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Sara A. Skiba
Kennesaw State University

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Sara A. Skiba

Kennesaw State University

Department of Ecology, Evolution and Organismal Biology

Master of Science in Integrative Biology Thesis

Major Advisor: Jared P. Taglialatela, Ph.D

Thesis Committee Members: William Ensign, Ph.D

Martin Hudson, Ph.D

Table of Contents

Abstract

Human spoken language represents the most elaborate communication system, however the selection pressures leading to its emergence are still uncertain. Unlike humans, bonobos and chimpanzees do not have language. However, bonobos may have been subjected to similar selection pressures as early hominins, subsequent to their phylogenetic split from chimpanzees roughly 1.5 million years ago. The current study investigated the similarities and differences in sociality and communicative production between bonobos and chimpanzees in captive settings, using 9, 10-minute focal follows for each individual. Analyses revealed a significant positive correlation between social proximity score and total communicative signals produced, as well as a significant positive correlation between the proportion of time spent playing and total communicative signals produced, for both bonobos and chimpanzees. Additionally, a significant negative correlation was found between the proportion of time spent grooming and total communicative signals produced. Furthermore, a MANOVA indicated a significant species differences in overall communicative production and social proximity score. Specifically, bonobos produced significantly more signals and spent more time in close proximity to conspecifics than chimpanzees. These data are consistent with previous findings that bonobos travel in larger social groups, have greater flexibility in their communicative production, and have the largest communicative repertoires of all non-human ape species. The multifaceted relationship between sociality and communication, and species differences in socio-communicative behavior observed in bonobos and chimpanzees, can provide insight into the evolutionary origins of human spoken language and complex social behavior.

Background and Introduction

Human spoken language represents the most elaborate communication system in the animal kingdom, however the selection pressures and adaptive value of behavioral adaptations leading to its emergence are still uncertain. Although these evolutionary factors are unknown, there is an evident relationship between communication and sociality; the fundamental purpose of language is to communicate socially relevant information (Bateson, 1972a,b; Pinker, 2003; Binkerton, 2017). Not surprisingly, it is proposed that the intricate communication system exhibited by humans may be the result of selection pressures associated with living in large, dynamic social groups (Bateson, 1982; McComb & Semple, 2005; Dunbar, 1996; Leavens, Taglialatela & Hopkins, 2014). The adaptive value of social living, and evidence of a complex socio-communicative relationship, is apparent in a number of avian and mammalian species (Silk, 2007a,b). These relationships, however, are highly diverse and vary across species and social group; therefore, we must first consider how the fundamental factors of sociality influence communicative complexity in order to better understand how these adaptations evolved.

The foundational aspects of a communication system involve a sender that encodes information into signals and transfers this information to a recipient, who then must decode the information. The sender is invested in the accurate transfer of information and intends for the signal to elicit a behavioral response. Additionally, complex communication systems are commonly linked to social contexts; for example, individuals will modify their communication depending on which social partners are in the audience (Pinker, 2003; Bickerton, 2017). Social complexity can be represented by multiple metrics including the number of social agents interacting with one another, the number of different social roles, and the diversity of interactions between social agents (Freeberg et al., 2012). As social groups become larger, there are more

possible social agents leading to more diverse interactions between individuals, and greater ambiguity in the system. In order to combat this uncertainty, and to communicate effectively with social partners, individuals must utilize increasingly complex and distinct communicative signals. Therefore, the increasing demands of large social groups, and complex social interactions that likely occurred in the hominin lineage may have necessitated increasingly elaborate communicative strategies (Leavens et al., 2014; Pinker, 2003; Freeberg et al., 2012). Most commonly referred to as the social complexity hypothesis, this theory highlights the important influential relationship between complex communication and sociality, and the consequences of living in large, dynamic social groups.

Although there is increasing evidence of an evolutionary link between complex communication and complex sociality, as it pertains to spoken language, there is much debate as to what communicative modality (vocal, gestural or multimodal) primarily influenced this adaptation (Lehmann, Kortjens & Dunbar, 2007; Silk, 2007; Taglialatela, Russell, Schaeffer & Hopkins, 2011). Theories in support of gestural origins of language evolution highlight that this communicative modality is virtually unique to humans and apes, while vocal communication is seen across a variety of species (Arbib 2005; Arbib, Liebal & Pika, 2008; Corballis 2003). Gestures are context specific and can have a variety of meanings and intentions making them a valuable communicative tool in complex social groups (Arbib et al., 2008). This has led Corballis and others to argue that intentional human communication originated in the hands and emerged as spoken language through the mouth and larynx. He states that as primates became bipedal their hands were freed up to perform more meaningful communicative gestures and these gestures were soon accompanied with facial and vocal signals (Corballis, 2003). These new

communicative strategies allowed for narratives and richer social interactions between conspecifics.

In contrast, theorists in favor of vocal origin theories argue that complex communication, specifically human spoken language, is an adaptive response to the increasing societal demands associated with increased group size (Dunbar, 1996; Fitch, 2000; Pinker, 2003). More specifically, theorists emphasize the facilitative effect communication has on the maintenance of social bonds (Freeberg et al., 2012; Dunbar, 1996). Grooming is one of the most crucial mechanism for maintaining social relationships in primates, and it is seen as a reciprocal social behavior, especially in species with shallow dominance hierarchies (Stevens, Vervaecke, de Vries & Van Elsacker, 2005; Watts, 2000). Previous work has demonstrated that grooming not only provides the receiver with physiological benefits (e.g. the removal of dead skin and parasites), but it also provides the groomer with social benefits at a later time including support from other individuals during agonistic interactions (Stevens et al., 2005; Watts, 2000). In social primates, grooming rates increase as group size increases; however there appears to be a limit to the number of social partners that can be attended to with manual grooming (Lehmann et al., 2007; Dunbar, 1996). Specifically, when group size exceeds a critical number, manually grooming each socially partner becomes unrealistic given the amount of time necessary for survival behaviors, such as foraging, (Dunbar, 1996; Lehmann et al., 2007; Leavens et al., 2014). Therefore, it has been proposed that the adaptive value of complex vocal communication is to act as an affiliative call, substituting the need for manual grooming, and allowing for more time to forage and travel. Most specifically, it is hypothesized that physical grooming was replaced with auditory communication in the hominin lineage as a mechanism to maintain strong bonds with a large number of social partners (Dunbar, 1996; Leavens et al., 2014).

