotion used by all members of both bonobo groups. In both groups, all bonobos engaged in postural behaviors more than locomotor behaviors (n=2,812 min in postural behaviors, n=473 min in locomotor behaviors). Overall, bonobos spent 39.0% of their time *sitting*, 37.6% *lying*, 11.6% *quadrupedal walking*, 5.1% *quadrupedal standing,* 2.0% *crouching*, 1.3% *climbing*, and 1.1% *riding* on others (for young only). All other positional behaviors made up less than 1.0% of the total focal sampling time. As with gorillas and chimpanzees, when time was divided by postures and locomotion, the most prominent postures for bonobos were *sitting*, *lying*, and *quadrupedal standing*, though in different proportions in each age-class (see Figure 4.11 for adults and Figure 4.12 for young). When I examined the frequency of each posture, these three behaviors remained the most used postural behaviors, but *quadrupedal standing* was used more frequently than *lying* by WAP bonobos (WAP: For *quadrupedal standing*: n=958 counts or 31.2%; for *lying*: n=710 counts or 23.1% of 3,068 posture counts; SDZ: For *quadrupedal standing*: n=426 counts or 18.7%; for *lying*: n=556 counts or 24.4 % of 2,275 posture counts). In general, WAP bonobos used a wider variety of postural behaviors than SDZ bonobos, particularly among young individuals. Young WAP bonobos relied less on *sitting* and *lying* and more on other postures such as *quadrupedal standing*, *bipedal standing*, and *hanging* than young bonobos in SDZ (Figure 4.12).

Because bonobos at SDZ and WAP varied in the proportions of time spent in various forms of locomotion (across groups and across age-classes), I present data for them separately. The most prominent modes of locomotion for both groups were *quadrupedal walking*, *climbing*, and *quadrupedal running* though in differing proportions across age-classes (see Figure 4.13 for adults and Figure 4.14 for young). In general, bonobos at SDZ were *climbing* more than WAP bonobos: Adult WAP bonobos used *climbing* 1.6% (n=3 min) of their total time in locomotion, while adult SDZ bonobos used *climbing* 9.9% (n=10 min) of their total time in locomotion (Figure 4.13). This difference was even greater in young bonobos: Young WAP bonobos spent 10.3% (n=10 min) of their total time in locomotion *climbing*, while young SDZ bonobos were *climbing* 24.7% (n=20 min) of their total time in locomotion (Figure 4.14). An increase in arboreal locomotion was also apparent when I examined the total counts of each mode of locomotion in addition to the time spent in each. The top three behaviors remained the most used locomotor behaviors, but *climbing* and *brachiating* were used more frequently by SDZ bonobos (for *climbing*: n=385 counts or 20.3%; for *brachiating*: n=72 counts or 3.8 % of 1,895 total locomotion counts) than WAP bonobos (for *climbing*: n=128 counts or 5.8%; for *brachiating*: n=6 counts or 0.3% of 2,220 total locomotion counts).

4.4.2 Arboreality versus Terrestriality

To establish a complete picture of bonobo locomotor profiles for these study groups, I also examined the proportions of time spent arboreally and terrestrially, as well as what positional behaviors were employed while on arboreal and terrestrial substrates. Bonobos exhibited less arboreality than gorillas and chimpanzees, and WAP bonobos were especially terrestrial. SDZ bonobos were arboreal for 9.9% (n=146 min) of their focal time and terrestrial for 90.1% (n=1,340 min) of their total 1,486 min of focal sampling time. WAP bonobos were only arboreal for 1.4% (n=25 min) of their focal time and terrestrial for 98.6% (n=1,773 min) of their total 1,798 min of focal sampling time. When examined by age-class (Table 4.5), adults in both groups were significantly more arboreal than terrestrial ($\chi^2=77.440$, $p<0.0001$, df=1 for SDZ adults and $\chi^2=96.040$, $p<0.0001$, df=1 for WAP adults). Adult bonobos in WAP exhibited the least amount of arboreality of any group (0.5%, n=7 min). Young individuals were also significantly more arboreal than terrestrial in both groups (Table 4.5): $\chi^2=38.440$, $p<0.0001$, df=1 for SDZ young and $\chi^2=84.640$, $p<0.0001$, df=1 for WAP young. Adults in both groups were less arboreal than young individuals.

Figure 4.15 shows the percentage of time bonobos spent in various postures when they were arboreal and terrestrial. When arboreal, both groups were *sitting* most of the time when they were not in locomotion (SDZ: 85.3%, n=94 min; WAP: 44.4%, n=7 min). WAP bonobos were also *hanging* for a large percentage of time when they were not in arboreal locomotion (39.0%, n=6 min). When terrestrial, both groups spent large percentages of time *lying* (SDZ: 47.1%, n=561 min; WAP: 45.1% n=672 min) and *sitting* (SDZ: 46.9%, n=560 min; WAP: 41.6% n=621 min) when they were not engaged in locomotion.

Figure 4.16 shows the percentage of time bonobos spent in various modes of locomotion when they were arboreal and terrestrial. Because SDZ and WAP bonobos were markedly different in terms of their positional behaviors, I present the groups separately for these analyses as well. *Climbing* took up the greatest proportion of time for bonobos of both groups when in arboreal locomotion (SDZ: 74.1%, n=27 min; WAP: 88.8% n=8 min). All other arboreal locomotion by WAP bonobos occurred for less than 1 min per locomotor mode. When terrestrial, all bonobos were most often *quadrupedal walking* (SDZ: 87.4%, n=128 min; WAP: 89.3% n=251 min) and *quadrupedal running* (SDZ: 7.6%, n=11 min; WAP: 6.9% n=20 min).

4.4.3 Positional Behavior While Gesturing

All gestures were categorized by those that required at least one upper limb, both upper limbs, or no upper limbs to determine if positional behavior influenced the use of certain gestures (Table 4.3). I predicted that bonobos would be engaged in bipedal postures and locomotion more often than the other species, and therefore they would take advantage of the freedom of their upper limbs to gesture more frequently with them. However, across the three species, bonobos spent the least amount of time bipedal. Figure 4.17 shows the most frequent positional behaviors used by bonobos during gestural signaling. Bonobos gestured most often when they were *lying* (24.0%, n=838 min of 3,486 total gestures), followed by *sitting* (21.6%, n=753 min), *bipedal standing* (11.2%, n=392 min), *crouching* (10.3%, n=360 min), *quadrupedal running* (9.1%, n=318 min), *quadrupedal walking* (6.3%, n=218 min), and *quadrupedal standing* (5.6%, n=195 min). Bonobos gestured in all other positional behaviors less than 5.0% of the cases in which gestures were produced. The five most frequent gestures used by SDZ bonobos were *grab, body on, embrace, pull,* and *chase*. *Grab, embrace,* and *pull* required the use of at least one limb, while *body on* and *chase* did not. The five most frequent gestures used by WAP bonobos were *grab*, *pull*, *embrace, body on*, and *touch*. All of these gestures except *body on* required the use of one or both upper limbs (Table 4.3). The gesture used most frequently (50.4%, n=128) when bonobos were *bipedal standing* was *grab*, and the two infants females were responsible for 95.3% (n=170 gestures) of those gestures. The average duration of a bipedal bout (posture or locomotion) was 6 seconds for SDZ and 5 seconds for WAP.

Like gorillas and chimpanzees, bonobos also used several gestures that had a locomotor component. *Object sliding* was a unique form of locomotion and a unique gesture used by WAP individuals of all age/sex-classes and one adult male in SDZ. It occurred 103 times as a gesture in WAP but only accounted for 43 total seconds of focal video data. *Object sliding* only occurred three times as a gesture in SDZ, but never in focal video data. A similar gesture that also served as a dominance display involving objects was *drag*, which involved quadrupedal running while dragging an object (usually a large branch) behind the individual, and this gesture was used exclusively by adult male bonobos in SDZ. This gesture occurred 24 times and accounted for 95.5% of *quadrupedal running full* counts in adult male focal videos.

4.5 Chapter Summary and Conclusions

I hypothesized that the locomotor profiles of African apes would dictate the availability of the upper limbs for gesturing and the frequency with which gestural communication was employed. Implicit in this hypothesis was the assumption that if upper limbs were not actively involved in locomotion, they would be recruited for communication. However, my results do not support this hypothesis. Rather, these results demonstrate that gestural signaling is not bound by the availability of the upper limbs. Furthermore, gestures and positional behaviors are sometimes one and the same (a concept that I will discuss in greater detail in Chapter 5 section 5.2.2).

All study groups spent more time using postural behaviors than locomotor behaviors, and more time terrestrial than arboreal. All groups also demonstrated clear age-class differences in arboreality and the percentages of time devoted to various positional behaviors. In general, young individuals used a wider array of positional behaviors than adults; this was particularly evident in young SLZ chimpanzees and young SDZ bonobos.

Gorillas expressed a uniform locomotor profile across groups: Young individuals were more arboreal and spent more time involved in locomotion, while adults were predictably more stationary (a finding that was not surprising given their large body sizes). I predicted that gorillas would gesture more because they would spend more time *sitting* than chimpanzees and bonobos. Gorillas did spend a large proportion of time *sitting*, however, it was not significantly more than bonobos or chimpanzees. All species gestured most frequently while *sitting*, which was also the most used positional behavior across all species. Moreover, gorillas did not use more gestures that required the use of the upper limbs than chimpanzees or bonobos (Table 4.3). Young gorillas used more bipedality than adult gorillas, typically while they were playing with other young gorillas. When using gestures that required the use of both hands (such as *chest beat* or *body beat*) gorillas often used a bipedal posture or locomotion rather than gesturing while *sitting*, even though the availability of the upper limbs is the same. Standing erect or moving bipedally was an easy way to make these gestures more apparent to the rest of the group and give the actor a more imposing appearance.

Chimpanzees and bonobos were not as uniform across groups in their locomotor profiles. Young chimpanzees in SLZ and LAZ expressed considerable variation in their arboreal locomotion. These differences stemmed mainly from the more extensive arboreal locomotor behaviors used by young individuals of SLZ. SLZ chimpanzees had more fire hose and large trees available to them than LAZ chimpanzees, and their increased arboreality and *climbing* locomotion could be interpreted as a reflection of the availability of enclosure features that encouraged more arboreal locomotion in SLZ chimpanzees (see photographs in Chapter 2, Figures 2.2 and 2.3).

Contrary to my prediction that bonobos would be more bipedal than chimpanzees (and therefore gesture more frequently with their upper limbs), chimpanzees were actually the most bipedal of the three species. Adult chimpanzees were *bipedal walking* for 3.6% of their time in locomotion, while gorilla and bonobo adults exhibited bipedal locomotion less than 1.0% of their time in locomotion. Part of this increase in bipedality in chimpanzees was due to the frequent use of the *bipedal swagger* gesture as a dominance display by adult male chimpanzees. This gesture involved *bipedal walking* locomotion, and it was the third most-used gesture in the LAZ chimpanzee repertoire.

Both bonobo groups were surprisingly terrestrial, though WAP bonobos were especially so. There was considerable variation between SDZ and WAP bonobos in terms of locomotor behaviors, particularly with respect to arboreal locomotion such as *brachiating* and *climbing* in young bonobos. These differences can perhaps also be attributed to specific features within each of the different bonobo enclosures. The SDZ enclosure was multi-leveled and filled with trees, fire hose, and sway poles (see photograph in Chapter 2, Figure 2.6). To reach the top level of the enclosure, all individuals needed to use these arboreal substrates. In this environment, bonobos (especially young ones) used more *climbing* and *brachiating* than WAP bonobos, whose enclosure was a large, open island in which all areas could be accessed without using arboreal substrates (see photograph in Chapter 2, Figure 2.5). Bonobos at WAP did not need to use the sway poles, trees, and other climbing structures in their enclosure, so unless they were using them for play, most individuals (particularly adults) chose not to use arboreal substrates. *Bipedal standing* and *bipedal walking* were used more often by young bonobos, but always less than 1.0% of the time for adult bonobos in both groups. Young SDZ bonobos used more arboreal locomotor behaviors for larger portions of their time than young gorillas or chimpanzees.

All species also used gestures that involved at least one upper limb in significant proportions, but these gestures were not used most frequently when *sitting* or bipedal. All species gestured most frequently while *sitting* and *lying*, but all species also gestured at least 10.0% of the time while in some sort of bipedal posture or locomotion. The gestures produced during this bipedality, however, were not always gestures that only involved the use of the upper limbs. Rather, many were gestures that relied on the positional behavior as part of the communicative act, such as *bipedal swagger* in chimpanzees. These forms of locomotion were coupled with the gestures themselves so that communication took place without expressly involving the upper limbs.

Table 4.1 Positional behaviors recorded by study group. Shaded rows signify positional behaviors recorded in all study groups.

	Gorillas		Chimpanzees		Bonobos	
	BZA	BZB	SLZ	LAZ	SDZ	WAP
Locomotor Behaviors:						
Bipedal Running	✓	✓	✓	✓		✓
Bipedal Running Full	✓					✓
Bipedal Swaggering			✓	✓		
Bipedal Walking	✓	✓	✓	✓	✓	✓
Bipedal Walking Full	✓	✓	✓	✓	✓	✓
Brachiating		✓	✓	✓	✓	✓
Climbing	✓	✓	✓	✓	✓	✓
Ice Skating	✓	✓		✓	✓	✓
Jumping	✓	✓	✓	✓	✓	✓
Object Sliding					✓	✓
Quadrupedal Running	✓	✓	✓	✓	✓	✓
Quadrupedal Running Full	✓	✓	✓	✓	✓	✓
Quadrupedal Walking	✓	✓	✓	✓	✓	✓
Quadrupedal Walking Full	✓	✓	✓	✓	✓	✓
Sliding	✓	✓			✓	✓
Somersaulting	✓	✓	✓	✓	✓	✓
Swingsetting	✓	✓		✓	✓	✓
Postural Behaviors:						
Bipedal Standing	✓	✓	✓	✓	✓	✓
Bipedal Standing Full	✓	✓	✓	✓	✓	✓
Crouching	✓	✓	✓	✓	✓	✓
Hanging	✓	✓	✓	✓	✓	✓
Headstanding	✓				✓	✓
Lying Dorsally	✓	✓	✓	✓	✓	✓
Lying Ventrally	✓	✓	✓	✓	✓	✓
Lying on Side	✓	✓	✓	✓	✓	✓
Quadrupedal Standing	✓	✓	✓	✓	✓	✓
Quadrupedal Standing Full	✓	✓	✓	✓	✓	✓
Riding	✓	✓	✓		✓	✓
Sitting	✓	✓	✓	✓	✓	✓

Table 4.2 Proportion of time gorillas spent arboreal and terrestrial by age-class. Young=Individuals ≤8 yrs; Adult=Individuals ≥9 yrs.

		% Arboreal	**% Terrestrial**
BZA	Adults (n=5)	19.0%*	81.0%*
	Young (n=5)	17.6%*	82.4%*
BZB	Adults (n=7†)	10.8%*	89.2%*
	Young (n=8†)	17.8%*	82.2%*

†Two females in BZB were included in both age-classes.
*p<0.0001
Total min for BZA Adults=303 arboreal, 1,294 terrestrial.
Total min for BZA Young=262 arboreal, 1,224 terrestrial.
Total min for BZB Adults=189 arboreal, 1,624 terrestrial.
Total min for BZB Young=263 arboreal, 1,132 terrestrial.

Table 4.3 Upper limb involvement in gestural signaling. Percentage of total gestures used per species. Gestures that required the use of at least one upper limb were predicted to be used more frequently in species that were more frequently *sitting* or engaged in bipedal postures/locomotion. *Gesture combos* are not included in the total number of gestures.