Similar to gestural and vocal origins, and building upon their commonalities, multimodal origins of language evolution argue multimodal signals, from *both* visual and auditory domains, allow for more complex information to be exchanged and therefore allow for more dynamic social interactions. These complex signals are said to be necessary when social groups become so large that there is increased uncertainty and diversity during signal production (Freeberg et al., 2012). In order to combat this ambiguity, individuals must utilize complex, distinct signals to provide the target recipient with accurate information. Multimodal theorists converge the theoretical frameworks of gestural and vocal origin theories, and have found support of communication originating in the hands, traveling to the mouth, and finally larynx, as well as evidence of affiliative auditory signals (Leavens et al., 2014) Most specifically, it is argued that complex communication, specifically spoken language, co-evolved through the visual and auditory modalities as a means of conveying social information and of facilitating social bonds (Leavens et al., 2014; Taglialatela et al., 2011).

Although there is great debate over which communicative modality human spoken language evolved through, most origin theories emphasize the important evolutionary link between complex sociality and communication, with human language representing the most elaborate form. Although it is not possible to examine the socio-communicative behaviors of our hominin ancestors, it is possible to examine the behavior of our closest extant relatives, bonobos and chimpanzees. These ape species have intricate social interactions and produce complex vocal and gestural signals, many of which are closely tied to the species' social behavior (Pollick & de Waal, 2007; Stanford, 1998). The present study will investigate the adaptive value of socio-communicative behaviors in bonobos and chimpanzees, to better understand the selection pressures that may have led to the emergence of spoken language in the hominin lineage.

Complex Socio-Communicative Behavior Across Animal Species

A consideration of the various ways complex socio-communicative behavior manifests across species is necessary in order to efficiently investigate the adaptive value of complex socio-communicative behavior. A variety of avian, cetacean and primate species living in large social groups exhibit greater communicative complexity and social diversity than species living in smaller social groups (Krams, Krama, Freeberg, Kullberg & Lucas, 2012; Marino, 2002; Freeberg & Harvey, 2008). Similarly, among these social species, there is a reoccurring, dynamically complicated relationship between sociality and communication. Although living socially may be inherently costly due to increased resource competition, species living in large social groups benefit from social living by experiencing increased protection from predators, increased mating opportunities and genetic diversity, improved access to consistent food resources, and occasionally direct benefits to reproductive fitness (Silk, 2007a,b; Engh, Esch, Smale & Holekamp, 2000; Henzi & Barrett, 2003).

As stated previously, larger group size leads to increased social complexity and therefore necessitates more flexible communicative systems (Silk, 2007a,b). For example, there is evidence that vocal repertoires of chickadees are influenced by the social complexity of the group (Freeberg & Harvey, 2008). In 2006 Freeberg found that Carolina chickadees, both in the wild and in captivity, living in larger social groups produced calls containing more information (greater level of uncertainty measured by bits) than individuals living in smaller social groups. It is important to note that individuals living in larger social groups did not produce more calls, however they produced more complex communicative signals, containing more informational bits (Freeberg, 2006). Complex socio-communicative relationships are also evident in cetacean species living in large social groups. Dolphins, for example, have intricate and complex

communication systems including vocal, tactile and visual signals (Marino, Connor, Fordyce, Herman, Hof, Lefebvre & Lusseau, 2007). Additionally, there is a link between tonal sound production, and social structure and composition in whales (May-Collado, Agnarsson, & Wartzok, 2007). Specifically, increases in tonal sound modulation were significantly correlated with overall group size and social structure, meaning whale species that live in large, more dynamic social groups exhibit greater vocal control and flexibility than whales living in smaller social groups (May-Collado et al., 2007). Similarly, sciurid rodents exhibit group size influences on communication; specifically, researchers found that social group size predicted whether or not individualized alarm calls were present in the sciurid species (Pollard & Blumstein, 2012). Furthermore, primate species living in larger social groups exhibit greater proportions of time spent grooming and also have larger vocal repertoire sizes than those living in groups with fewer individuals (Lehman et al., 2007; McComb & Semple, 2005). Consistent across all of these studies is a clear relationship between group size and socio-communicative behavior, which supports the idea that increases in group size lead to more social roles and more diverse social interactions, therefore requiring more complex communication; however, more relevant to the understanding of human spoken language is in what various ways communication and social diversity interact (Freeberg et al., 2012).

There is an increasing number of studies that critically demonstrate the varying interactions between aspects of sociality and communication. In addition to group size influences on vocal production, Freeberg, along with Harvey (2008), also found an association between male sociality and call production in Carolina chickadees; individual males that spend more time perched in close proximity to their female cage-mate produce higher call rates than males that spend less time perched near the female (Freeberg & Harvey, 2008). The authors conclude that

these contextually dependent vocalizations may function to facilitate social cohesion. Most specifically, is it possible that the species typical "chick-a-dee" calls may act as affiliative calls, which is consistent with Dunbar's hypothesis that vocalizations initially acted as affiliative calls early in the hominin lineage (Freeberg & Harvey, 2008; Dunbar, 1996; Leavens et al., 2014). Similar to Freeberg and Harvey's findings, the vocal repertoire sizes of wren males from polygynous species are significantly larger than the vocal repertoire sizes of monogamous males, suggesting potential influences of social structure and mating systems on vocal repertoire size (Kroodsma, 1977; Freeberg et al., 2012). In addition to the group size influences on communication observed in sciurid rodents, researchers also found that diversity of social roles predicted vocal repertoire size among sciurid species (Pollard & Blumstein, 2012). The experimenters concluded that varying aspects of sociality differentially drive certain aspects of communicative complexity, and that the complex socio-communicative relationship observed across animal species is multi-faceted and deserves considerably greater attention (Pollard & Blumstein, 2012).

When considering primates specifically, there are multiple non-human species that produce context dependent communicative signals and exhibit complex communicative strategies in relation to larger group sizes and increased diversity of social interactions (McComb & Semple, 2005; Gros-Louis, 2002; Krams et al., 2012). The calls of white-faced capuchin monkeys, for example, have been found to facilitate social interactions and are produced more often in contexts where there is an anticipated behavioral response (Gros-Louis, 2002). Similarly, some sooty mangabeys vocalizations, for example grunts, screams and copulation calls, are specific to the behavioral context they're produced in, and in comparison to other monkey species, are suggestive of a phylogenetic influence on communicative complexity,

meaning across evolutionary time the communicative signals of primate species became more complex (Range & Fischer, 2004). In addition to monkey species, apes also exhibit elaborate socio-communicative behaviors. Among the two ape species most closely related to humans, chimpanzees and bonobos, it has been reported that individuals modify vocalizations depending on behavioral context and social audience (Gruber & Clay, 2016; Liebal, Waller, Slocombe & Burrows, 2014). Not surprisingly, it has been proposed that complex vocal communication and complex sociality co-evolved in primates with specific emphasis given to the facilitative role communicative signals serve in the evolution of complex sociality (McComb & Semple, 2005). This co-evolution in primates was assessed by comparing the vocal repertoire sizes, grooming rates, and group size of 42 primate species (McComb & Semple, 2005; Rowe, 1996). Researchers found that among primate species, increases in vocal repertoire size were associated with increased grooming rates and group size. Additionally, there is a positive relationship between vocal repertoire size and grooming rates, suggesting communication has facilitative effects on primate sociality (McComb & Semple, 2005). More recently, it has been proposed that complex sociality is "an ecological determinant of increased vocal complexity", specifically within the hominin lineage (Leavens et al., 2014; Dunbar, 1996).