	Gorillas	**Chimpanzees**	**Bonobos**
Both upper limbs involved:			
Bipedal Swagger	n/a	4.2%	n/a
Body Beat	1.2%	n/a	n/a
Chest Beat	4.6%	n/a	n/a
Charge	0.4%	0.7%	1.1%
Chase	2.6%	0.8%	5.7%
Clap	2.6%	n/a	3.5%
Dropkick	n/a	0.5%	n/a
Drum	1.0%	n/a	n/a
Head Bang	1.0%	n/a	n/a
Object Slide	n/a	n/a	3.1%
Slap Ground	4.4%	n/a	0.5%
At least one upper limb involved:			
Arm Raise	0.3%	3.9%	1.4%
Arm Shake	n/a	0.4%	n/a
Back Pounce	n/a	3.7%	0.9%
Bite Offer	n/a	0.3%	n/a
Embrace	3.4%	5.3%	9.8%
Grab	16.8%	12.3%	22.1%
Gallop	2.5%	n/a	n/a
Long Touch	2.6%	1.3%	0.7%
Poke	n/a	0.5%	0.6%
Pull	4.9%	12.5%	10.0%
Push	7.1%	10.1%	4.1%
Object Shake	0.7%	2.1%	0.3%
Slap	4.7%	0.3%	0.3%
Smack	7.8%	3.3%	3.7%
Swat	1.8%	1.4%	n/a
Take	2.7%	2.9%	2.5%
Throw	n/a	0.3%	n/a
Touch	8.6%	7.5%	3.6%
Touch Genitals	1.1%	2.0%	3.0%
No upper limbs involved:			
Bite	3.1%	2.3%	1.4%
Body On	1.0%	1.8%	9.3%
Bow	n/a	1.9%	0.3%
Foot Clap	n/a	n/a	3.3%

n/a=not applicable because the gesture was not observed in that species.
Gorillas: n=2,418 total gestures
Chimpanzees: n=1,963 total gestures
Bonobos: n=3,473 total gestures

Table 4.3 Upper limb involvement in gestural signaling (continued).

	Gorillas	Chimpanzees	Bonobos
No upper limbs involved:			
Formal Bite	0.3%	n/a	n/a
Genito-Genital Rub	n/a	n/a	0.2%
Head Nod	n/a	0.7%	n/a
Head Nuzzle	3.6%	1.2%	0.5%
Head Shake	n/a	n/a	0.5%
Ice Skate	0.7%	n/a	n/a
Inspect Genitals	n/a	2.6%	0.3%
Mount Pelvic Thrust	0.4%	n/a	0.1%
Nibble	1.1%	0.3%	0.4%
Peer	6.0%	6.7%	2.9%
Present Genitals	n/a	2.5%	1.7%
Rock	n/a	3.5%	n/a
Somersault	0.5%	n/a	0.5%
Staredown	0.2%	n/a	n/a
Stomp	n/a	n/a	0.9%

n/a=not applicable because the gesture was not observed in that species.
Gorillas: n=2,418 gestures
Chimpanzees: n=1,963 gestures
Bonobos: n=3,473 gestures

Table 4.4 Proportion of time chimpanzees spent arboreal and terrestrial by age-class. Young=Individuals ≤8 yrs; Adult=Individuals ≥9 yrs.

		% Arboreal	**% Terrestrial**
SLZ	Adults (n=9)	17.1%*	82.9%*
	Young (n=2)	34.9%**	65.1%**
LAZ	Adults (n=10)	2.5%*	97.5%*
	Young (n=3)	11.3%*	88.7%*

*p<0.0001; **p=0.0027
Total min for SLZ Adults=513 arboreal, 2,486 terrestrial.
Total min for SLZ Young=231 arboreal, 429 terrestrial.
Total min for LAZ Adults=90 arboreal, 3,452 terrestrial.
Total min for LAZ Young=122 arboreal, 953 terrestrial.

Table 4.5. Proportion of time bonobos were arboreal and terrestrial by age-class. Young=Individuals ≤8 yrs; Adult=Individuals ≥9 yrs.

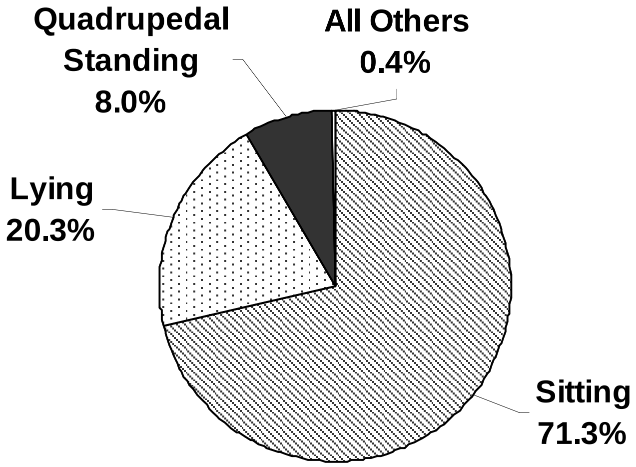
		% Arboreal	**% Terrestrial**
SDZ	Adults (n=6)	6.0%*	94.0%*
	Young (n=2)	18.5%*	81.5%*
WAP	Adults (n=5)	0.5%*	99.5%*
	Young (n=3)	4.3%*	95.7%*

*$p<0.0001$

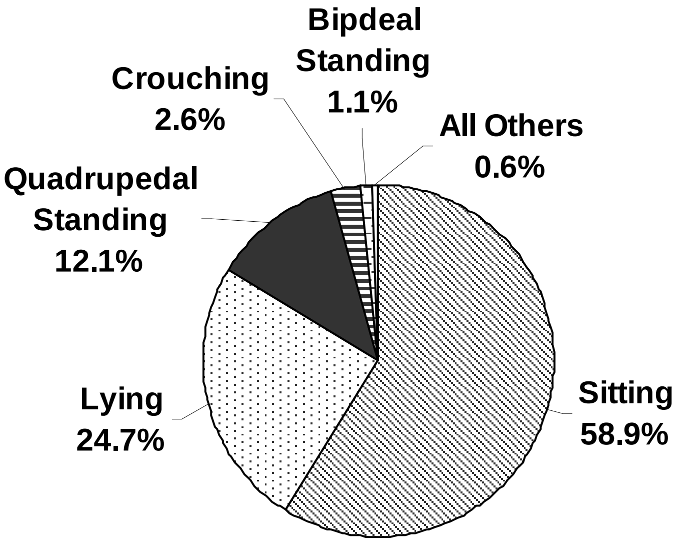
Total min for SDZ Adults=61 arboreal, 965 terrestrial.
Total min for SDZ Young=85 arboreal, 375 terrestrial.
Total min for WAP Adults=7 arboreal, 1,375 terrestrial.
Total min for Young=18 arboreal, 398 terrestrial.

Figure 4.1 Postures used by gorillas. Percentages of time spent in different postures for both groups. Adults=12 individuals; Young=13 individuals. Total min in postures: Adults=3,077; Young=2,581.

Postures Used by Adult Gorillas

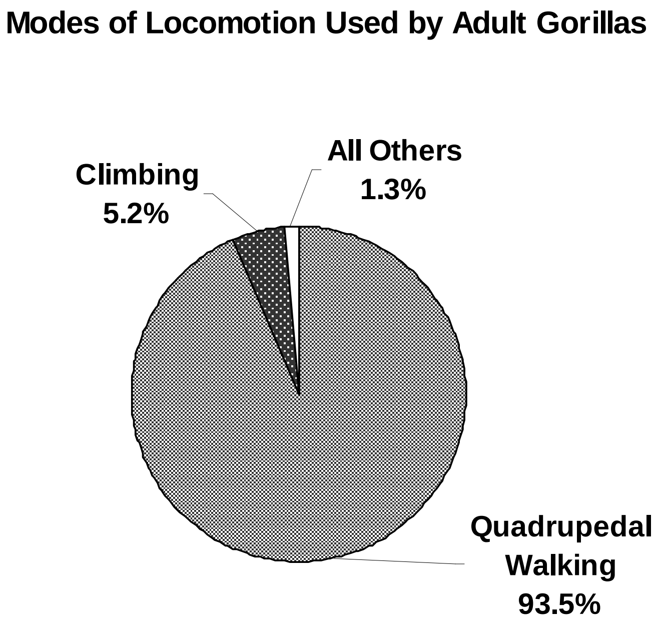


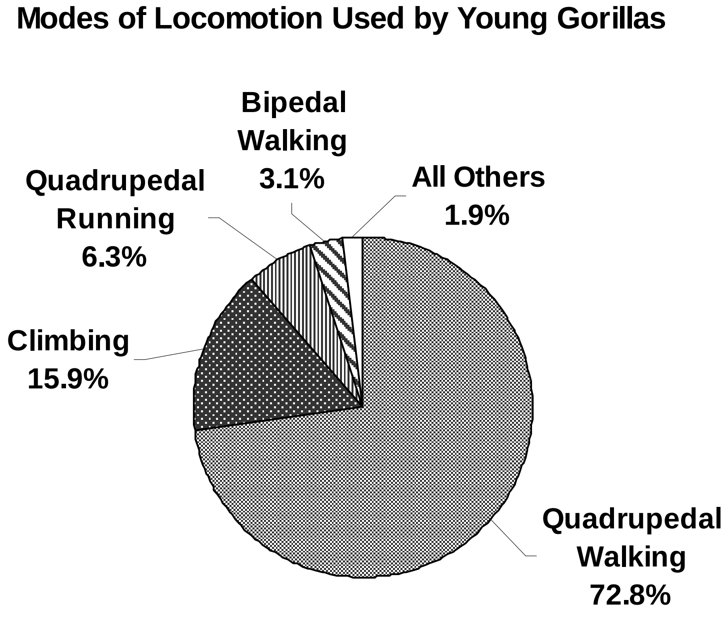
Postures Used by Young Gorillas



All Others=All postures used <1% of the time combined.
Lying includes *Lying Dorsally*, *Lying Ventrally*, *Lying on Side*.
Quadrupedal Standing also includes *Quadrupedal Standing Full*.
Bipedal Standing also includes *Bipedal Standing Full*.

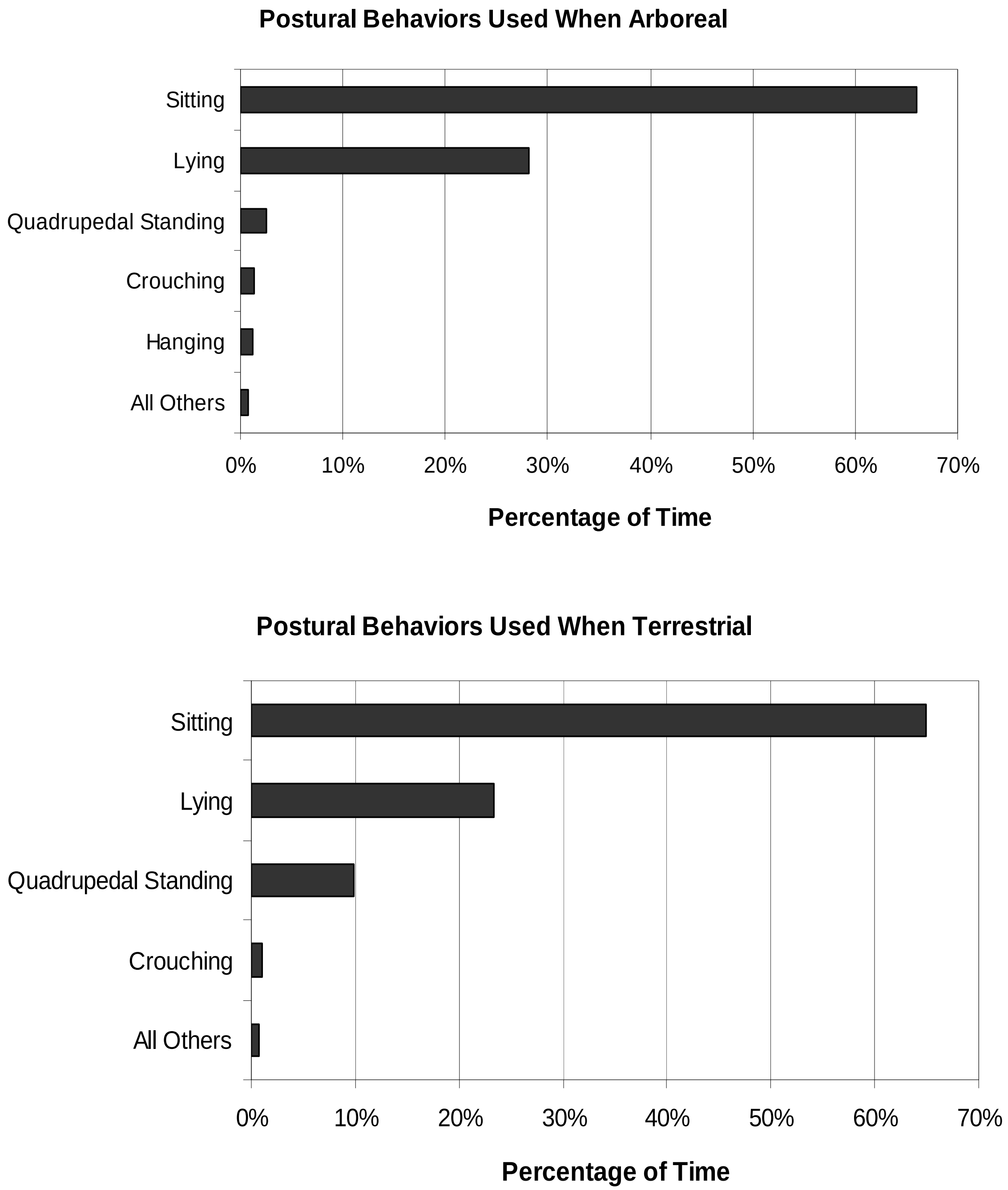
Figure 4.2 Modes of locomotion used by gorillas. Percentages of time spent in different modes of locomotion for both groups. Adults=12 individuals; Young=13 individuals. Total min in locomotion: Adults=232; Young=402.





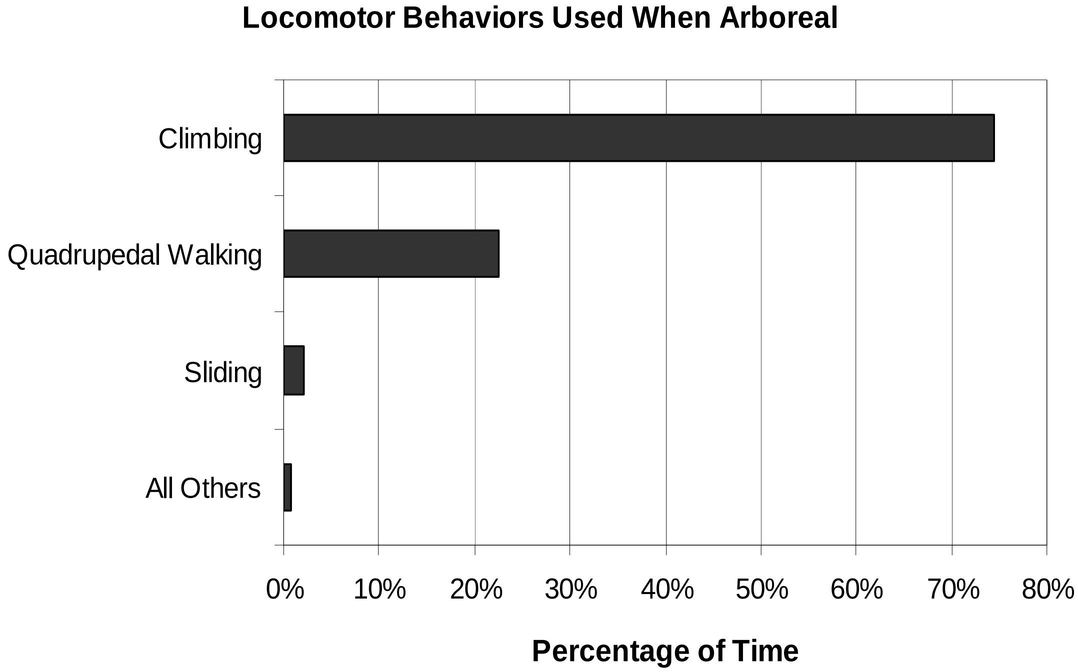
All Others=All modes of locomotion used <1% of the time combined.
Quadrupedal Walking also includes *Quadrupedal Walking Full.*
Quadrupedal Running also includes *Quadrupedal Running Full*
Bipedal Walking also includes *Bipedal Walking Full.*

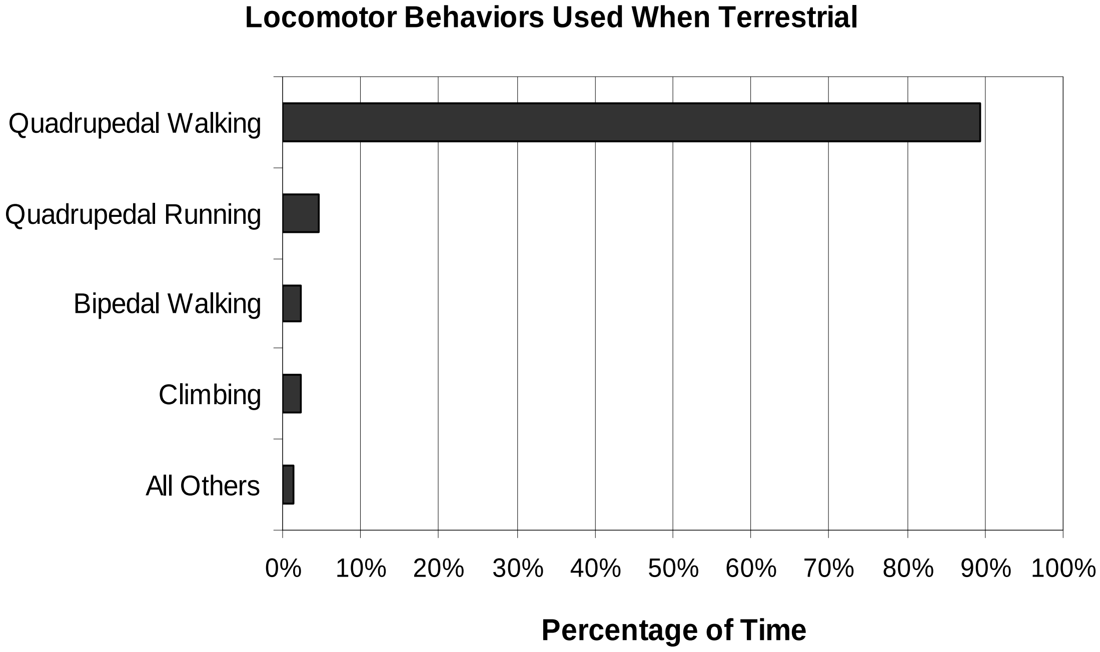
Figure 4.3 Arboreal postures versus terrestrial postures for gorillas. The percentages of total focal sample time for both groups. Total min in postures on arboreal substrates=932; total min in postures on terrestrial substrates=2,746.