As indicated above, living socially can provide species with a number of benefits including protection from predators and increased reproductive success. In bird species for example, living socially is associated with reduced predation risk and increased reproductive success. Brewer's blackbirds, for example, live in a variety of nesting patterns, and predation risk was found to be highest amongst nest sites that were widely dispersed, and lowest among clumped nest colonies (Horn, 1968). Similarly, individual birds living in clumped nest colonies

had higher reproductive success than individuals living in linearly dispersed nest sites (Horn, 1968).

In addition, there is evidence that increased social diversity can be a predictor of reproductive fitness in mammals as well (Frere, Krutzen, Mann, Connor, Bejder & Sherwin, 2010). In wild bottlenose dolphins, social variance explained 44% of the variation in calving success; female dolphins living in larger, more diverse social groups produced more viable offspring. (Frere et al., 2010). Another example of the direct reproductive benefits to living in large, socially complex groups has been observed in female baboons; higher ranking female baboons have shorter inter-birth intervals and produce offspring that are more likely to survive past the first year, than lower ranking females (Bulgar & Hamilton, 1986). Theorists postulate that the socially influenced reproductive rates of baboon females are indicative of the adaptive benefits of living socially and of holding higher status in the group. Furthermore, it is proposed that an individual's sociality is important for counterbalancing hierarchy discrepancies in large social groups, and complex socio-communicative behavior facilitates the necessary social advances. (Silk, 2007; Henzi & Barrett, 2003).

Considered collectively, these findings provide evidence of an adaptive link between increases in social diversity and communicative complexity, as a function of living in large social groups. Living socially is adaptive for a number of reasons, including lowered predation risk, increased mating opportunities, and improved reproductive success. As such, it is not surprising that a complicated relationship between sociality and communication exists in numerous species including birds, rodents, cetaceans, and most importantly for this discussion, primates. This relationship is also evident in humanity's closest living relatives, chimpanzees and bonobos; therefore, the current study investigated the socio-communicative behavior of these

two species. By studying how the two species most closely related to humans differ in their social behavior and communication, we hope to better understand how human spoken language evolved to be the most complex socio-communicative system.

Justification for Studying Bonobos and Chimpanzees

Bonobos and chimpanzees exhibit similarly complex socio-communicative behavior, have the largest foraging party sizes and vocal repertoire sizes of all non-human apes, and have the highest rates of grooming among all ape species (Stanford, 1998; McComb & Semple, 2005). Additionally, bonobos and chimpanzees demonstrate levels of flexibility in the production and perception of gestural signals, as well as vocalizations to some extent; individuals are able to intentionally produced signals and modify them depending on social context (Liebal et al., 2014; Gruber & Clay, 2016; Hopkins, Taglialatela & Leavens, 2007). These two species live in highly social, multi-male, multi-female groups, and have been observed to use socio-communicative behaviors to influence overall social standing (Liebal et al., 2014; Gruber & Clay, 2016). The communicative flexibility and social complexity exhibited by bonobos and chimpanzees, as well as their genetic similarities to humans, make them unique models for human socio-communicative behavior, and can provide unprecedented insight into the evolution of the complex socio-communicative behavior exhibited by humans.

Despite the fact that chimpanzees and bonobos only diverged from a common ancestor approximately 1.5 million years ago, the two species display noted differences in social structure, vocal flexibility, and feeding ecology, which may provide additional insights into the origins of human spoken language. Bonobos are a matriarchal species that is seen to be more tolerant and participates in high levels of socio-sexual behavior (Parish, de Waal & Haig, 2000; Stanford, 1998). On the contrary, chimpanzees are considered to be a more belligerent and territorial

species that participates in higher levels of intra- and inter-specific aggression, and is primarily lead by a single alpha male (de Waal, 2007; Stanford, 1998). Bonobos travel in larger feeding parties and live in larger social groups in the wild, which has led to the common perspective that bonobos are more social than chimpanzees (Doran, Sugiyama, Fleagle & Heesy, 2002; Stanford, 1998). It has also been shown that bonobos have more flexibility in their vocal production, have larger vocal repertoires, and rely more heavily on auditory communication while foraging than other ape species (Moore, 2014; McComb & Semple, 2005; Bernejo & Omedes, 1999; Rowe, 1996). Therefore, it is proposed that because of the increased group size and accompanying social complexity and vocal flexibility observed in bonobos relative to chimpanzees, recent bonobo evolution (i.e. in the approximately 1 million years since their divergence from chimpanzees) may be analogous to hominin evolution following the split between the most recent common ancestor of bonobos, chimpanzees, and humans.

The present study aims to examine the rich and complex social behaviors of bonobos and chimpanzees in a captive setting through behavioral observations, while also recording the frequency of communicative production. Given bonobos' increased vocal repertoire size and larger social group sizes in the wild, it was hypothesized that bonobos would spend more time engaged in social behaviors and in closer proximity to conspecifics, and would produce more communicative signals than chimpanzees. Additionally, it was hypothesized that there will be a positive association between communicative production and social behavior. Specifically, individuals that produce more communicative signals will exhibit more prosocial behaviors than individuals that produce less communicative signals; Most specifically, highly communicative individuals will spend more time engaged in grooming, playing, and in closer proximity to conspecifics. Overall, the project aimed to understand the adaptive value of being

communicative by observing the social behaviors of bonobos and chimpanzees; two species

demonstrating similarly complex social behaviors, cognitive abilities and communication

systems as humans. In this way, this study investigated whether or not socio-communicative

behavior facilitates the maintenance of strong social bonds.