All Others=All postures used <1% of the time combined.
Lying includes *Lying Dorsally*, *Lying Ventrally*, *Lying on Side*.
Quadrupedal Standing also includes *Quadrupedal Standing Full*.

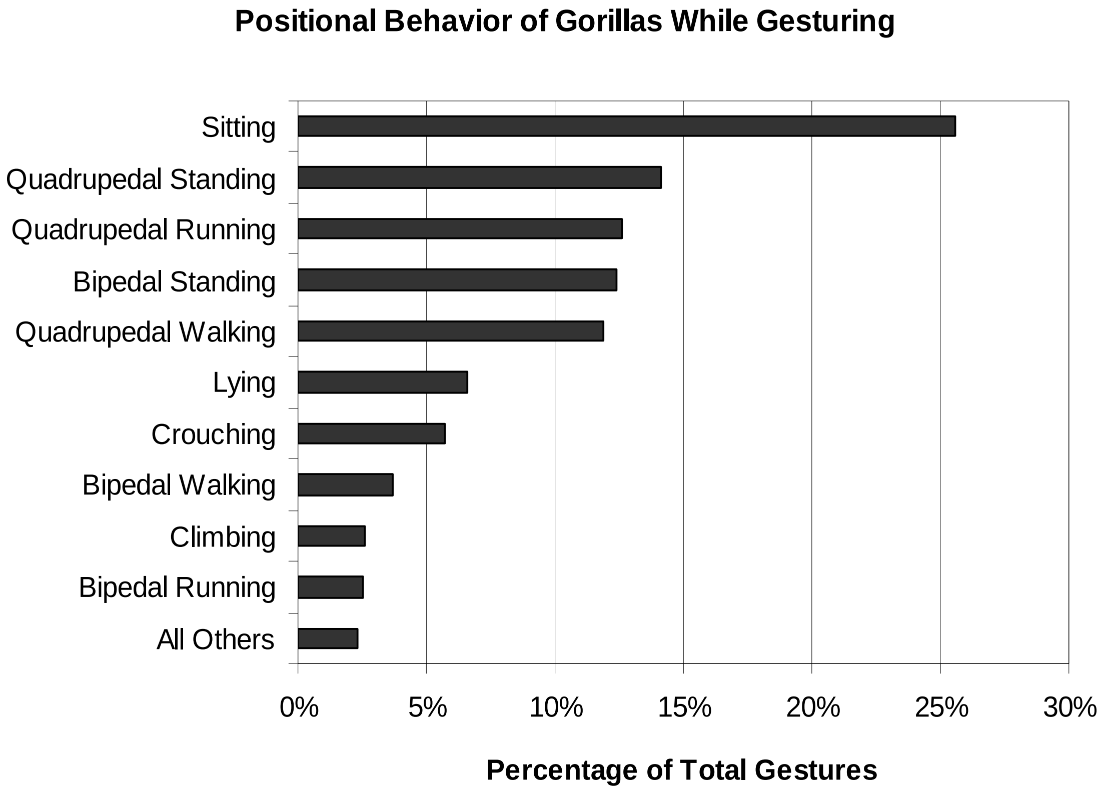
Figure 4.4 Arboreal locomotion versus terrestrial locomotion for gorillas. The percentages of total focal sample time devoted to locomotion for both groups. Total min in locomotion on arboreal substrates=85; total min in locomotion on terrestrial substrates=549.





All Others=All modes of locomotion used <1% of the time combined.
Quadrupedal Walking also includes *Quadrupedal Walking Full.*
Quadrupedal Running also includes *Quadrupedal Running Full.*
Bipedal Walking also includes *Bipedal Walking Full.*

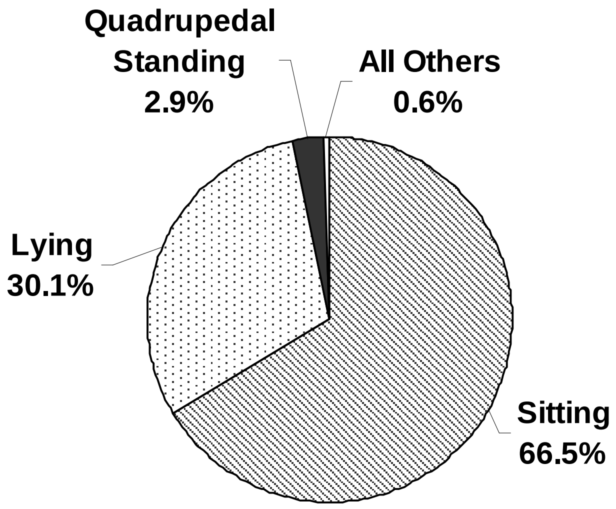
Figure 4.5 Positional behavior of gorillas while gesturing. The percentages of gesturing that occurred while in each positional behavior for both groups (n=2,463 total gestures).



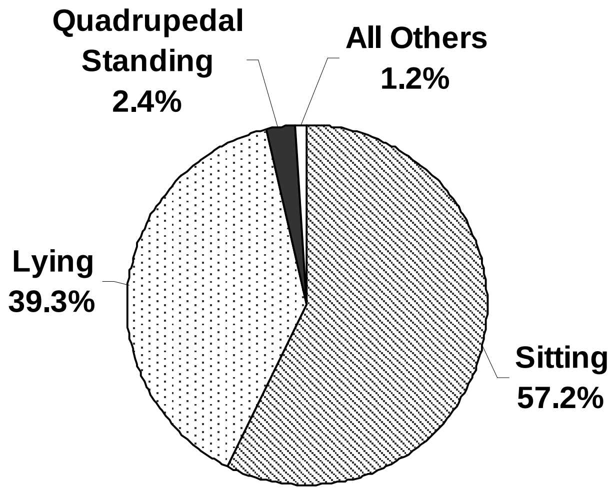
All Others=All positional behaviors in which gorillas gestured <1% combined.
Quadrupedal Standing also includes *Quadrupedal Standing Full.*
Quadrupedal Running also includes *Quadrupedal Running Full.*
Bipedal Standing also includes *Bipedal Standing Full.*
Quadrupedal Walking also includes *Quadrupedal Walking Full.*
Lying includes *Lying Dorsally*, *Lying Ventrally*, *Lying on Side.*
Bipedal Walking also includes *Bipedal Walking Full.*
Bipedal Running also includes *Bipedal Running Full.*

Figure 4.6 Postures used by chimpanzees. Percentages of time spent in different postures for both groups. Adults=19 individuals; Young=5 individuals. Total min of postures: Adults=5,970; Young=1,582.

Postures Used by Adult Chimpanzees

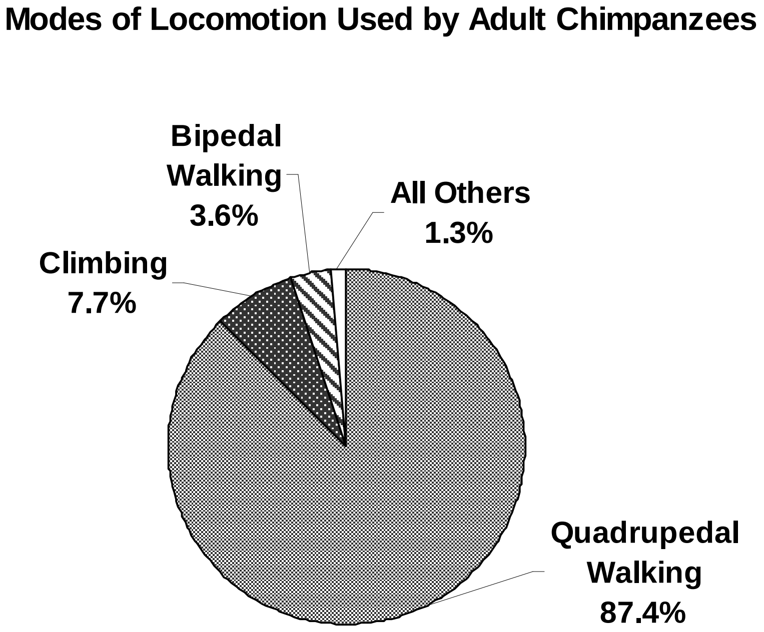


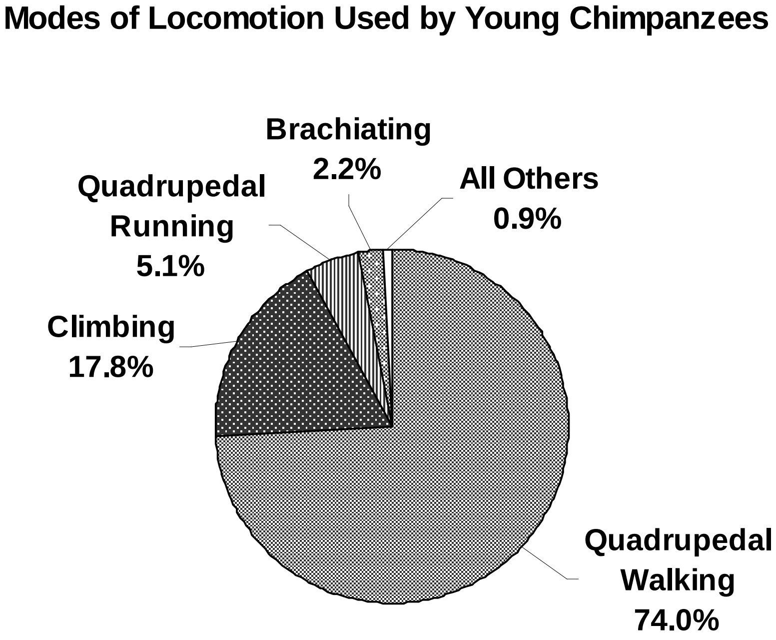
Postures Used by Young Chimpanzees



All Others=All postures used <1% of the time combined.
Lying includes *Lying Dorsally*, *Lying Ventrally*, *Lying on Side*.
Quadrupedal Standing also includes *Quadrupedal Standing Full*.

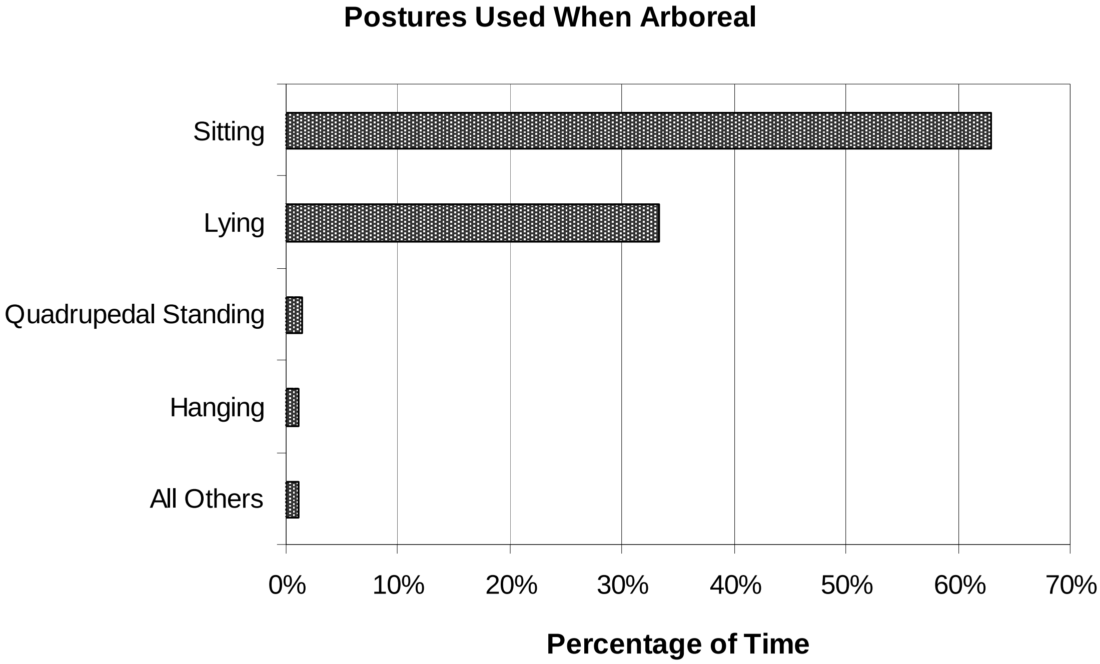
Figure 4.7 Modes of locomotion used by chimpanzees. Percentages of time spent in different modes of locomotion for both groups. Adults=19 individuals; Young=5 individuals. Total min in locomotion: Adults=572; Young=152.

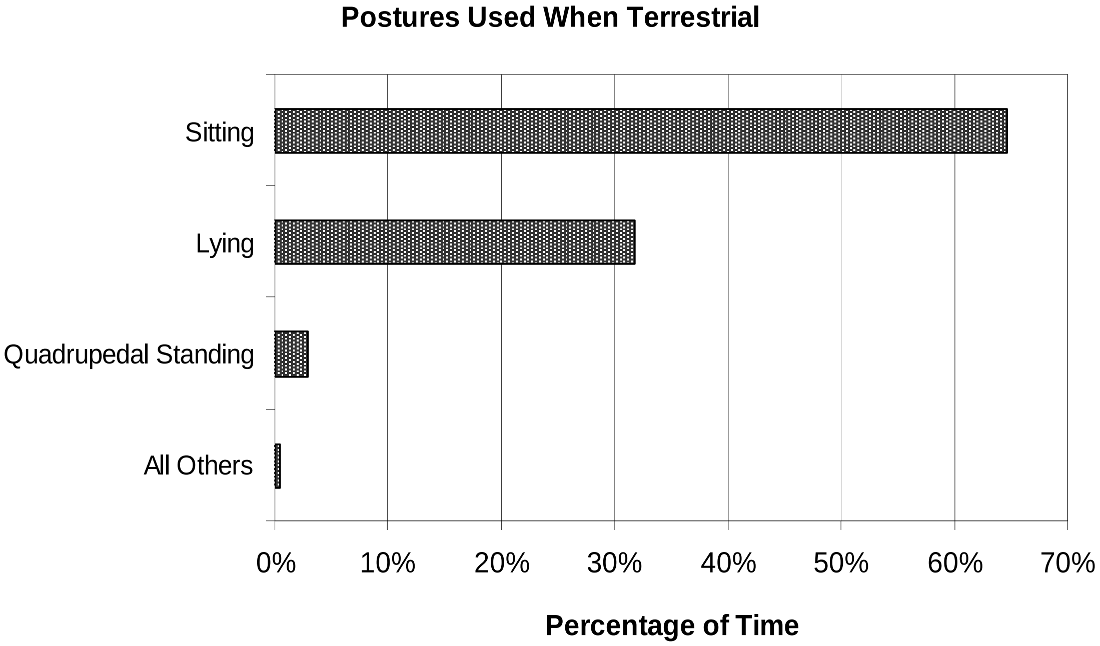




All Others=All modes of locomotion used <1% of the time combined.
Quadrupedal Walking also includes *Quadrupedal Walking Full.*
Bipedal Walking also includes *Bipedal Walking Full and Bipedal Swaggering*.
Quadrupedal Running also includes *Quadrupedal Running Full.*

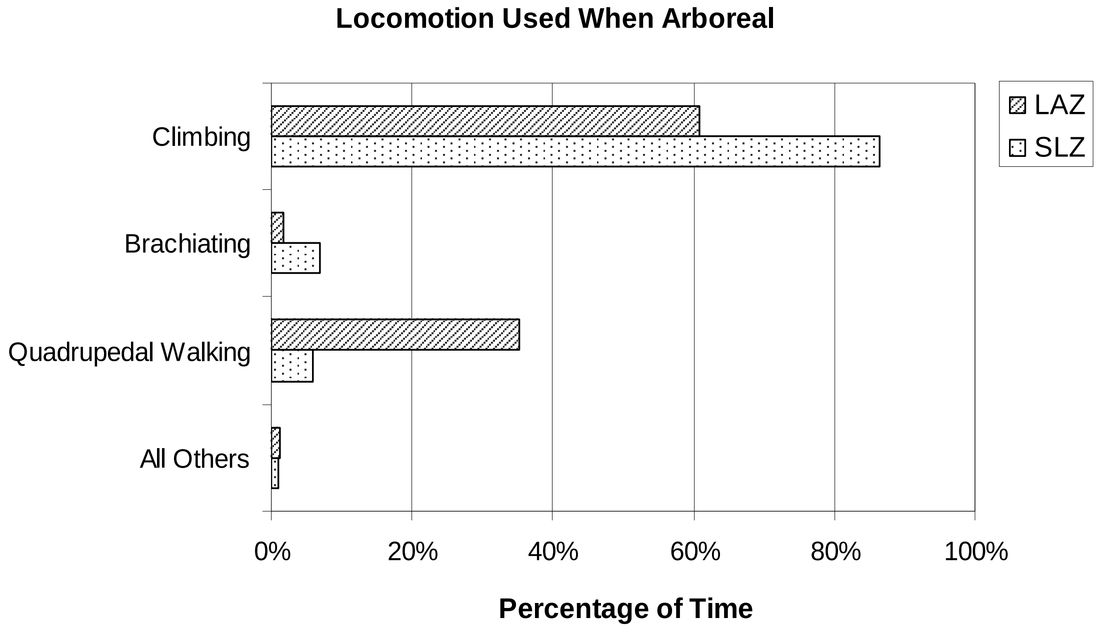
Figure 4.8 Arboreal postures versus terrestrial postures for chimpanzees. The percentages of total focal sample time devoted to postures for both groups. Total min in postures on arboreal substrates=892; total min in postures on terrestrial substrates=6,659.

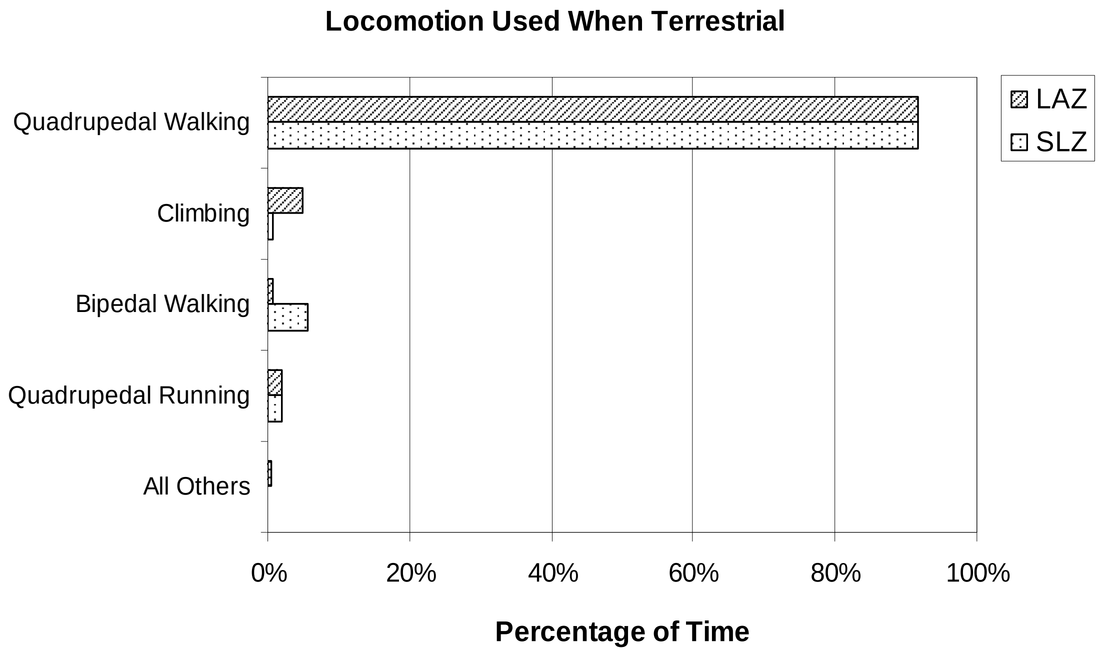




All Others=All postures used <1% of the total time arboreal combined.
Lying includes *Lying Dorsally*, *Lying Ventrally*, *Lying on Side*.
Quadrupedal Standing also includes *Quadrupedal Standing Full*.

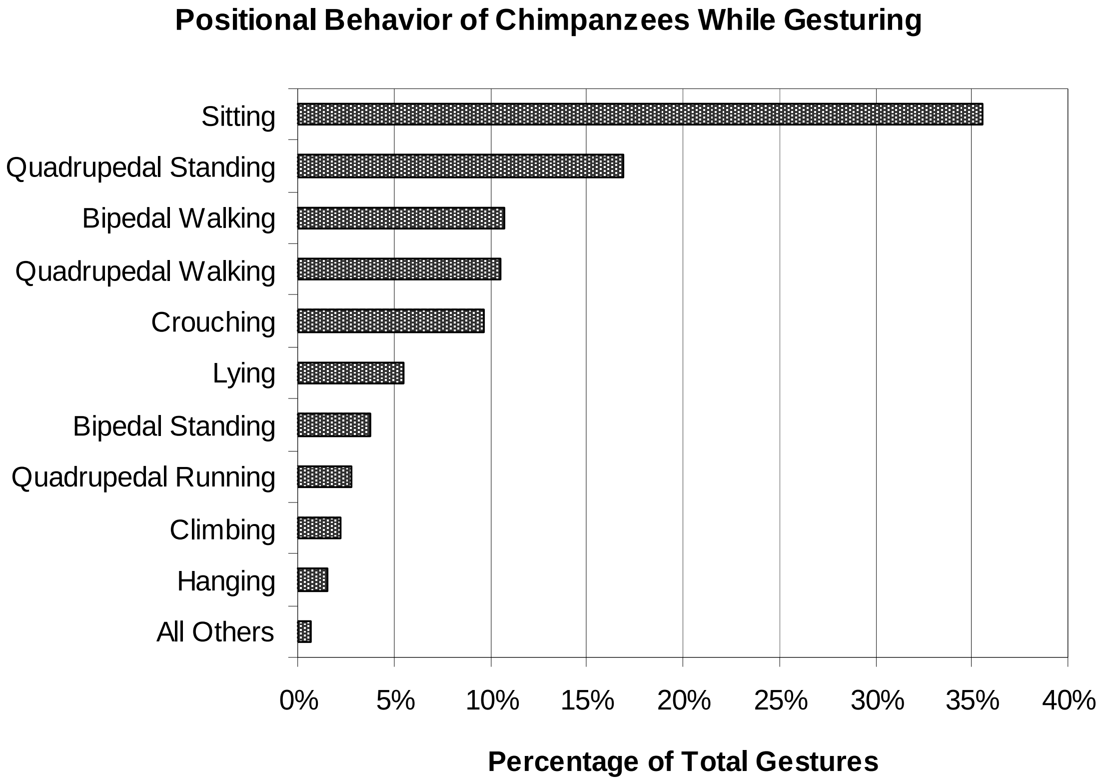
Figure 4.9 Arboreal locomotion versus terrestrial locomotion for chimpanzees. The percentages of total focal sample time devoted to locomotion for both groups. Total min in locomotion on arboreal substrates=63; total min in locomotion on terrestrial substrates=661.





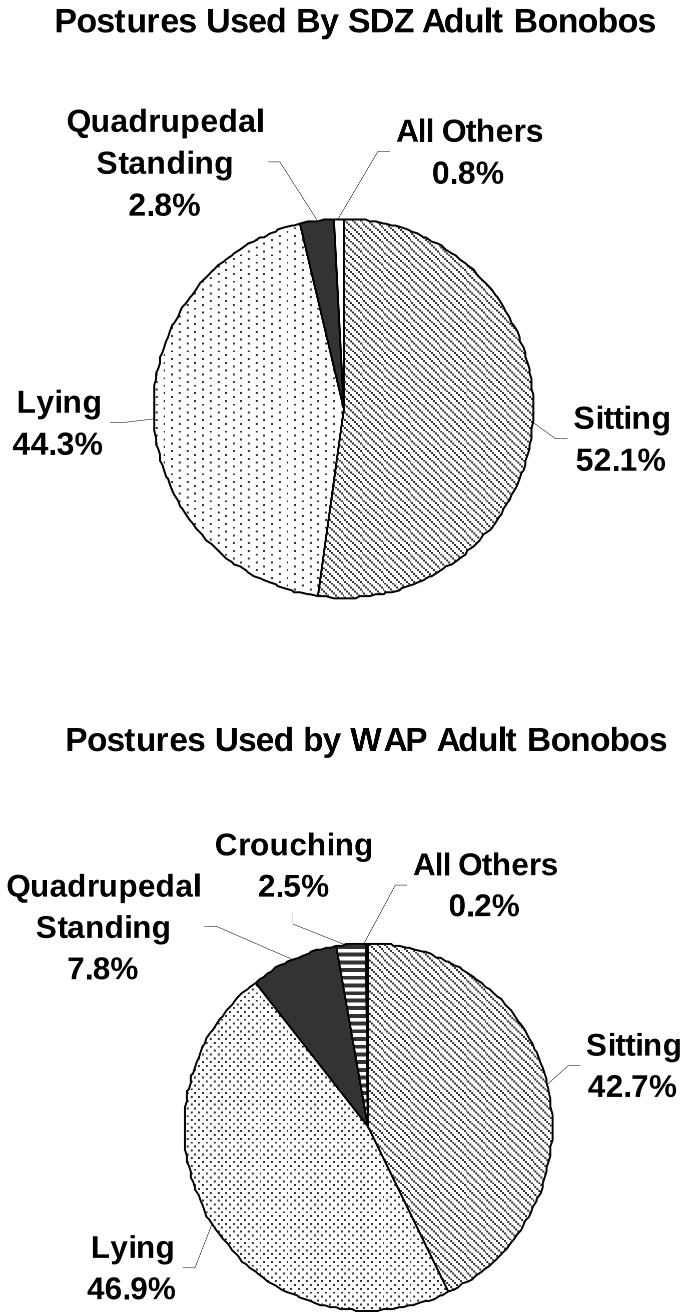
All Others=All modes of locomotion used <1% of the total time pooled together.
Quadrupedal Walking also includes *Quadrupedal Walking Full.*
Bipedal Walking also includes *Bipedal Walking Full and Bipedal Swaggering*.
Quadrupedal Running also includes *Quadrupedal Running Full.*

Figure 4.10 Positional behavior of chimpanzees while gesturing. The percentages of gesturing that occurred in each positional behavior for both groups (n=2,041 total gestures).



All Others=All positional behaviors in which chimpanzees gestured <1% combined.
Quadrupedal Standing also includes *Quadrupedal Standing Full.*
Bipedal Walking also includes *Bipedal Walking Full and Bipedal Swaggering*.
Quadrupedal Walking also includes *Quadrupedal Walking Full.*
Lying includes *Lying Dorsally*, *Lying Ventrally*, *Lying on Side.*
Bipedal Standing also includes *Bipedal Standing Full.*
Quadrupedal Running also includes *Quadrupedal Running Full*

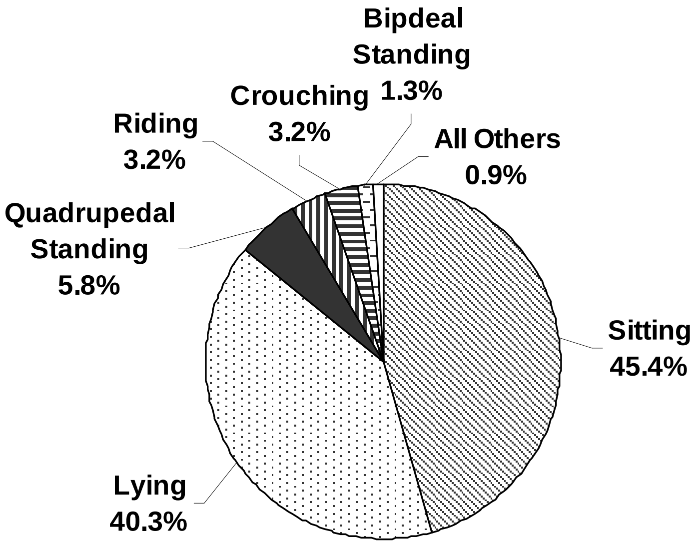
Figure 4.11 Postures used by adult bonobos. Percentages of time spent in different postures for both groups. SDZ=5 individuals; WAP=6 individuals. Total min in postures: SDZ=926; WAP=1,186.



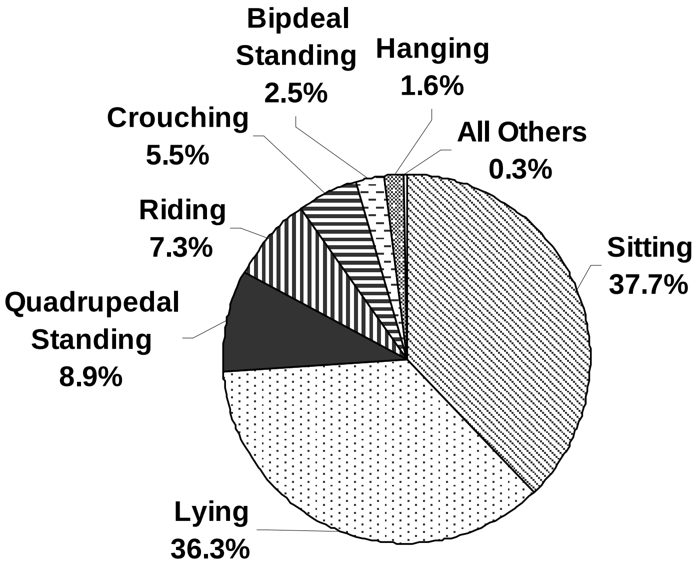
All Others=All postures used <1% of the time combined.
Lying includes *Lying Dorsally*, *Lying Ventrally*, *Lying on Side*.
Quadrupedal Standing also includes *Quadrupedal Standing Full*.

Figure 4.12 Postures used by young bonobos. Percentages of time spent in different postures for both groups. SDZ=3 individuals; WAP=2 individuals. Total min in postures: SDZ=378; WAP=322.