Materials and Methods

Behavioral Observation Data Collection

In order to investigate the relationship between sociality and communicative production

and assess the socio-communicative behavior of chimpanzees and bonobos, focal follow data

were collected on 24 chimpanzees (6 males and 18 females, mean age = 24.0) housed at the

North Carolina Zoo (NCZ), in Asheboro, North Carolina (N=16, 5 males), the Yerkes National

Primates Research Center (YNPRC) in Lawrenceville, Georgia (N=8, 1 male), and on 25

bonobos (11 males and 14 females, mean age = 18.84) housed at the Columbus Zoo and

Aquarium (CZA) in Powell, Ohio (N=15, 7 males), and Jacksonville Zoo and Gardens (JZG) in

Jacksonville, Florida (N=10, 4 males). Subjects live in indoor holding cages with adjacent

outdoor enclosures. A majority of focal follows were collected while subjects were in their

outdoor enclosure, periodically with indoor access, (NCZ: outdoor enclosure is approximately

45,000 square feet; YNPRC: outdoor enclosure is approximately 6,300 square feet; CZA:

outdoor enclosure is approximately 15,000 square feet; JZG: outdoor enclosure is approximately

6,500 square feet), and a portion of follows from CZA were collected while apes only had indoor

access (CZA: each indoor enclosure is approximately 800 square feet).

All bonobos and chimpanzees over the age of 24 months were considered subjects, while individuals that were 9-24 months were considered social partners (during the collection of behavioral data from other subjects) but not considered subjects themselves. Since most infants younger than 9 months of age spend a considerable amount of time attached to their mothers, these infants did not count as social partners when considering the mother's proximity measure, nor were they considered subjects. Any social behaviors that the focal engaged in with an infant (0-24 months) were counted in said focal's sociality measures (nursing, play, grooming, etc.). Only individuals older than 9 months were counted in social group size measures and social proximity measures.

Focal follow data were collected on a quasi-randomized list of individuals from the time the apes were allowed access to the outdoor enclosure/exhibit (roughly 9 AM) until they were brought back inside/into holding (roughly 5 PM). Follows lasted 10 minutes and at least 9 follows were collected from each subject (minimum 90 minutes of observations per chimpanzee and bonobo). Follow order was determined by randomly assigning each subject a number and conducting follows numerically as long as this order did not violate the following rules: For each focal individual, no 2 follows were collected within 60 minutes of one another and no more than 3 follows were collected on an individual in any given day, as long as access permitted (exceptions were made for 2 bonobos at JZG and 1 bonobo at CZG, where 4 follows occurred in the same day because of access limitations). If the focal individual went out of view for more than 3 minutes, or their proximity could not be determined for 3 or more consecutive data points, the follow was thrown out and not used in data analysis.

A series of sociality and communicative production measures were coded in real-time using Behavioral Observation Research Interactive Software (BORIS) version 3.0 operating on a

MacBook Air (see socio-communicative measures below). Social proximity was recorded instantaneously at 1-minute intervals (starting at time zero) for a total of 11 proximity data points per follow (see proximity measures below). All other social behavior measures were recorded continuously during the 10-minute follow (see state behaviors below) or on an all-occurrence basis (see event behaviors below). Social group sizes varied across facilities and across data collection days and were recorded for every single follow (NCZ: average group size = 8; YNPRC: G2 compound group size = 8; CZA: average group size = 5; JZG: average group size = 5). All focal follows were also recorded using a Canon VIXIA HF G30 camcorder and a Sennheiser ME 66 short shotgun microphone with K6 power module. On occasion, follow videos were utilized post hoc to verify socio-communicative measures upon data entry. The same experimenter coded all focal follows.

Any communicative signals directed towards an external source (e.g. a human caregiver) was noted during data collection and later excluded from analyses. Signals were coded as external if the signaler emitted the communicative signal while either 1) performing a focused look or glance towards a human, or 2) approaching a human. Similarly, chimpanzee idiosyncratic grooming sounds (e.g. raspberries, teeth chomping, lip smacking) were noted during data collection and later excluded from analyses; bonobos do not produce an equivalent vocalization, and all analyses were not affected by the inclusion or exclusion of chimpanzee grooming sounds. Often times, the individual chimpanzee produced grooming sounds (raspberries, lip smacking, etc.) prior to initiating grooming behavior or just subsequent to ceasing the behavior. Any signals produced before or after grooming behavior occurred were not scored as a grooming sound and were included in analyses. Only sounds made while the focal was actively engaged in grooming were excluded.

All communicative signals were coded as either a vocalization (any vocal event produced by focal individual not directed towards humans; see vocal types below), gesture (any gestural signal produced by focal individual not directed towards humans; see gesture types below), facial expression (any facial expression produced by focal individual not directed towards humans that occurs without a vocal component; see facial expression types below), or concomitant signal (any two signals from different types occurring at the same time or within one second of one another; see concomitant signal types below). When a facial expression was produced while vocalizing, and was necessary for the production of the vocalization, the event was scored as a vocalization, and if the facial expression occurred during or within one second of a vocalization or gesture, and was not necessary for the other signal's production, it was coded as a concomitant signal. For example, a 'hoo' vocalization that contains a 'hoo' face was coded as a vocalization because the facial expression was necessary to produce the 'hoo' sound. In contrast, a play face is not necessary for the production of a laugh vocalization therefore if the focal produced a play face while laughing the event was coded as concomitant. A communicative event was considered a separate/new signal if it occurred at least 3 seconds following the production of another signal, or was of a different signal type and did not fit the concomitant signal criteria. For example, if an individual vocalized at the beginning of an agonistic event and 2 seconds later, slapped the conspecific, these communicative events were coded as a separate vocalization and gesture.

<u>Facilities</u>

Chimpanzees – North Carolina Zoo – Asheboro, North Carolina

The chimpanzees living at the North Carolina Zoo in Asheboro have access to an approximately 45,000 square foot outdoor enclosure with natural grass substrate. This outdoor yard contains multiple fallen trees, both real and fake, as well as flat rocks and a large, hollow, fake tree roughly 20 feet tall. The outdoor trees are strung with fire hoses and contain multiple hammocks. The yard also contains a dry moat that is approximately 6-8 feet deep. The outdoor enclosure is open-topped and visual access was available through 15-foot glass windows on one side of the enclosure (2 public viewing areas). Observations occurred between 8:00AM and 5:00PM while the chimpanzees had access to the outdoor yard, and were made from 15-foot public, glass viewing windows.

A total of 16 chimpanzees, 5 males and 11 females, live in two social groups at the North Carolina Zoo (ages 2-46, mean age = 20.93). The two groups remain relatively constant, with two adult females and one juvenile male switching between social groups on any given day. One social group consistently contains three adult males and six females (Jon's group) while the other is composed of one male and three females (Kendall's group). The most common group compositions were 3 males and 6 females in Jon's group (ages 5-44, mean age = 16.33) and 2 males and 5 females in Kendall's group (ages 2-46, mean age = 26.57).

Weather dependent, chimpanzees in the social group that had outdoor access overnight were brought inside in the morning so keepers could bait the yard with food. This social group was then let into the outdoor enclosure, at approximately 8:30AM, and remained outdoors until 2PM. At this time, keepers would bring the chimpanzees inside and re-bait the outdoor yard.

Keepers then gave outdoor access to the other social group, which remained on exhibit until 2PM the following day (with a short period inside while keepers baited the yard for the AM forage). On days where temperatures were too low (below 40) chimpanzees were not given access overnight and only one social group had access to the outdoor yard during the day, from roughly 8:30AM – 4:00PM.

Chimpanzees – Yerkes National Primate Research Center – Lawrenceville, Georgia

At the Yerkes National Primate Research Center (YNPRC), the outdoor corral has a wooden climbing structure with multiple features including hammocks, fire hoses, bridges and ladders. The outdoor corral is open-topped, surrounded by metal mesh on all four sides and is approximately 6,300 square feet and combined with the indoor runs is roughly 7,000 square feet. The yard is natural dirt substrate with some grass patches and contains large barrels placed throughout. Each indoor run has a substrate of wood-wool, cardboard, burlap, etc., and contains between one and two bed board(s) and some runs contain hammocks.

The G2 group of chimpanzees consists of 1 male and 7 females (mean age = 24.5) and never changed social composition during the entire period of data collection. Focal follows were conducted from an observation tower that had visual access of the entire outdoor corral. When the focal subject went indoors, follows were conducted from human space adjacent to the indoor runs (metal mesh). Follows were conducted during the times of 9:00AM - 4:00PM while the chimpanzees had indoor and outdoor access. On some of the days, chimpanzees were given short training sessions, or enrichment was handed out at roughly 2:00PM. Follows were conducted as

normal during these times as long as visual access was available and the follow was already taking place when activity began; no new follows were started during training/enrichment times.

Bonobos – Columbus Zoo and Aquarium – Powell, Ohio

The bonobo exhibit at the Columbus Zoo and Aquarium includes three separate enclosures, two of which are indoors and one of which is an approximately 15,000 square foot outdoor yard. The indoor enclosures, which are viewable from 10-foot outdoor, public viewing windows, are adorned with playground equipment including brachiating bars, bedding platforms and slides. Each indoor enclosure is roughly 800 square feet and 15 feet tall at its highest. The outdoor yard features multiple fallen trees, both real and fake, and multiple tall wooden climbing platforms, connected with fire hoses. The outdoor yard also features a 30 foot deep dry moat, an artificial termite mound, and slow flowing waterfall. Follows were conducted from outdoor, public, glass viewing windows for all follows, and from open access areas over the moat for outdoor follows, and were collected during the times of 9 – 5:30PM.

There are a total of 18 bonobos living at the Columbus Zoo, 15 of which were considered subjects, 7 males and 8 females (ages 2-38, mean age = 18.48). Social group composition changed on a daily basis and typically consisted of 4 groups. Only a few individuals had restrictions on particular social partners and each individual moved groups at least once during the data collection process. The group sizes ranged from 3 to 7 individuals (mean group size = 4.94).

On any given day, the bonobos that slept in one indoor exhibit enclosure (enclosure A) were moved into holding at 9:30AM and the enclosure was sanitized. Following enclosure

sanitization and food baiting, roughly 11AM, the other social group that slept on exhibit would be moved into the clean enclosure (enclosure A). The now empty exhibit enclosure (enclosure B) would then be sanitized and baited, and a new group would be shifted into this space. While enclosure A was being cleaned, a third group would move out into the outdoor yard, at roughly 10AM. On some of the data collection days, enrichment (in the form of frozen treats) was given to the individuals in the outdoor yard around 2PM. Each afternoon the bonobos in exhibit enclosure A would be shifted into holding, the enclosure would be baited, and then the individuals inside enclosure B would be shifted over into enclosure A. Enclosure B was then baited and the group from the outdoor yard was shifted in for evening forage. The groups then slept in this arrangement until the following morning. This shifting typically occurred at 4:30PM.

Bonobos – Jacksonville Zoo and Gardens – Jacksonville, Florida

The bonobos living at the Jacksonville Zoo and Gardens have access to an approximately 6,500 square foot outdoor enclosure with natural grass substrate. The outdoor enclosure is surrounded by a 2-foot deep moat on one side and a tall cement wall on the other side. The bonobos have access to a multi-story wooden climbing structure that is adorned with hammocks, ladders, fire hoses, rope swings, etc. The enclosure is open-topped and approximately two stories below the public viewing areas. All focal follows were conducted from the public viewing areas while the bonobos had outdoor access only (between 9:00AM and 4:00PM).

At JZG there are a total of 11 bonobos, 5 males and 6 females, 10 of which were considered subjects (4 males: 6 females, ages 2-47, mean age = 19.4). The bonobos live in 2 separate social groups, each containing an adult male (mean group size = 5.17). Most of the

females and juveniles switch groups on a daily basis, however a female and her 2 male offspring are always in the same group. Group sizes ranged from 3 to 8 individuals. The most common groupings were 3 males with 3 females (group a, mean age = 12.83) and 1 male with 3 females (group b, mean age = 29.25).

The bonobos were let into the outdoor enclosure each morning after the yard was baited with food for forage (approximately 9:00AM). On some of the observation days the bonobos were brought inside at 12PM, the yard was baited again, and the other social group was given outdoor access. On other days, the social group remained outdoors from roughly 9:00AM until they were brought off exhibit at 4:00PM. On days where only one social group was given outdoor access, the keepers handed out an enrichment item at approximately 2PM.

Data Analyses

Individual focal follow data and averaged focal follow data per subject were analyzed for both species using SPSS v.24 operating on a MacBook Air. In terms of grooming, a total time spent grooming was collected for each focal follow by adding up the total time spent giving grooming, receiving grooming and mutually grooming, and subtracting out the time when the individual was engaged in more than one grooming behavior (groom overlap). Grooming proportion was collected for each focal follow using the following formula: (total time spent grooming) / (600 – time out of view), where 600 is the total observation time (in seconds) and time out of view (mean across 498 follows = 8.90 seconds; total out of view time never exceeded 180 seconds, or the follow was thrown out) is specific to each individual focal follow. Play proportions were also calculated in this way: (total time spent playing) / (600 – time out of view).