Postures Used by SDZ Young Bonobos

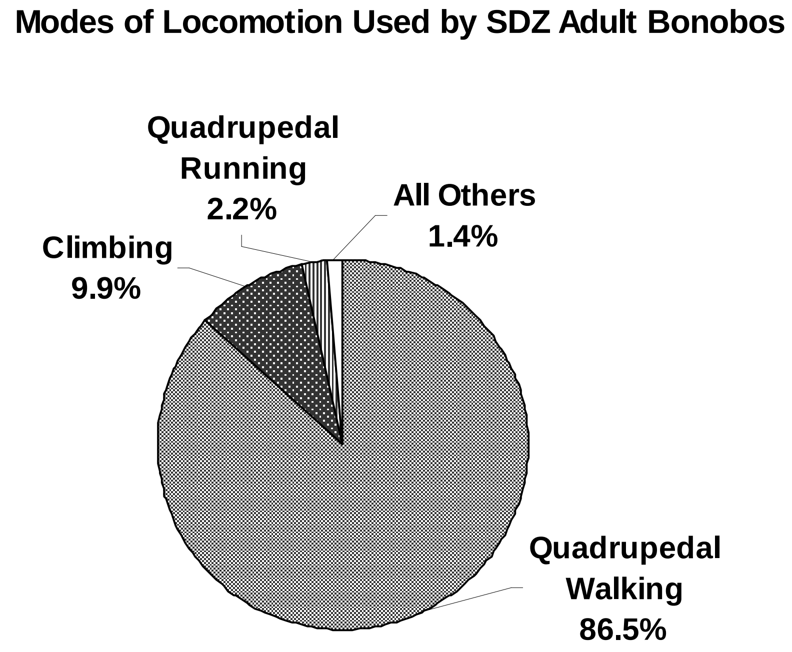


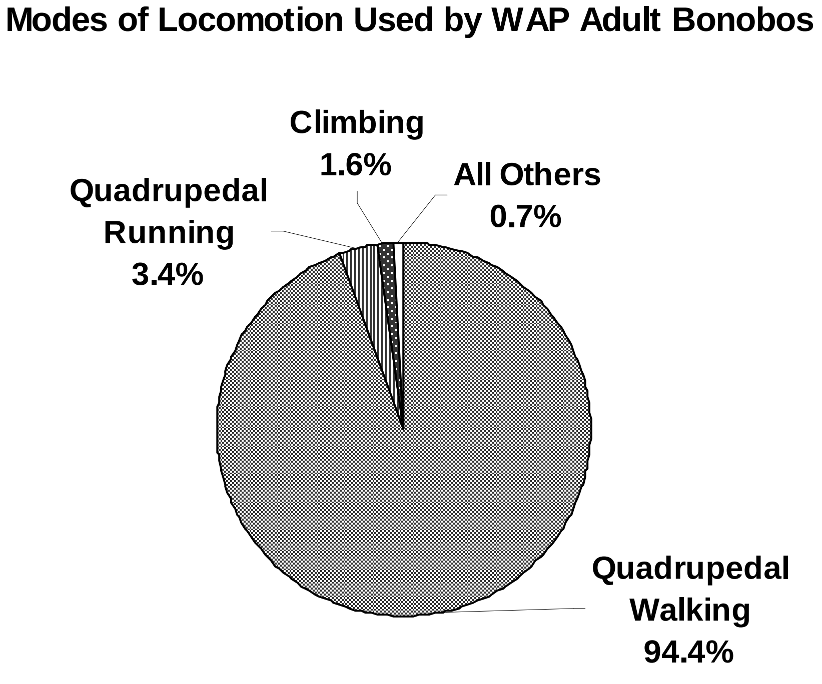
Postures Used by WAP Young Bonobos



All Others=All postures used <1% of the time combined.
Lying includes *Lying Dorsally*, *Lying Ventrally*, *Lying on Side*.
Quadrupedal Standing also includes *Quadrupedal Standing Full*.
Bipedal Standing also includes *Bipedal Standing Full*.

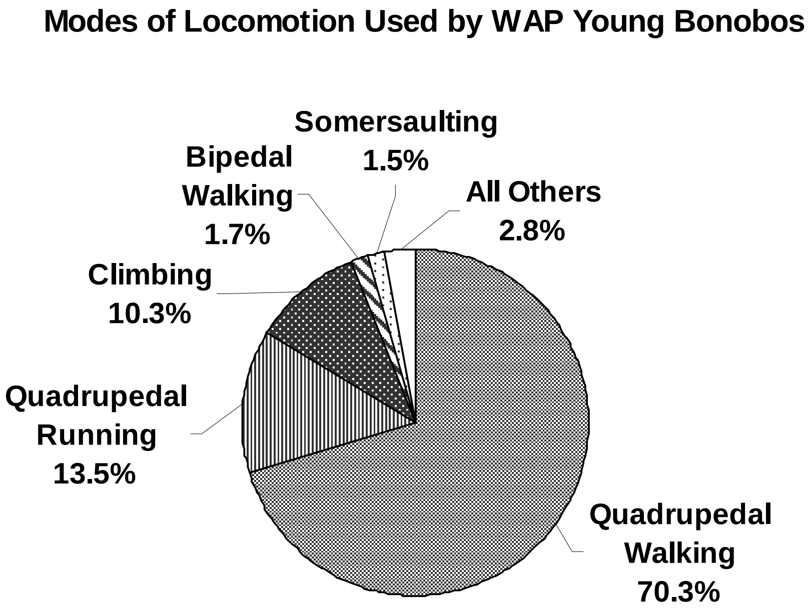
Figure 4.13 Modes of locomotion used by adult bonobos. Percentages of time spent in different modes of locomotion for both groups. SDZ=5 individuals; WAP=6 individuals. Total min in locomotion: SDZ=100; WAP=196.

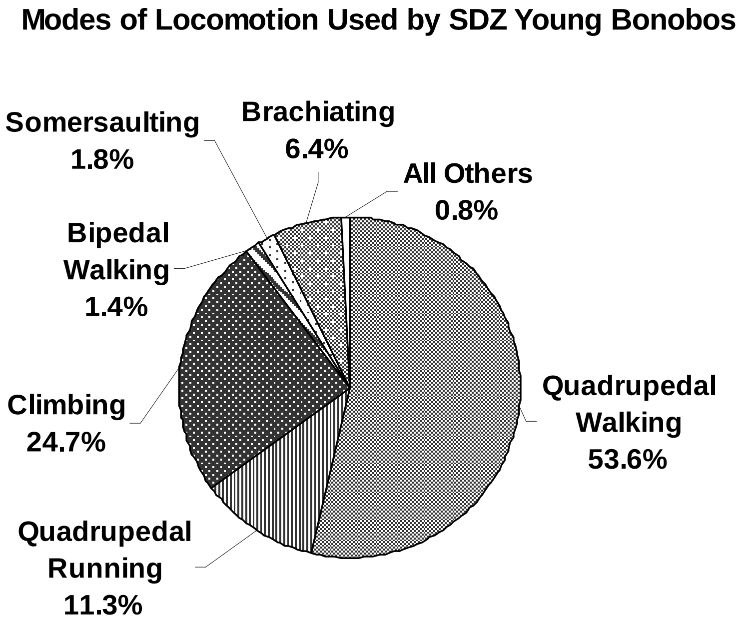




All Others=All modes of locomotion used <1% of the time combined.
Quadrupedal Walking also includes *Quadrupedal Walking Full.*
Quadrupedal Running also includes *Quadrupedal Running Full*
Bipedal Walking also includes *Bipedal Walking Full.*

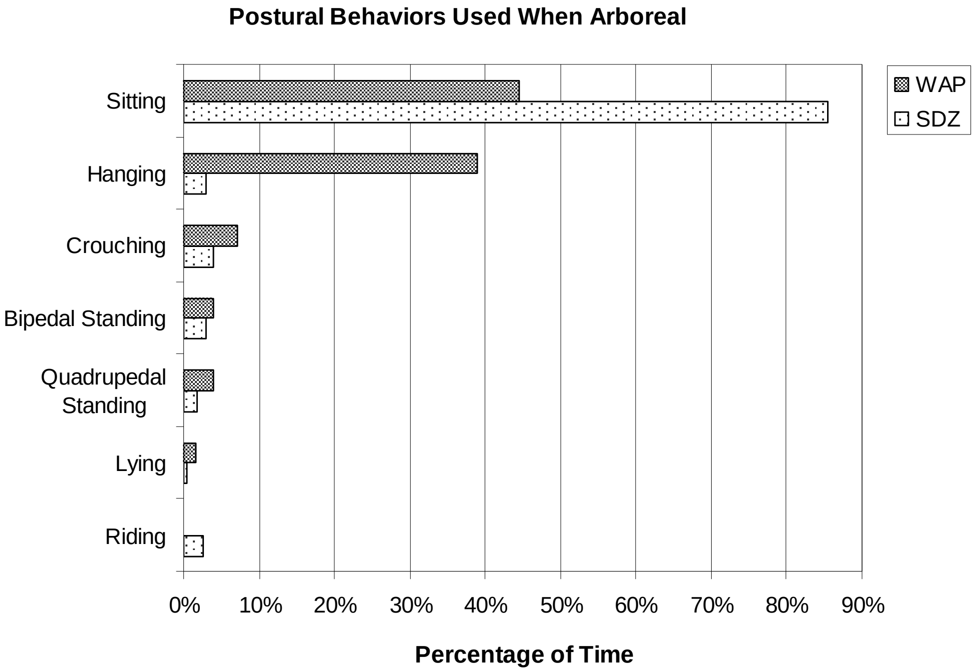
Figure 4.14 Modes of locomotion used by young bonobos. Percentages of time spent in different modes of locomotion. SDZ=3 individuals; WAP=2 individuals. Total min in locomotion: SDZ=82; WAP=95.

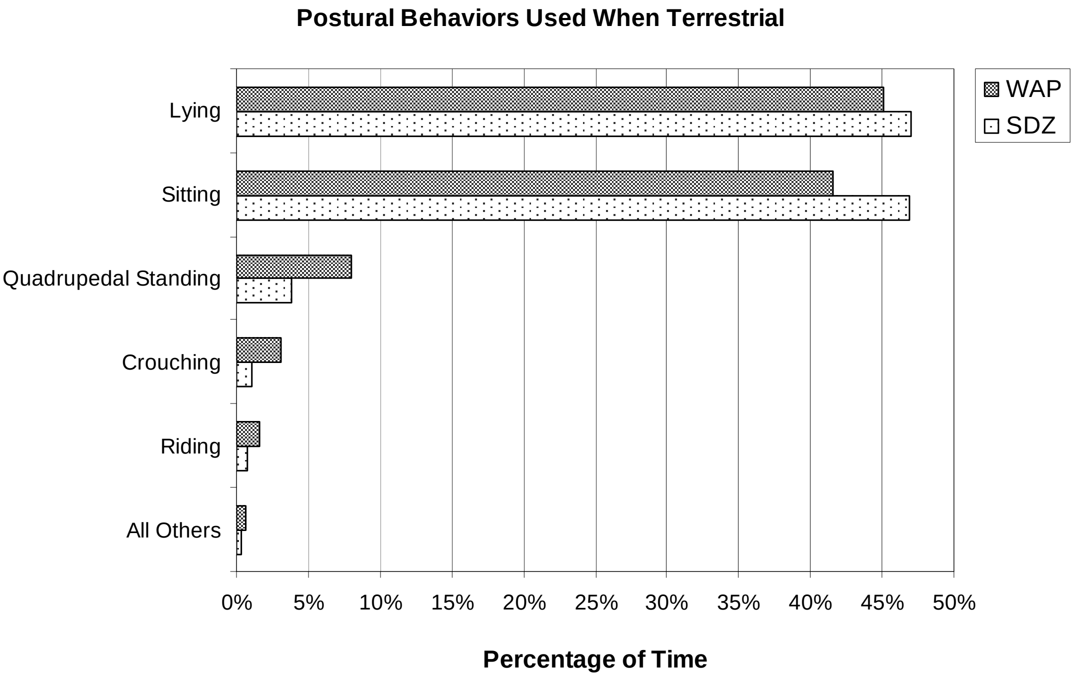




All Others=All modes of locomotion used <1% of the time combined.
Quadrupedal Walking also includes *Quadrupedal Walking Full.*
Quadrupedal Running also includes *Quadrupedal Running Full*
Bipedal Walking also includes *Bipedal Walking Full.*

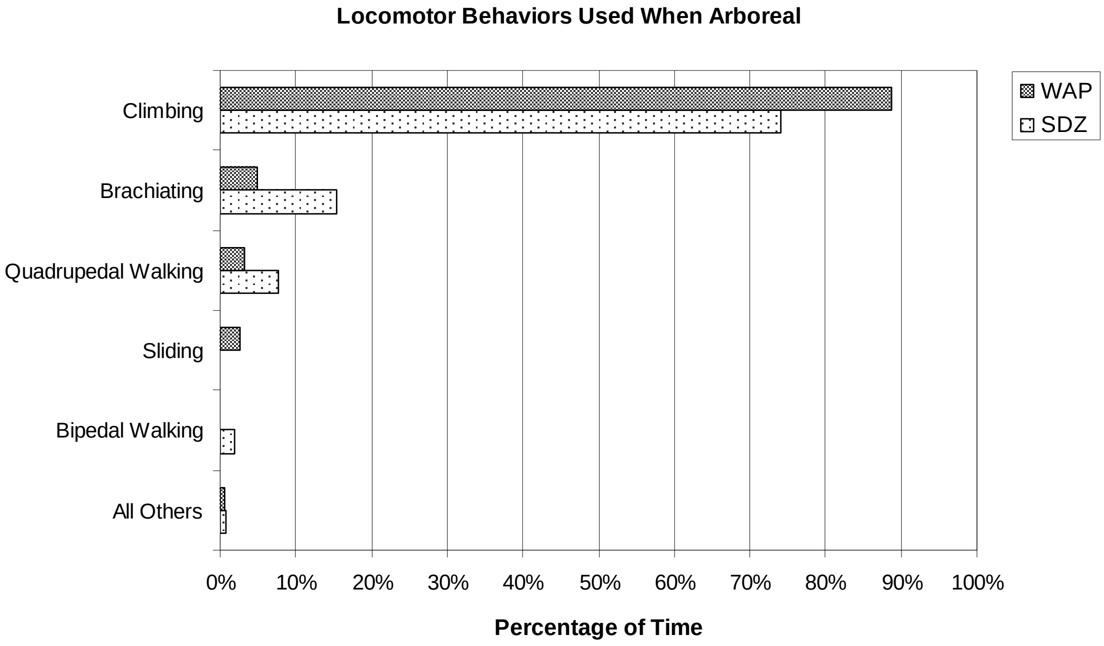
Figure 4.15 Arboreal postures versus terrestrial postures for bonobos. The percentages of total focal sample time devoted to postural behaviors for both groups. Total min in postures on arboreal substrates=126; total min in postures on terrestrial substrates=2,685.

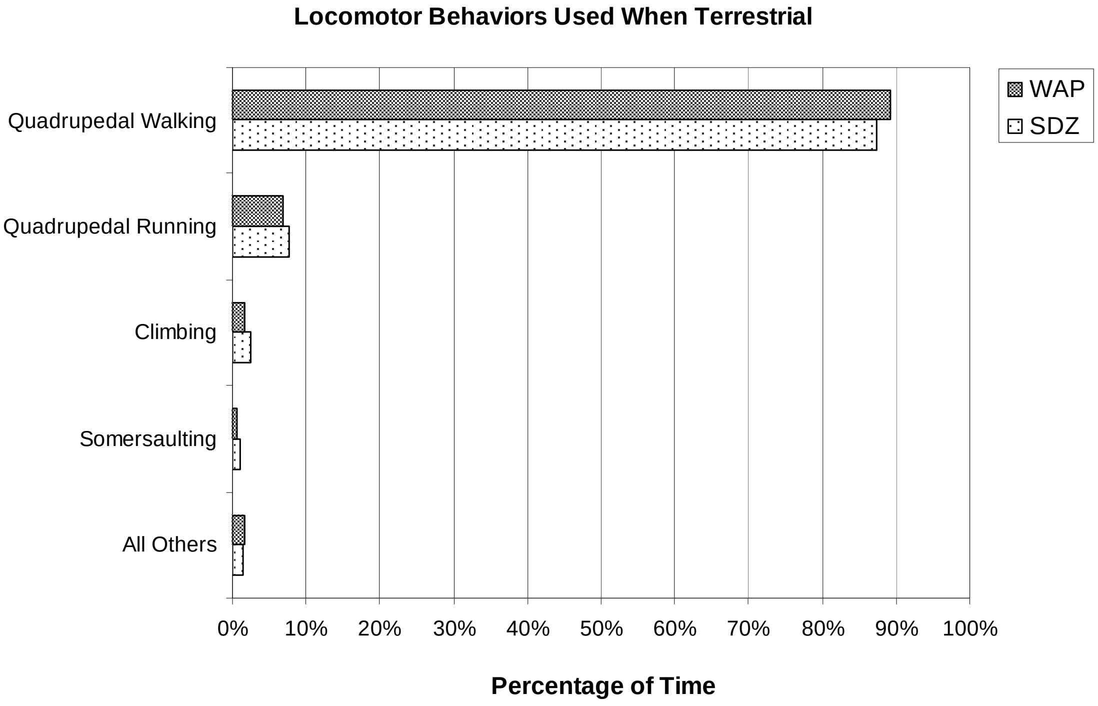




All Others=All postures used <1% of the total time arboreal combined.
Bipedal Standing also includes *Bipedal Standing Full*.
Quadrupedal Standing also includes *Quadrupedal Standing Full*.
Lying includes *Lying Dorsally*, *Lying Ventrally*, *Lying on Side*.