For each focal follow, proximity score was calculated using the following formula:

$$\frac{(3 * \text{\# touching data points}) + (2 * \text{\# socially close data points}) + (1 * \text{\# solitary data points}) + (0 * \text{\# isolated data points})}{(11 - \text{\# cannot be determined data points})}$$

where 11 is the total number of proximity points per focal follow. Scores range from 0-3.

In order to standardize sociality measures, grooming proportion, play proportion, and social proximity score were transformed into z-scores, and only z-score values were used in the analyses. The total number of vocalizations, gestures, facial expressions and concomitant signals were summed to generate a total communicative signals produced value per focal follow.

The relationship between communicative production (total communicative signals produced) and sociality (transformed grooming proportion, transformed play proportion and proximity score) was assessed using Pearson correlations for each species, while controlling for individual subject. For correlational analyses the first 9 focal follows per individual were analyzed. A total of 225 bonobo focal follows and 216 chimpanzee focal follows were collected. Therefore, a total of 4,410 minutes (73.5 hours) of direct observations were analyzed for the two species combined.

In order to assess differences in overall communicative production and sociality, a multivariate ANOVA was conducted with species and sex as fixed factors and group size as a covariate; an independent-samples t-tests revealed bonobos live in significantly smaller group sizes than chimpanzees ($t(47) = -9.245$, $p < 0.001$; mean bonobo group size = 5.052, mean chimpanzee group size = 8.492). A MANOVA was selected in order to investigate how multiple independent factors, and the interaction between them, may influence multiple socio-

communicative measures. Therefore, for all analyses of variance, focal follow data were averaged per individual subject (Bonobo n = 25, Chimpanzee n = 24).

RESULTS

Pearson correlation analyses revealed a significant positive correlation between social proximity score and total communicative signals produced for bonobos (r = 0.146, p = 0.029), and chimpanzees (r = 0.237, p < 0.001) (Figure 1). Similarly, a significant positive correlation between play proportion and total communicative signals produced was found for bonobos (r = 0.503, p < 0.001) and chimpanzees (r = 0.596, p < 0.001) (Figure 2). When considering communicative modalities, a significant positive correlation between play proportion and total gestures produced was found for bonobos (r = 0.369, p < 0.001) and chimpanzees (r = 0.465, p < 0.001), as well as a significant correlation between play proportion and total facial expressions produced for bonobos (r = 0.579, p < 0.001) and chimpanzees (r = 0.727, p < 0.001), and a significant correlation between play proportion and total concomitant signals produced for bonobos (r = 0.574, p < 0.001) and for chimpanzees (r = 0.493, p < 0.001) (Figures 3A, 3B and 3C, respectively). For bonobos specifically, analyses revealed a significant negative correlation between grooming proportion and total communicative signals produced (r = - 0.153, p = 0.022) (Figure 4), and a significant positive correlation between group size and proximity score (r = 0.185, p = 0.005).

MANOVA results revealed a significant main effect for species when considering total communicative signals produced (F (1,44) = 9.636, p = 0.003), total gestures produced (F (1,44) = 5.479, p = 0.024) (Figure 5), and social proximity score (F (1,44) = 7.641, p = 0.008) (Figure 6). Additionally, a significant main effect for sex was found when considering proximity score (F (1,44) = 4.882, p = 0.032) (Figure 7). No interactions between sex and species were found for

overall grooming proportion, play proportion, social proximity score or total communicative signals produced.

DISCUSSION

The current study's primary investigation involved observing the similarities and differences in socio-communicative behavior of our closest living relatives, bonobos and chimpanzees, to better understand the selection pressures leading to the emergence of complex sociality and communication, which occurred in the hominin lineage. When considering bonobos and chimpanzees, we found a significant positive correlation between proximity score and total communicative signals produced. In other words, individuals that communicated more also spent more time in close proximity to conspecifics. This positive relationship between communication and spending time in close proximity to conspecifics is also evident in birds, and these results are suggestive of a socially relevant function of communication; communication is the commonly proposed purpose of human spoken language (Freeberg & Harvey, 2008; Pinker, 2003). Individuals that spent more time in close proximity to conspecifics also produced more gestural signals, which may support a gestural origin of language, however further data analyses, discussed here shortly, suggest otherwise.

In addition to proximity being positively correlated with communicative production in chimpanzees and bonobos, we found that individuals from both species that play more often also produce more total communicative signals, most specifically gestures, facial expressions and signals from more than one modality. This result is not surprising considering the highly dynamic and obscure nature of play, which likely necessitates increased communicative production and complexity (Bekoff & Allen, 1998). Together these data are supportive of multimodal origin theories, demonstrating associations between sociality and a diversity of

communicative signals in different modalities. Other researchers have similarly concluded that evidence of multiple modalities being associated with varying levels of socio-communicative behavior is indicative of a multimodal origin of language (Taglialatela et al., 2011; Leavens et al., 2014). However, more comprehensive investigations of the role communicative modality plays in the expression of complex sociality will need to be conducted.

In bonobos specifically, analyses indicated a negative relationship between communicative production and grooming proportion; specifically, individual bonobos that produce more communicative signals engage in grooming behaviors less often than individuals that produce fewer communicative signals. This finding is consistent with current theories proposing that complex communication replaced manual grooming, within the hominin lineage, as a way to maintain strong bonds in large social groups (Leavens, et al., 2014; Dunbar, 1996). Bonobos are exhibiting an individual level representation of a phylogenetic relationship between grooming rates and communication; at some point in our hominin lineage, individuals must have shown this replacement of communication for grooming which became adaptive across generations. Therefore, the socio-communicative behaviors of bonobos are an exemplary model for the elaborate social and communication system exhibited by humans, and can provide insight into the social pressures leading to the emergence of spoken language. Overall, our correlational findings are consistent with previous work demonstrating chimpanzees and bonobos live in the large social groups, engage in high levels of affiliative behaviors including grooming, and display uniquely complex communicative signals (McComb & Semple, 2005; Gruber & Clay, 2016).

Although there is evidence of a comparable relationship between sociality and communication in chimpanzees and bonobos, it is also important to highlight the substantial

differences these two species exhibit in socio-communicative behavior. A MANOVA revealed bonobos (mean = 3.530 signals/follow) communicate significantly more than chimpanzees (mean = 1.354 signals/follow). This is consistent with previous findings that bonobos travel in larger foraging parties in the wild, rely more heavily on auditory communication while foraging, and have the largest vocal repertoires of all non-human ape species (Bernejo & Omedes, 1999; McComb & Semple, 2005). In addition, we found a trend towards a species difference in total vocalizations produced, with bonobos (mean = 0.9704 vocalizations/follow) producing more vocalizations than chimpanzees (mean = 0.2192 vocalizations/follow), however this species difference only approached significance (F (1,44) = 4.025, p = 0.052). Bonobos did produce significantly more gestures than their chimpanzee counterparts, (bonobo mean = 1.491, chimpanzee mean = 0.650 gestures/follow), and this is consistent with previous findings that bonobos have greater gestural flexibility than chimpanzees (Pollick & de Waal, 2007). Together our findings indicate that bonobos may be the more socially and communicatively complex of the two ape species.

Analyses also revealed that bonobos spend significantly more time in closer social proximity to conspecifics than their chimpanzee counterparts (bonobo mean = 2.058, which is between socially close and close touching; chimpanzee mean = 1.850, which is between solitary and socially close), suggesting bonobos are in fact the more social species. These results are not surprising considering bonobos have been found to live and travel in larger social groups, and are the only species to exhibit high levels of socio-sexual behavior such as genital-genital rubbing, which is used as a form of social cohesion among social partners during particularly stressful events (Stanford, 1998; McComb & Semple, 2005; Gruber & Clay, 2016; Rowe 1996). Additionally, we found that regardless of species, females had significantly higher proximity

scores than males (female mean = 2.029, male mean = 1.818), which makes sense given bonobos are matriarchal, and female bonding is critical in bonobo societies, and to lesser extent, in chimpanzees (Gruber & Clay, 2016; Stanford, 1998). Our analyses however, did not reveal a significant interaction between sex and species in regards to proximity score. Furthermore, post hoc analyses revealed bonobos were kept in significantly smaller social groups than chimpanzees (mean social group size = 5.052 and 8.492 respectively), and were the only species to exhibit a positive association between group size and proximity score. Despite the fact that bonobos are being kept in smaller social groups than chimpanzees, these data indicate that bonobos communicate more often and are more social than chimpanzees.

The objective of the current study was to investigate the relationship between sociality and communication in our closest living relatives, bonobos and chimpanzees, to better understand how complex socio-communicative behavior developed as a result of selection pressures encountered by early hominins. Both bonobos and chimpanzees exhibited a notable positive association between sociality and communication. This relationship is even more pronounced in bonobos given their greater overall communicative production and higher social proximity measures than chimpanzees. Bonobos demonstrated an increase in sociality as group size increased, as well as a positive relationship between sociality (social proximity and play proportion) and communicative production; a relationship that has been observed among social primate species. Additionally, bonobos demonstrated an individual level pattern analogous to the phylogenetic association between grooming and communication; most specifically, complex communication is replacing physical grooming as a tool for maintaining strong bonds. These observed associations between communicative production and sociality in bonobos, make bonobos an exemplary model for the evolution of complex socio-communicative systems,

specifically those demonstrated by hominins. Given the multifaceted nature of this relationship, however, it is essential to continue to study this association comparatively. The similarities and differences observed in bonobo and chimpanzee socio-communicative behavior could provide unprecedented insights into the evolutionary origins of human spoken language.

TABLES

Subjects Table

Facility	Species	Number of Subjects	Male:Female	Age Range	Average Social Group Size
Jacksonville Zoo and Gardens	Bonobo	10	4:6	2-48	5
Columbus Zoo and Aquarium	Bonobo	15	7:8	2-38	5
North Carolina Zoo	Chimpanzee	16	5:11	2-46	8
Yerkes NPRC G2 Compound	Chimpanzee	8	1:7	18-29	8
	Bonobo	25	11:14	2-48	
	Chimpanzee	24	6:18	2-46	
	Total	49	17:32	2-48	

Socio-Communicative Measures

State Behaviors	Description
Groom Give (GG)	Focal individual initiated and is grooming social individual without any grooming returned.
Groom Receive (GR)	Focal individual is receiving grooming initiated by another social individual and is not returning any grooming.
Mutual Groom (MG)	Both the focal individual and the social partner(s) are actively grooming each other –grooming partner.
Aggression Give (AG)	Focal individual is slapping, biting, hitting, and/or chasing a conspecific, while pilo-erect.
Aggression Receive (AR)	Focal individual is being slapped, bitten, hit, and/or chased by a pilo-erect conspecific.
Mutual Aggression (MA)	Both the focal individual and the social partner(s) are actively slapping, biting, hitting, or chasing each other, while pilo-erect.
Play (PL)	Focal individual engages in lively activity with another individual by wrestling, tickling and/or chasing the conspecific.
Nursing Give (NG)	Focal individual supplies a conspecific (usually offspring) with milk

	while conspecific is attached to focal individual's nipple.
Nursing Receive (NR)	Focal individual suckles on nipple of conspecific female (usually mother) to receive milk.

Event Behaviors	Description
Genital - Genital Rubbing / Copulation (GG)	Focal individual is actively engaged in sex or genital-genital contact with a conspecific.
Displaying (DS)	Focal individual is swaying, charging, drumming, slapping the ground/walls/barrels, or throwing objects; accompanied by pilo-erection.
Communicative Signal (CS)	Any vocal, gestural, facial or concomitant signal produced by the focal individual. In order to be considered a separate/new signal, the signal must be produced at least three seconds following a prior signal or must be of different signal type than the prior signal. See communicative signal types below.
Social Proximity (SP)	Social proximity was recorded instantaneously at 1-minute intervals. See proximity measures and descriptions below.

Communicative Signals	Description
Vocalization (VO)	Any vocal signal produced by focal individual. See vocal types and definitions below. This includes idiosyncratic sounds produced during manual grooming by chimpanzees.
Gesture (GE)	Any gestural signal produced by focal individual. See gestural types and definitions below.
Facial Expression (FA)	Any facial communicative signal produced by focal individual that is not produced in conjunction with a vocalization that may necessitate it. (For example 'hoo' faces produced without a 'hoo' vocalization are considered facial expression, while 'hoo' vocalizations with a 'hoo' face are considered vocalizations, not concomitant signals). See facial expression types below.
Concomitant Signal (CO)	Any vocalization, gesture, facial expression or body posture that occurs within two seconds of an initial communicative signal of different type. (VO+GE, GE+FA, VO+FA)

Social Proximity	Description
Close/Touching (TOU)	Focal individual is in physical contact with a conspecific or close enough that it could touch a conspecific without relocating (≤ 1.5

	meters).
Socially Close (CLO)	Focal individual is ~ 1.5-3 meters from the nearest conspecific.
Solitary (SOL)	Focal individual is ~ 3-5 meters from the nearest conspecific.
Isolated (ISO)	Focal individual is > 5 meters from the nearest conspecific.