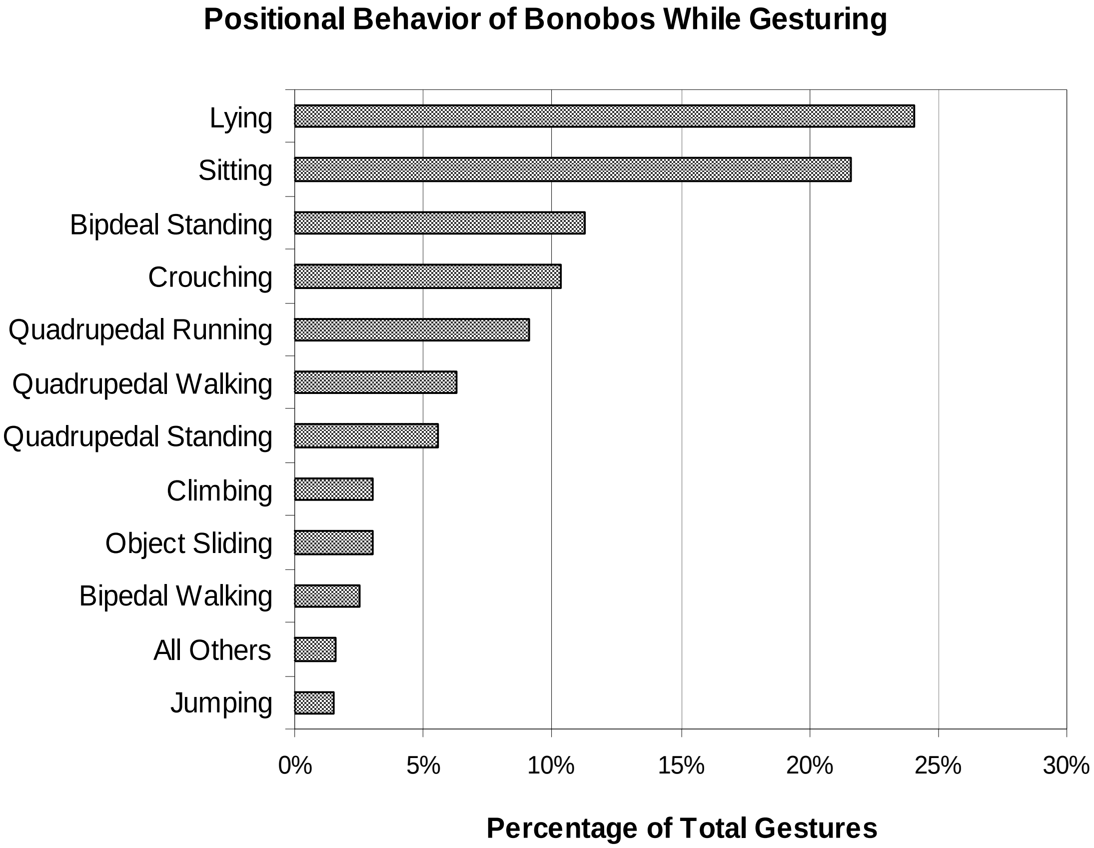
Figure 4.16 Arboreal locomotion versus terrestrial locomotion for bonobos. The percentages of total focal sample time devoted to locomotion for both groups. Total min in locomotion on arboreal substrates=45; total min in locomotion on terrestrial substrates=427.





All Others=All modes of locomotion used <1% of the time combined.
Quadrupedal Walking also includes *Quadrupedal Walking Full.*
Quadrupedal Running also includes *Quadrupedal Running Full.*
Bipedal Walking also includes *Bipedal Walking Full.*

Figure 4.17 Positional behavior of bonobos while gesturing. The percentages of gesturing that occurred in each positional behavior for both groups (n=3,486 total gestures).



All Others=All positional behaviors in which bonobos gestured <1% combined.
Lying includes *Lying Dorsally*, *Lying Ventrally*, *Lying on Side*.
Bipedal Standing also includes *Bipedal Standing Full*.
Quadrupedal Running also includes *Quadrupedal Running Full*
Quadrupedal Walking also includes *Quadrupedal Walking Full*.
Quadrupedal Standing also includes *Quadrupedal Standing Full*.
Bipedal Walking also includes *Bipedal Walking Full*.

CHAPTER 5

DISCUSSION, IMPLICATIONS, AND FUTURE DIRECTIONS

In this thesis, I examined the influence of social dynamics and positional behavior on gestural signaling in African apes. This research was the first to take into account the effects of both of these factors on gestural signaling across the African apes. In this chapter, I summarize and interpret the results from Chapters 3 and 4 and discuss them in relation to the evolution of gestural signaling in early hominins and its implications for the origins of language. Then, I discuss the limitations of this study, and conclude by proposing ways in which this research can be expanded in future work.

5.1 Summary of Social Dynamics and Gestural Signaling

The social dynamics for each of the species studied here were ascertained from multiple field and captive studies that have investigated various aspects of dominance hierarchies, mother-offspring relationships, and the nature of agonistic, sexual, and affiliative interactions between age/sex-classes (see Chapter 1, section 1.2). These data were the basis for my expectations of the social dynamics of these study groups and informed my original predictions about how gestural signaling may be influenced by social dynamics. In this section, I discuss whether the patterns of gestural signaling observed in these study groups matched our understanding of African ape social dynamics, and whether meaning can be ascribed to the various gestures observed in these study groups.

5.1.1 The Role of the Recipient

All species gestured significantly more frequently when recipients were attentive to them, but these effects were particularly apparent for visual gestures (such as *arm raise*, *peer*, or *object shake*). This provides evidence that actors were sensitive to whether recipients were able to receive certain gestures. Sensitivity to the attentional state of the recipient is a key component of effective communication because communication can only take place if both the actor and the recipient are engaged. An auditory or tactile gesture may still be effective if the recipient is not oriented toward the actor at the time of gesturing, but a visual gesture such as a *head nod* is not an effective tool for communication if it cannot be seen by the recipient.

The intimate relationship between actor and recipient separates gestural signaling from vocal signaling because most gestures require a direct interaction between individuals (Cartmill & Byrne 2010). Tactile (and to some degree auditory) gestures require close physical proximity, and visual gestures depend on the orientation of the recipient. By contrast, vocal signaling does not require direct contact or depend on the engagement of a potential recipient. Vocal signals are generally widely-broadcast and may be received by all group members indiscriminately. Group-living primates could certainly obtain adaptive advantages by using non-vocal signals that could be intentionally withheld from certain individuals or restricted to particular dyads.

Although the exact cognitive skills associate with sensitivity to audience effects are unclear (Tomasello 2006), being able to adjust gestural signaling based on the attentional state of a recipient may be a crucial first step towards the development of more advanced cognitive abilities such as joint attention and theory of mind (Povinelli *et al.* 2003; Liebal & Tomasello 2009). Referential gestures like declarative pointing to direct one's attention to something external or imperative pointing to recruit another to cooperate or attend to a shared goal have not been observed to occur naturally in any non-human primate, but these kinds of gestures are crucial to opening up the dyadic interactions between actors and recipients to involve third parties or external objects (Povinelli & Davis 1994; Tomasello & Call 1997). Humans develop these abilities in infancy as they learn to follow their mothers' gazes, focus jointly on objects or events with others, and begin pointing to direct others' attentions elsewhere (Striano & Stahl 2005; Liebal & Tomasello 2009). Understanding the thoughts and intentions of others and being able to communicate about external events or objects are essential skills necessary for language development, and these skills were presumably important for the evolution of language as well.

Since communication is a dynamic process between individuals, examining the response of the recipient is another way to measure how successful particular signals are and what potential functions specific gestures serve. For example, if recipients frequently respond to an *arm raise* gesture by grooming the actor, we can deduce that the *arm raise* gesture is used to communicate the desire to be groomed (see Figure 5.1 for an illustration of an *arm raise* gesture). Rather than a clear-cut relationship of "gesture X always leads to response Y in context Z," most gestures elicited many different responses and were used in several different social contexts. In other words, an *arm raise* gesture by an infant to her mom may lead to riding ventrally on her, but an *arm raise* by an adult male to an adult female may lead to the female grooming the male. Tactile gestures, in particular, were incredibly flexible in the ways in which they were used and the responses they garnered, which could explain why so many of them were used by all three species. Certain gestures (particularly auditory ones like *body beat* or *dropkick*) often elicited no response at all, which indicates that these gestures may not function to initiate contact or alter the behavior of the recipient, but could be important in displaying status or expressing an emotional state to one or more group members.

5.1.2 Interpreting Gestures

Ascribing meaning to a gesture is a complicated process. Measuring whether a recipient responds reliably to a certain gesture or whether the social context always changes after the use of a certain gesture can provide clues as to what the inherent message (*e.g.,* intention or motivation) may be behind each gesture. But, as with human gestures, one gesture can have several meanings or multiple gestures can have the same meaning depending on the context, the relationship between members of the dyad, and other behavioral cues. A *grab* can mean "let's play," or "get away from my food" depending on the circumstance and which individuals are interacting.

Understanding the meaning of a specific signal and its functional role in certain contexts also hinges on whether the communicative interaction is examined through the perspective of the actor or the receiver (Seyfarth and Cheney 2003; Seyfarth *et al.* 2005; Pollick & de Waal 2007; Cartmill & Byrne 2010). Cartmill and Byrne (2010) make a distinction between a gestural signal's "functional meaning" and its "intentional meaning" (p. 794). The functional meaning is understood from the recipient's perspective and is inferred from the response of the recipient. The intentional meaning is understood from the actor's perspective and is inferred from the actor exhibiting signs of expecting a certain response or outcome after the gesture. Most studies examine the functional meaning of gestures because the intentional meaning is much more difficult to interpret. A signal may be misinterpreted by the receiver, or the meaning of a signal may change depending on the inferred intent of the actor.

As is the case in other studies of non-human primate gestural signaling that examine meanings behind gestures (*e.g.*, Pollick & de Waal 2007; Genty *et al.* 2009; Cartmill & Byrne 2010), reliably predicting one particular response or a subsequent social context was nearly impossible for most gestures studied here. Instead, gestures that were more frequently associated with particular contexts or responses were those that were used less flexibly and perhaps had more narrow meanings. Only two gestures were used reliably in all three species: *Bite* and *peer*. *Bite* led to *playing* more frequently than any other context in all three species and *peer* was used in the context of *feeding* more than any other context in all three species. There was only one gesture (*stomp*) that was associated with only one context (*grooming*) every time it was used by bonobos.

While the flexibility of gestural signals makes understanding their functional and intentional meanings problematic, it also illustrates the complexity of this mode of communication (Tomasello & Zuberbühler 2002; Cartmill & Byrne 2010). Gestures can be used in a variety of social contexts and their meanings rely on complex behavioral interactions and context clues. For example, the function of a gesture may depend not only on the signal itself, but also previous interactions between the members of the dyad, the presence of other individuals, the relative dominance ranks of the actor and recipient, and other behavioral cues such as vocalizations or facial expressions. As Pollick and de Waal (2007) point out, "recipients need to interpret gestures within a larger combinatorial context," which leads to a dizzying array of potential outcomes that researchers must attempt to interpret (p. 8188).

There were several gestures that were unique to a particular group, much like the *grooming hand clasp* is only found in certain populations of chimpanzees (Bonnie & de Waal 2006). Cultural variants are intriguing because they can shed light on how new gestures are acquired, and they can provide more information on the function of certain signals within a group or species (Whiten *et al.* 1999). Several gestures I observed were variants of the same basic gesture that served similar communicative functions. For example, the *drag* gesture used by SDZ bonobos and the *object slide* gesture used by bonobos in both groups were both dominance displays incorporating a large and/or novel object used mainly by adult males (though *object slide* was also used by members of other age/sex-classes). WAP bonobos integrated cardboard boxes into their displays while SDZ mainly used browse for theirs (but when *object slide* was observed in SDZ it was on a day when a cardboard box was given as enrichment). Both gestures served the same purpose in their groups, but they took on different forms. The *gallop* display in gorillas and *bipedal swagger* in chimpanzees also serve the similar function of asserting dominance, but in unique ways (see Figure 5.2 for an illustration of a *bipedal swagger* gesture). The *rock* gesture assumed the same form in chimpanzees, but its usage was very different across groups. At SLZ, certain adult female chimpanzees used this gesture to initiate a particular type of stereotypical traveling (training). At LAZ, adult males used *rock* during dominance displays. Wild bonobos at Wamba have been observed using a *rock* gesture to initiate grooming or other types of body contact, depending on the intensity of the rocking and whether it was used in conjunction with other gestures (Kuroda 1984). In these cases, the form of the signal may be the same, but its function varied depending on the particular group. If transmitted via social learning, this variation can lead to the development of different cultural traditions across groups and populations.

While some gestures have a clear function, others are more difficult to interpret. The frequent *foot clap* gesture used by bonobos was used most often when grooming was already taking place and rarely resulted in a response from the recipient or a change in social context. Ingmanson (1987) and de Waal (1988, 1994) also observed this gesture in San Diego bonobos. De Waal (1994) reported that this gesture was a cultural variant unique to San Diego bonobos and suggested that it was the result of bottle-rearing that spread throughout the group via social learning. According to de Waal (1994), "hand and foot clapping have never been reported for other bonobos captive or wild, and the gestures appear to serve the same communicative function during grooming in the San Diego bonobos as the typical tooth clacking, sputtering, and lip smacking of grooming chimpanzees" (p. 256). However, this gesture has also been observed during grooming in wild chimpanzees at Mahale (Nishida *et al.* 1999), suggesting that the gesture is not exclusive to bonobos in San Diego. The communicative function of this gesture may just be to express a state of arousal while grooming, but since there was no response or change in context, the exact function remains ambiguous.

There were other gestures whose function also seemed to be to express a playful mood or affiliative intent. In bonobos, the *head shake* gesture was used when an individual was approaching another and sometimes led to play between the two, but also often resulted in the actor just being in proximity to the recipient, in the same way a person might extend a hand for another to shake when he approaches to indicate to the other person that the approach is a friendly one. *Ice skate* (gorillas at

BZA), *bow* (chimpanzees and bonobos), and *somersault* (gorillas at BZA and bonobos) were used in similar manners.

5.1.3 Gestural Signaling as a Predictor of Social Dynamics

Gorillas, chimpanzees, and bonobos each have unique social systems, and the distinctive ways in which individuals interact with each other serve to characterize each species. Examining who actors gesture to most frequently, the social contexts in which they gesture, and the patterns that emerge within groups of the same species is a useful means of understanding these social dynamics. My results indicated that the social dynamics of each of these species (particularly for chimpanzees and bonobos) is flexible across groups, such that distinguishing a particular species by their patterns of gestural signaling may not be a straightforward task. However, certain patterns emerged with respect to how often individuals of different age/sex-classes gestured to each other and in what social contexts, and these similarities can be used to differentiate each species. In fact, patterns of gestural signaling can possibly even be used to predict the nature of social relationships within a species. For example, if gestural signaling is infrequent between females in a particular species, it can be reasonably assumed that female-female interactions are also infrequent and those relationships are not critical ones within the social system of that species. Or, if there is a high frequency of gesturing in the context of *agonism*, such a finding is a strong indicator that agonism is a large component of that species' social dynamics.

An examination of the overall patterns of gorilla gestural signaling revealed that gestural communication in gorillas functioned mainly to maintain mother-offspring bonds and relationships between young members of the group. Although there was only one silverback present (in BZA), he gestured infrequently and his gestures were directed mainly to adult females, then equally to young males and multiple individuals within the group. As I predicted, adult females gestured very little to the silverback: Only 1.2% of all adult female gestures were directed at the silverback (n=2 gestures) and both were visual gestures (*head bang* and *staredown*) produced by one female named Imani. These finding are corroborated by the available data from wild gorillas, which describe affiliative behavior as rare and typically limited to interactions between mothers and offspring (Stokes 2004). The absence of older males in BZB perhaps led to the variation in gestural signaling between the two groups. There were only two infant males present in BZB, so adult females gestured more often to each other and to the offspring in the group. The dynamics of the group were more fluid and the offspring interacted frequently with all group members, rather than mainly with their mothers. There was a low occurrence of gesturing in the context of grooming across gorilla groups, which also set them apart from chimpanzees and bonobos. There was also very little gesturing in the context of *agonism*, which was contrary to expectation. In the wild, frequent agonism has been observed between adult females and the silverback, as well as between adult females (Stokes 2004; Harcourt & Stewart 2007). However, the agonism I observed in gorillas was both rare and brief, and did not involve a high frequency of gesturing before or after the interaction. The *gallop* gesture was the main dominance display in gorillas, and it rarely led to prolonged displays or full-blown conflict in the group in the way that *bipedal swagger* or *object slide* gestures often did in chimpanzees and bonobos, respectively. Perhaps the level of agonism in these gorilla groups was lower than that observed in wild groups because there was no potential threat from outside males or immigrant females, which are main sources of conflict for wild groups (Harcourt & Stewart 2007). In any case, the low frequency of agonistic gestures I recorded would appear to accurately reflect the low frequency of agonism that I observed among these gorillas.

Chimpanzees exhibited a different pattern of gestural signaling than gorillas, but there was also significant inter-group variation within chimpanzees, particularly with respect to gesturing among adult females. There were fewer predictable responses to chimpanzee gestures than in gorillas and bonobos, and the social contexts in which gestures occurred were also variable among chimpanzees. However, there were more gestures associated with *grooming* and *agonism* than observed in gorillas or bonobos, which is a strong indicator of the prevalence of those contexts within chimpanzee societies. In both chimpanzee groups, adults gestured more frequently to other adults, but young individuals gestured more frequently to adults than to members of their own age-class. There was only one mother-offspring pair in which the offspring was still nursing (Rosebud and Utamu in SLZ), so young individuals gestured often to adults who were not their mothers. In both groups, male chimpanzees gestured more frequently to group females than to group males. But, there were group differences in the most frequent recipients of adult female gestures: In SLZ, adult females gestured most often to other adult females, while adult females in LAZ gestured most often to juvenile males.

A possible explanation for the variation between gestural communication in the two chimpanzee groups is the type of alpha male present in the respective groups. In SLZ, the alpha male was very solitary and spent almost 95% of his focal sample time *sitting* or *lying* apart from the majority of the group. By contrast, the alpha male in LAZ was much more active and he engaged in many more dominance displays in proximity to the rest of the group. These personality differences certainly could have affected the group dynamics and influenced how often certain individuals gestured with each other and under what contexts. Chimpanzees in the wild and in captivity elsewhere have demonstrated behavioral plasticity similar to that observed in these chimpanzee groups (Baker & Smuts 1994; Goodall 1986; Nishida 1989; Mitani *et al.* 2002). The inter-group variation I observed here with regard to the degree of agonism and the frequency of interaction between adult males and females was accurately reflected in the different patterns of gestural signaling.

Bonobos had unique patterns of gestural signaling that differentiated them from gorillas and chimpanzees. Bonobos gestured at very high rates (particularly WAP bonobos) and the median gestures per individual were greater than any other group or species studied here. The same pattern observed in gorillas and chimpanzees of frequent mother-offspring gesturing was also present in bonobos. Three out of the six adult females across both groups had dependent offspring throughout the course of this study. A unique situation for the dominant individuals in these bonobo groups is that the alpha females were also mothers of nursing infants, thus both alpha females gestured much more frequently than the silverback gorilla or the chimpanzee alpha male because they gestured often to their infants as well as to other group members. However, gestural signaling was not only frequent between mothers and their offspring. In general, gestural signaling was much more fluid across age/sex-classes in bonobo groups. As with chimpanzees, young bonobos gestured more frequently to adults than to members of their own age-class. But, unlike gorillas or chimpanzees, female bonobos gestured almost equally to males as they did to females, and adults gestured almost equally to young individuals as they did to other adults. This frequent male-female gesturing, particularly between adults, reflects a more tolerant social environment in which males and females regularly communicate in a variety of social contexts. Strong relationships between sexes have also been observed in wild bonobos at Lomako, regardless of their relatedness (Hohmann *et al.* 1999). Bonobos used many gestures associated with play and they were used frequently by members of all age/sex-classes. *Bite, bow, head nuzzle, head shake,* and *somersault* were all followed by *playing* in more than 50% of the cases in which those gestures were used. Bonobos have been characterized as more playful than the rest of the African apes (Palagi & Paoli 2007), and many studies have also shown that adult bonobos engage in frequent play behaviors (de Waal 1988; Palagi & Paoli 2007; Palagi 2008). Gestures were not used as frequently in the context of *sex* as I predicted, but *genito-genital rub* and *present genitals* led to a sexual context more frequently in bonobos than in gorillas or chimpanzees (see Figure 5.3 for an illustration of a *genito-genital rub* gesture). Sexual gestures occurred most frequently between females of different age-classes, and as reported for other bonobos (Hohmann & Fruth 2000), these gestures were used in periods of high tension (such as *agonism* or *feeding*) but also during *playing*. Often, play behaviors were interspersed with sexual behaviors, making the recording of purely sexual gestures difficult. It was not uncommon to observe a *genito-genital rub* or *present genitals* during a play bout, particularly bouts involving adult males with young females.

This research was the first to systematically compare the influence of social dynamics on gestural signaling across multiple groups of Africa apes. While there was inter-group variation at some level in all species, patterns of gestural signaling provided clues to the nature of social relationships in a given species and may even be a useful tool in predicting the frequency of interactions between members of certain age/sex-classes and in particular social contexts. The variation between groups of the same species indicates that gestural signaling is flexible enough to meet the needs of a particular group's dynamics; but the major patterns of gestural signaling expressed by each species (*i.e.*, frequency of gesturing between dominant individuals and other group members, mother-infant gestural signaling, and the frequency of gesturing between age/sex-classes) conformed to predictions based on the particular social dynamics that differentiate each species.

5.2 Summary of Positional Behavior and Gestural Signaling

Establishing the locomotor profiles of gorillas, chimpanzees, and bonobos enabled me to clarify the relationship between positional behaviors and gestural signaling. Because I was able to examine not only frequencies of certain positional behaviors, but also the proportions of time spent in those behaviors, I was able to obtain a more complete picture of how the African apes differ. These data were informative for determining how gestural signaling was affected by positional behavior and vice versa. In this section, I summarize the results from my analyses of these data and discuss the implications of these results.

5.2.1 Establishing Locomotor Profiles for Each Species

African apes demonstrated clear similarities in the types of positional behaviors they used. Not surprisingly, there was much more overlap with positional behaviors between groups and across species than there was for types of gestures. All study groups spent less time engaged in locomotion than in postural behaviors, and all individuals were more terrestrial than arboreal. Young individuals of all groups were also significantly more arboreal and used a wider variety of positional behaviors than adults, which was expected since young individuals typically spend more time being active than larger-bodied adults (particularly for gorillas).

Although the range of different positional behaviors was consistent across species, there was variation within species with regard to the proportions of time spent in those behaviors. The environment was a key factor in shaping locomotor profiles, particularly with respect to how much time individuals spent engaged in different modes of locomotion. All groups that had more arboreal substrates available to them spent more time engaged in locomotor behaviors such as *climbing* and *brachiating*. In the wild, African apes also use arboreal substrates for feeding, so positional behaviors like *climbing* and *brachiating* are expected to be used more often in wild populations of all African apes. However, because of their large body sizes, gorillas (especially males) have not been observed to be as arboreal as chimpanzees and bonobos (Remis 1995, 1998; Doran 1996). None of the arboreal structures in any study groups was utilized for feeding, so the function of arboreal substrates was mainly to access areas of the enclosures, to play, to and secure higher vantage points.

Contrary to my predictions, bonobos were not more bipedal than gorillas or chimpanzees. In fact, bonobos exhibited the least amount of bipedality. In all species, bouts of bipedal locomotion or postures were brief (the longest average duration was 12 sec for SLZ chimpanzees) and served different purposes for different age/sex-classes. Bipedality was more frequent and took up a larger percentage of locomotor time in young individuals than in adults for all species except chimpanzees. This bipedality was generally postural and used during play bouts between young individuals or when infants requested rides on the backs or ventrums of their mothers. Wild adult and young bonobos at Lomako have been observed to use bipedality for displays, during feeding, and when carrying food or infants (Susman *et al.* 1980). Videan and McGrew (2001) also found that bonobos in captivity used bipedality mainly for carrying and vigilance, and that bipedality was more frequent in younger individuals. The bonobos in this study used bipedality occasionally for vigilance or for carrying objects, but they did not use bipedality for displays. Rather, bonobos used cardboard boxes provided for enrichment to slide (the *object slide* gesture) or large branches to drag (the *drag* gesture) past group members.

The largest percentage of time spent in bipedal locomotion was observed in adult chimpanzees (3.6% of total time spent in locomotion), which was just slightly above the total for young gorillas (3.1%). The bipedality observed in adult chimpanzees at SLZ was mainly *bipedal standing* (55 counts) and *bipedal walking full* (50 counts). Ninety-eight percent of the *bipedal walking full* counts were by Holly (the adult female who engaged in training locomotion), who often held a burlap sac or other object while traveling with the adult female Bakhari. The average duration of a bipedal bout in SLZ was higher than in LAZ because of these lengthy training bouts. The bipedality observed in adult chimpanzees at LAZ was mainly *bipedal standing* (41 counts) and *bipedal swaggering* (17 counts). *Bipedal swaggering* was primarily done by adult males during dominance displays (88.2% of the counts). This particular locomotion was also recorded as a gesture in data collection because the locomotion was more than just a means of traveling; it was a signal of dominance status to the rest of the group. Other chimpanzees have also been reported to use bipedality more for displays than bonobos in captive environments (Videan & McGrew 2001).

This research was the first to take into account the influence of postures and locomotion on gestural signaling in any African ape species. Collecting comparative data on not only frequencies of positional behaviors but also on the durations of these behaviors was instrumental in establishing overall locomotor profiles for these species and determining the impact of positional behavior on gestural signaling. These data can now be compared to future studies of other captive and wild groups to establish a more complete understanding of how African apes differ in terms of their positional behavior, what variables influence these behaviors, and how postures and locomotion are related to gestural signaling.

5.2.2 Locomotion as Communication

I hypothesized that upper limb availability would lead to increased gestural signaling using the upper limbs, but this prediction was not supported. In fact, it appears that gestural signaling can (and frequently does) occur even when both of the upper limbs are actively involved in locomotion. During the use of gestures like *chase* and *charge*, the upper limbs are actively involved in locomotion. Other visual gestures like *head nod*, *peer*, or *present genitals* do not rely on the upper limbs and can occur in various postures or modes of locomotion. Rather than positional behavior being a hindrance to the use of certain gestures, it instead appears that positional behavior can enhance certain gestures. For example, it is certainly possible to *chest beat* while *sitting*, but it is much more effective to chest beat while standing or moving bipedally (see Figure 5.4 for an illustration of *chest beat* gesture). For example, when an actor is standing, the signal can be received by more group members and an erect posture is much more imposing in a dominance display. This was the case among gorillas that used the *chest beat* gesture more frequently when bipedal than *sitting* even though *sitting* was a more frequent posture. Thus, the relationship between gestural signaling and positional behavior may not really be determined by upper limb availability but more by the need to raise the body for maximum effect when producing gestures. Alternatively, gestural signaling may actually be influencing the locomotor repertoire of the species. This was especially apparent with *bipedal swagger* in chimpanzees, *object slide* and *drag* in bonobos, and *gallop* in gorillas. The acts of moving through the group with a large object in hand or even just piloerected with an erect posture were more powerful displays to group members than *sitting* or *lying* and gesturing with the upper limbs. Other gestures like *ice skate* and *somersault* were also labeled as distinct modes of locomotion since they were used for multiple purposes. For instance, in addition to being a means of moving from place to place, these gestures also indicated the desire to play or were an expression of playfulness by individuals. These types of gestures were used more often by young individuals, but many adult bonobos also used *somersault* as a way of initiating or extending play bouts with each other or with other young group members.

5.3 Repertoire Size and Rates of Gesturing

I predicted that, in all species, juveniles and infants would gesture more frequently and use a greater number of gestures because younger individuals interact frequently with each other, especially in the context of *playing*. This prediction was supported in every group but the LAZ chimpanzees. In that group, there was no significant difference between the average number of gestures produced by adult and young age-classes. The lower average gesturing by young chimpanzees in LAZ may have been the result of there being only three juveniles in the group, all of whom were eight years old. There were no dependent offspring in the group and the juveniles did not engage in as many play behaviors as younger juveniles and infants in other groups.

I also predicted a high frequency of gesturing between mothers and their offspring for all species. This prediction was supported. Mothers and infants were each other's favored gesturing partners in every group in which they were both present (the infant male, Makasi, in SDZ was an orphan). In all African apes, infants nurse for an extended period and ride ventrally and dorsally on their mothers for several years, so there is a constant need for communication during an infant's early years. Bonobos and chimpanzees, in particular, form strong bonds between mothers and offspring that persist past infancy, and offspring will seek out protection or support from their mothers throughout their lives. Some chimpanzee and bonobo mothers also gestured frequently to their adult sons; this was not surprising since more frequent grooming and other affiliative behaviors have also been observed between mothers and their adult offspring (particularly males) in other captive and wild groups (Goodall 1986; Hohmann *et al.* 1999; Stevens *et al.* 2006).

Finally, I predicted that the increased terrestriality and seated postures of gorillas (which frees their upper limbs for gesturing) and the increased bipedal locomotion of bonobos (whose upper limbs would also be free to gesture), would enable them to gesture at higher rates using their upper limbs than chimpanzees. These predictions were not supported by my data for a number of reasons. First, gorillas were not *sitting* more than chimpanzees or bonobos, and bonobos were the least bipedal of the study species (rather than the most bipedal), therefore, their upper limbs were not more available for communication than chimpanzees. Second, gorillas and bonobos did not use gestures that involved the upper limbs more frequently than chimpanzees. All species used a variety of gestures that involved some or no use of the upper limbs to a similar degree.

Most importantly, there was considerable variation with regard to rates of gesturing within species. In all three species, social groups gestured at significantly different rates from each other, so there was no clear pattern of how frequently a certain species gestured. There was also significant variation in how frequently individuals gestured within groups. All groups had a very wide range of gestures produced per individual, with adults typically at the lower end and young individuals typically at the higher end. Bonobos were at the high end of the gesture frequency scale, with 45 being the lowest number of gestures produced by a single individual (an adult female in SDZ) and 954 being the highest number of gestures produced by a single individual (an infant female in WAP). WAP bonobos used 36.1 gestures per hour, which was much higher than all other groups and more than twice the rate of SDZ bonobos. By contrast, the lowest-gesturing gorilla used 4 gestures (an adult female in BZB) and the highest-gesturing gorilla used 315 gestures (a juvenile female in BZA). But, BZA gorillas had the next highest rate of gesturing at 17.7 gestures per hour. It is unclear why gesturing rates differed so much between two groups of the same species or why bonobos gestured so frequently, but it is evident that gestural signaling rates vary widely within groups and within species. Perhaps rearing histories influenced the rates of gesturing within a group. Gestural signaling rates could also have been influenced by individual personalities or age differences. Groups with older individuals may gesture less than groups with younger individuals or particularly gregarious or agonistic group members may affect gestural signaling rates within groups to a greater degree than anticipated.

5.4 Implications for the Origins of Human Language

This investigation of gestural signaling in African apes yielded new and valuable data regarding how social dynamics and positional behavior influence the rates of gesturing within groups, the frequency of gesturing among age/sex-classes, and the social contexts in which gestural signaling occur. The overarching finding is that gestural signaling is flexible, variable, multi-functional, and often interchangeable with positional behaviors. But, what does this research contribute toward our understanding of the origins and evolution of human language? Is gestural signaling a viable precursor to human language?

The theory that language originated from gestures is based, in part, on the flexibility of gestures in human and non-human primates, and the fact that gestures are universal in modern human communication. A growing body of research has shown that neural networks involved in language production and comprehension are also active during body movements and gesture production and processing, and these networks have correlates in non-human primates. In humans, even observing a hand grasping an object has been shown to influence syllable pronunciation (Gentilucci 2003). These findings demonstrate evolutionary continuity between language and bodily actions in primates (Kelly *et al.* 2002; Arbib 2005) as well as highlight an important feature of gestural signaling- that body movements and language comprehension and production are inherently connected.

Tomasello and Call (2007) assert that: 1) flexible gestural signaling, 2) increased sensitivity to audience effects inherent in comprehending visual signals, and 3) the development of an interest in sharing intentional states with others were three milestones of language evolution. The authors argue that these developments were more likely the basis for symbolic communication than were vocalizations

(Tomasello & Call 2007). These results provide evidence for flexible gestural signaling and sensitivity to audience effects across the African apes studied here, but I did not find any support for they type of referential gestural signaling that involved shared intentions such as declarative or imperative pointing or iconic gestures that represented external actions or objects.

Limited evidence for referential gesturing has been reported among non-human primates, and no observations of pointing have been reported for untrained captive or wild non-human primates. Iconic gestures have been observed, but they are certainly not abundant in the African ape gestural repertoire. Savage-Rumbaugh *et al.* (1977) reported the use of iconic gestures in language-trained bonobos, and Tanner and Byrne (1996) reported that a captive silverback gorilla used iconic gestures to direct a female's movements. More recently, referential gesturing was reported between pairs of adult male chimpanzees in the wild when actors used a "directed scratch" gesture to direct recipients' attention to their own bodies, presumably to request that the recipients groom there (Pika & Mitani 2006). This type of signaling has never been reported elsewhere and the gesture was not referential in the sense that it directed another's attention to an external referent since the gesture was directed at the actor's own body.

If gestural signaling is indeed a precursor to human language then an obvious questions is: Why don't apes point or use other referential signals such as pantomimes or emblems in similar ways to humans? Tomasello (2006, 2008) argues that the difference between human and ape gesturing lies in the cognitive underpinnings of certain types of gesturing. Pointing (whether declarative or imperative) and other referential gesturing involves a more cooperative mode of communication in which two parties work together to achieve a shared goal or direct attention elsewhere, and the actor may adjust communication or incorporate other behaviors such as gaze following depending on whether the recipient responds appropriately.

Evidence from experimental studies conducted by various research groups demonstrates that apes (particularly chimpanzees) know something about what humans and conspecifics see and know (*e.g.*, Call & Tomasello 1999; Hare *et al.* 2001; Povinelli *et al.* 2003; Vonk & Povinelli 2006), but the field is divided about whether these experiments are actually testing the abilities they are designed to test. Regardless of experimental protocol, naturally occurring referential gestures are rare in the African ape gestural repertoire. In order for a pointing gesture to be effective, the actor needs to direct the recipient's attention to an external object or event and the recipient needs to have some kind of shared understanding of the motivation behind the gesture. Is the actor requesting an object? Is the actor directing the recipient's attention to something useful or interesting, and if so, what should happen next? This sort of communication relies not only understanding another's orientation and attentional state, but also on being able to read the intentions or motivations of others and respond accordingly. These skills develop in human infants prior to linguistic development (even in congenitally blind children who cannot actually see what others see: Bedny *et al.* 2009), but they are not apparent in non-human primates (Tomasello 2006, 2008; Liebal & Tomasello 2009; Tomasello & Herrmann 2010).

The great divide between human gestural signaling and that of the African apes may therefore lie in the acquisition of cognitive abilities that enable one individual to interpret the intentions and motivations of another and cooperate to achieve a similar goal (Tomasello 2006, 2008; Liebal & Tomasello 2009; Tomasello

& Herrmann 2010). Perhaps pointing and other forms of gestural signaling like pantomimes and icons involve more complex cognitive processes (like theory of mind and joint attention) that were not acquired until later in hominin evolution, and thus are not present in other apes. Tomasello and Moll (2010) propose that these cognitive abilities may have evolved in humans because of collaborative thinking and actions, cooperative communication, social cognition, and cultural learning.

The theory that language originated in gestures is also based on a shift toward bipedality in early hominins that provided an opportunity for the upper limbs to become more available for gestural signaling. Using the upper limbs (along with facial expressions), communication could be achieved between group members over long distances without drawing attention from predators like vocalizations potentially could. However, my findings do not provide support for this argument. I hypothesized that bonobos would be more bipedal than gorillas and chimpanzees, and as a result, they would gesture with their upper limbs more frequently. However, bonobos were not more bipedal and gestures involving the use of one or both upper limbs occurred in similar frequencies across all three species. Young individuals of all three species gestured when bipedal (mainly during play bouts) more frequently than adults, with one exception: Adult male chimpanzees. The prominent dominance display of adult male chimpanzees was *bipedal swagger*, which was also a frequent mode of locomotion. Adult males gestured when in bipedal locomotion, but the gesture was not restricted to the upper limbs. Rather, the gesture was the locomotion itself. Nine of the 49 total gestures observed in all species had a locomotor component, and four could only be done in specific postures. For example, *ice skate, somersault, charge, gallop,* and *back pounce* were all gestures that were defined by their specific locomotion. Gestures and positional behavior are clearly strongly connected, just not in the limited manner involving the upper limbs that I predicted.

Kelly *et al.* (2002) argue that “the original functions of communication and language systems were perfectly suited for the body, and that the body continued to shape language over time (p. 324).” These results demonstrate that gestural signaling expresses the kind of behavioral and locomotor plasticity that could have given rise to a flexible, complex form of communication that eventually became language. Body movements can speak volumes about the mood or intentions of another, and gestures can be made more powerful when they are tied to erect postures or locomotion. My results do not provide support for the freedom of the upper limbs as an impetus for a shift in gestural signaling related to bipedality. But, perhaps the types of gestures already being used by early hominins when bipedality became more habitual were modified and adjusted to fit within a changing locomotor profile. If early hominins were already using gestures similar to *bipedal swagger*, *back pounce*, and *charge* as dominance displays (in addition to a suite of other tactile, visual, and auditory gestures) before the transition to habitual bipedality, then incorporating the upper limbs and an erect body posture would have been a natural transition. Donald (1991) argues that the transition to obligate bipedality could have sparked the development of “mimetic culture,” in which mimed movements of the hands and body were used to communicate about external events. This type of gesturing, along with the use of increasingly controlled speech, could have been the basis of human language. The use of body postures and locomotion as communicative tools has remained crucial to communication, even after speech blossomed. We often talk about reading each other’s “body language” and seem to take for granted the importance of manual gestures and body postures in our every day interactions.

Evidence of the importance of the body as vehicle for communication can be found in child development, sign languages, dance and other performance art, and even in the brain with the discovery of the mirror neuron network. Language may now be dominated by speech, but communication is still in many ways rooted in the body.

5.5 Limitations of This Research

No research conditions are ever perfect and every project could always benefit from a larger sample size. This study was made more robust by the inclusion of two groups of each species, but the addition of a third group may have clarified patterns and enriched the picture of gestural signaling across species. Increasing the sample size would also contribute to our understanding of just how flexible the gestural and locomotor repertoires of these species are and what other factors may influence gestural signaling in African apes.

Conducting this research in a captive setting was instrumental in enabling me to capture subtle movements and social interactions, but this also brought about a unique set of issues such as the diverse rearing histories of individuals and constant interaction with humans that are not necessarily factors in a wild setting. As I discussed in Chapter 1 (section 1.1.3), social dynamics can certainly be altered in captivity, and one way that this may have influenced my research was the inability for individuals to transfer to other groups of their own volition. At almost every study site, individuals were transferred to other facilities or new individuals were introduced either while I was collecting data or immediately before or after the study period. This obviously serves the same purpose and individuals must navigate changing group compositions and social relationships. But the fact that individuals are not in control of this process may have increased levels of agonism between certain individuals or even increased affiliations between unlikely partners because they associated more with each other than they may have in the wild. I did not observe any patterns of gesturing signaling or other social interactions that I could directly attribute to the captive setting (though the rocking and training behavior observed in SLZ does not appear to be typical chimpanzee behavior). Nonetheless, the possibility existed that social relationships (and thus gestural signaling) could have been influenced by close associations or other aspects of captive life.

Clear differences in positional behavior, however, could be pinpointed based on environmental features of certain enclosures. All groups that had access to more arboreal substrates (and the need to use these substrates to access different areas of the enclosure or secure better vantage points) exhibited more arboreal positional behavior (particularly at SLZ and SDZ). Even though the structural differences between enclosures were not quantified, variation in arboreal locomotion and time spent on arboreal substrates between groups of the same species was most extreme in groups that were housed in enclosures that contained a greater number and variety of arboreal substrates. Other factors such as female reproductive cycles, dominance rank, and kinship may have also played a part in shaping gestural signaling in these study groups, but these were not explored within the scope of this thesis.

The social dynamics I used as templates for each species were ascertained from the published literature. I used descriptions of the nature of social relationships and the frequency of interactions for each species as the basis for my predictions about the social dynamics expected for these study groups. Thus, I did not collect independent data to verify the social dynamics of these particular study groups. Therefore, differences in patterns of gestural signaling may have been a reflection of some unique aspect of the dynamics of these particular groups rather than the established social relationships used to characterize these species as a whole. However, based on my months of observation while collecting data on these groups, I feel confident that the social relationships within these groups were well within the variation reported elsewhere for each species.

Researchers attempt to simplify communication into actors, signals, and recipients, but it is an intricate dance that often involves several individuals, multiple modalities, and unclear outcomes (King 2004). Many gestures were used in combination with each other and gestures were often used repeatedly until the desired effect was achieved. Chimpanzees have been shown to use these types of gestural sequences when recipients are unresponsive or when stringing together tactile gestures during play bouts (Liebal *et al.* 2004a). Not only were gestures used in combination, but other modes of communication were also used along with gestures, such as facial expressions and vocalizations. For example, when bonobo infants requested rides from their mothers, they often used a *grab* or *pull* gesture while also pursing their lips and sometimes grunting softly. I did not study this multimodal communication in the framework of this study, but it would be intriguing to explore whether using gestures, facial expressions and vocalizations in concert with one other enhances the communicative message and affects how recipients respond (Partan & Marler 1999). Recently, Slocombe *et al.* (2011) have argued for an integrative, multimodal approach to studying primate communication that considers the roles of facial expressions, vocalizations, and gestures in shaping human language. Triadic interactions were also common, particularly during agonism when several group members who were not originally involved in the encounter would gesture to each other and to the original dyad. These interactions were difficult to interpret and analyze in this study, but nonetheless, they were a relevant component of gestural signaling.

5.6 Avenues for Future Research

An obvious next step for this research is to do a comparative study with each species in the wild to determine exactly how patterns of gestural signaling and types of gestures compare to wild populations. As more groups are studied, we can also answer more questions about cultural variants of certain gestures. For example, how prevalent is the *foot clap* gesture or something equivalent to it across bonobo groups? It would also be interesting to explore how gestural signaling varies in bachelor groups of wild western lowland gorillas or how gestural signaling changes between the silverback and younger males as young males approach maturity. I am also interested in testing the effects of party size and composition on gestural signaling in chimpanzees and bonobos, since these are variable across field sites. Much more comparative data are needed for locomotor profiles of wild African apes as well. It is important to not only collect data on frequencies of positional behaviors but also data on the durations of these behaviors so that we can determine how much time African apes spend in various positional behaviors and how proportions of time spent in certain behaviors differ by age/sex-class.

Another interesting facet of gestural signaling is how it is affected by relatedness. Do related individuals gesture more with each other? Does this end after the juvenile period or extend into adulthood? Enciso *et al.* (1999) showed that silverbacks in captivity were significantly more affiliative and tolerant with their own offspring than with other infants in their social groups who were unrelated. The effects of relatedness were difficult to determine in these groups because many animals were related to some degree, even across zoos. But, it would be fascinating to study those relationships systematically and explore gesturing between parents and offspring and the role of social learning in gesture acquisition of young individuals.

Finally, this research has obvious connections to the study of cognitive psychology. Patterns of communication infer underlying cognitive abilities associated with shared intentionality, decision-making, joint attention, theory of mind, and self awareness (Pika & Mitani 2006; Pollick & de Waal 2007; Liebal & Tomasello 2009; Tomasello & Herrmann 2010), yet how these abilities evolved and how they relate to human language evolution are not fully understood. Gestures like declarative and imperative pointing, emblems, and pantomimes are vital components of human gestural signaling, yet there seems to be a great divide between the symbolic and referential gestures of humans and the meaningful yet limited gestures of African apes (Tomasello & Herrmann 2010).

The ability to adjust communication based on the attentional states of others was likely a building block for the development of more advanced cognitive abilities like joint attention and theory of mind, and these abilities were no doubt important to human language evolution, perhaps even forming the basis for intermediate stages of “protosign” and “protolanguage” (Arbib *et al.* 2008). More research that aims to explicitly examine the functional and intentional meanings behind ape gestures (*e.g.*, Cartmill & Byrne 2010), explore the nature of collaborative and triadic interactions (*e.g.*, Tanner & Byrne 2010), and discover new experimental approaches for investigating the cognitive underpinnings of gestures (*e.g.*, Hare *et al.* 2001; Vonk & Povinelli 2006) will aid in our understanding of this flexible, multi-functional, highly variable mode of communication. Understanding how certain cognitive abilities differ within and between humans and African apes can provide more information about the origins and evolution of these abilities and their impact on the evolution of language. Gestures are clearly tied to speech and connected to bodily actions. Future work regarding the relationships between cognition, language comprehension and production, positional behavior, and gestural communication will shed more light on just how intimately connected gestural signaling is to our bodies and minds and how it may have evolved in early hominins.

Figure 5.1 Illustration of the *arm raise* gesture by a young male bonobo.

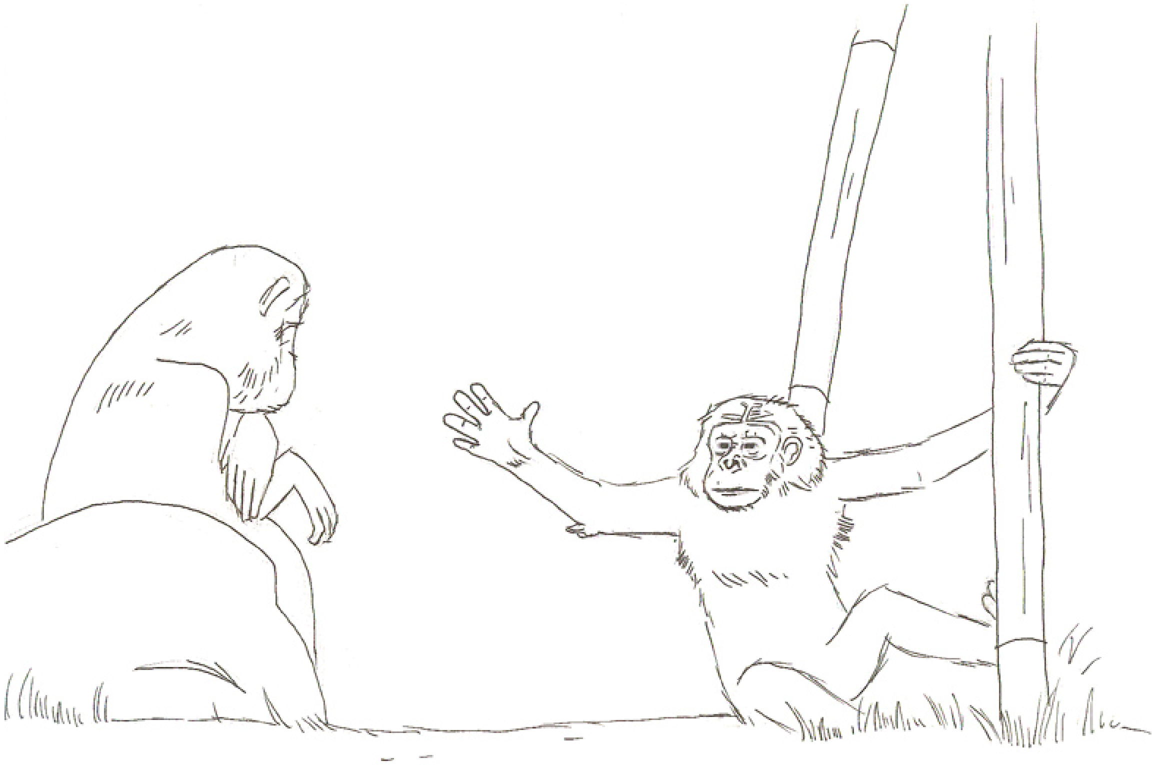


Figure 5.2 Illustration of the *bipedal swagger* gesture by an adult male chimpanzee.

Figure 5.3 Illustration of the *genito-gential rub* gesture between two adult female bonobos.

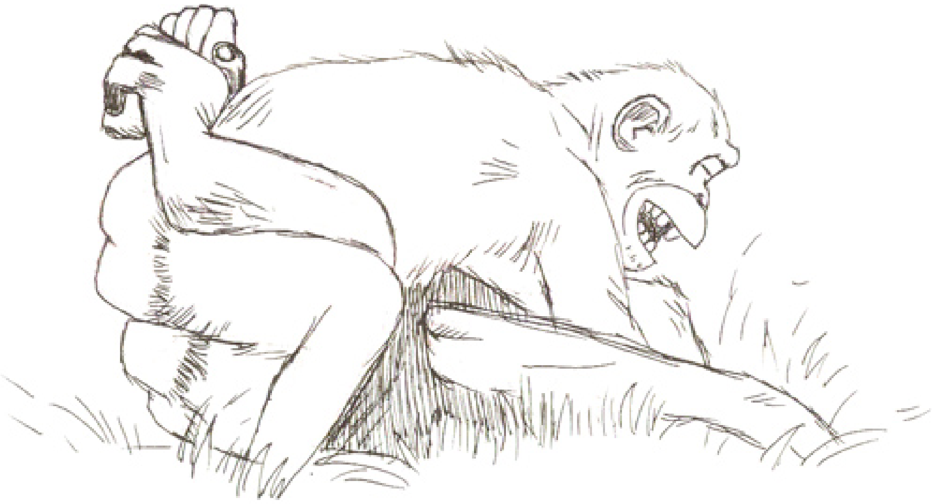


Figure 5.4 Illustration of the *chest beat* gesture by a young male gorilla.

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