Bonobo Vocal Types

Vocalization Types	Description
Hoots (HO)	Relatively loud vocalizations that are produced in a series and are voiced on both inhalation and exhalation. Hoots are often produced by a number of individuals simultaneously.
Alarms (AL)	Loud, sharp vocalizations that may sound like a "wraa" or "waa". Alarms are given in the context of real or perceived danger (snake, truck, etc.).
Peeps/Peep Yelps (PE)	Generally short, tonal, high-pitched vocalizations that are produced in a variety of contexts. They may occur in series or as a single call. They may be modulated or not (i.e. no change in frequency).
Pants/Grunts (PG)	Relatively low frequency, noisy vocalizations that are usually produced in a series. Pants are fast, repetitive, low frequency vocalizations made on both inhalation and exhalation (e.g. panting laugh). Grunts are also relatively quiet (but louder than pants) and sound like a series of "ohoh" or "uhuh" sounds made in quick succession.
Screams (SC)	Very loud, high pitched, relatively long vocalizations that have both tonal and noisy components.
Copulation Scream (CS)	Much like that of regular screams but higher pitched and produced during copulation or g-g rubbing.
Other (OT)	A vocalization that does not meet any of the above requirements for a category should be classified as other.

Chimpanzee Vocal Types

Vocalization Types	Description
Pant Hoots (PH)	Voices on both inhalation and exhalation and incorporate a series of "hoo" sounds which may or may not escalate to a climactic scream or piercing "ahh" vocalization.
Alarms (AL)	Loud, sharp vocalizations that may sound like a "wraa" or "waa". Alarms are given in the context of real or perceived danger (snake, truck, etc.). Some chimpanzees may also make a quieter "hoo" sound in this context. Alarms are often made by bystanders during a fight.

Barks/Grunts (BG)	Vocalizations that are produced by short exhalations sounding like 'aaa'. They are often produced in a series and can range in pitch from low to high. Grunts are relatively low frequency and noisy while barks tend to be more tonal and higher in frequency than grunts. These calls are typically associated with the anticipation of eating, receiving food, or other positive experiences.
Pants/Grunts (PG)	Pants are fast, repetitive, low frequency vocalizations made on both inhalation and exhalation (e.g. panting laugh). Pants are very quiet and breathy and are sometimes accompanied by placing an open mouth on another individual while panting. Pant grunts (PG) can be difficult to hear from a distance and are most easily recognized by quick, rhythmic movements of the body. Pant grunts are also relatively quiet (but louder than pants) and sound like a series of "ohoh" or "uhuh" sounds made in quick succession.
Screams and Whimpers (SC)	Screams are loud, high pitched, voiced shrieks and at its most intense can be raspy or even hoarse sounding. Screams are associated with fear, submission, distress or agitation. Whimpering sounds a bit like modulated, high-pitched 'hoo' sounds or crying and often progresses into screams. Whimpering occurs in chimpanzees of all ages during distress or fear and by infants when being weaned.
Other (OT)	A vocalization that does not meet any of the above requirements for a category should be classified as other.

Bonobo/Chimpanzee Gesture Types

Gesture Types	Description
Food Beg (FB)	Focal individual extends arm towards another individual with palm facing up and hand maintained in a cupped posture. May include placing one or both hands around or under the other's lips and or chin.
Wrist/Finger Present (WP)	Focal individual flexes the wrist while holding the back or side of hand out toward another individual, may include placing a finger or hand into another individual's mouth. Note whether or not contact occurs.
Point (PO)	Focal individual directs either his/her whole hand or one or more digits to recipient, another individual or object in the environment. Subject holds out a hand toward another individual or object by extending the arm, wrist and hand. May end in contact but gesture initiates without contact.
Touch (TO)	Focal individual makes any sort of contact with another individual with the front or back of their hand or fingers. Common Touch Gestures: GT=Gentle touch, DB=Dab, PT=Pat, EM=Embrace, AH=Aggressive hit, GR=Grab and GI=Genital inspect (with hand), PK=Poke.
Threat Gesture (TG)	Focal individual swings arm in a quick, upward motion towards another individual with palm facing down (AR=Arm raise) or shakes the hand

	vigorously and repeatedly with a flexible wrist towards another individual (WS=Wrist shake).
Other (OT)	Focal individual produces a gesture that does not fall into one of the other categories. Common Other Gestures: AO=Arm over, CB=Cage bang, TH=Throw, CL=Clap, SH=Self hit, RK=Rap knuckles

Bonobo/Chimpanzee Gesture – Sub Types

Touch Gestures	Description
Aggressive Hit (AH)	Individual uses hand to strike recipient with force, pilo-erect.
Dab (DB)	Subject touches recipient with back of flexed fingers whereafter touching hand is withdrawn immediately; sequence is repeated in quick succession.
Embrace (EM)	Individual places one or two arms around another, generally around their back from the front but can be from the back around their middle.
Genital Inspect (GI)	Subject touches recipient's swelling or penis with fingertip(s) or hand.
Grab (GR)	Subject uses his/her hand(s) to forcefully grasp recipient.
Gentle Touch (GT)	Subject makes any sort of contact with another individual with the front or back of their hand or fingers, without appreciable force, that does not fall into one of the more specific categories of touch.
Poke (PO)	Subject pushes one or more fingertips with sudden movement onto body part of recipient, repetitive.
Pat (PT)	Subject rapidly and repeatedly contacts another individual with flattened palm surface of hand.
Touch (TO)	Any touch that does not fit into one of the above categories. Provide description.

Threat Gesture	Description
Arm Raise (AR)	Subject swings arm in a quick, upward motion towards another individual with palm facing down.
Wrist Shake (WS)	Subject shakes the hand vigorously and repeatedly with a flexible wrist towards another individual.

Other Gestures	Description
Arm Over/Hunchover (AO)	Subject sweeps one arm over the back of another individual but without hugging or extended contact.

Cage Bang (CB)	Subject uses hand to forcefully strike a substrate with the apparent intention of creating noise.
Throw (TH)	Subject uses hand to toss debris (dirt, feces, etc.) towards a recipient.
Clap (CL)	Subject contacts hands together forcefully to create noise.
Self Hit/Clasp Self (SH)	Subject crosses one or more hands across torso and slaps their own body repeatedly.
Rap Knuckles (RK)	Subject hits the knuckles of one or both hands against the ground or other substrate without creating a loud noise, repetitive.

FIGURES

Figure 1.
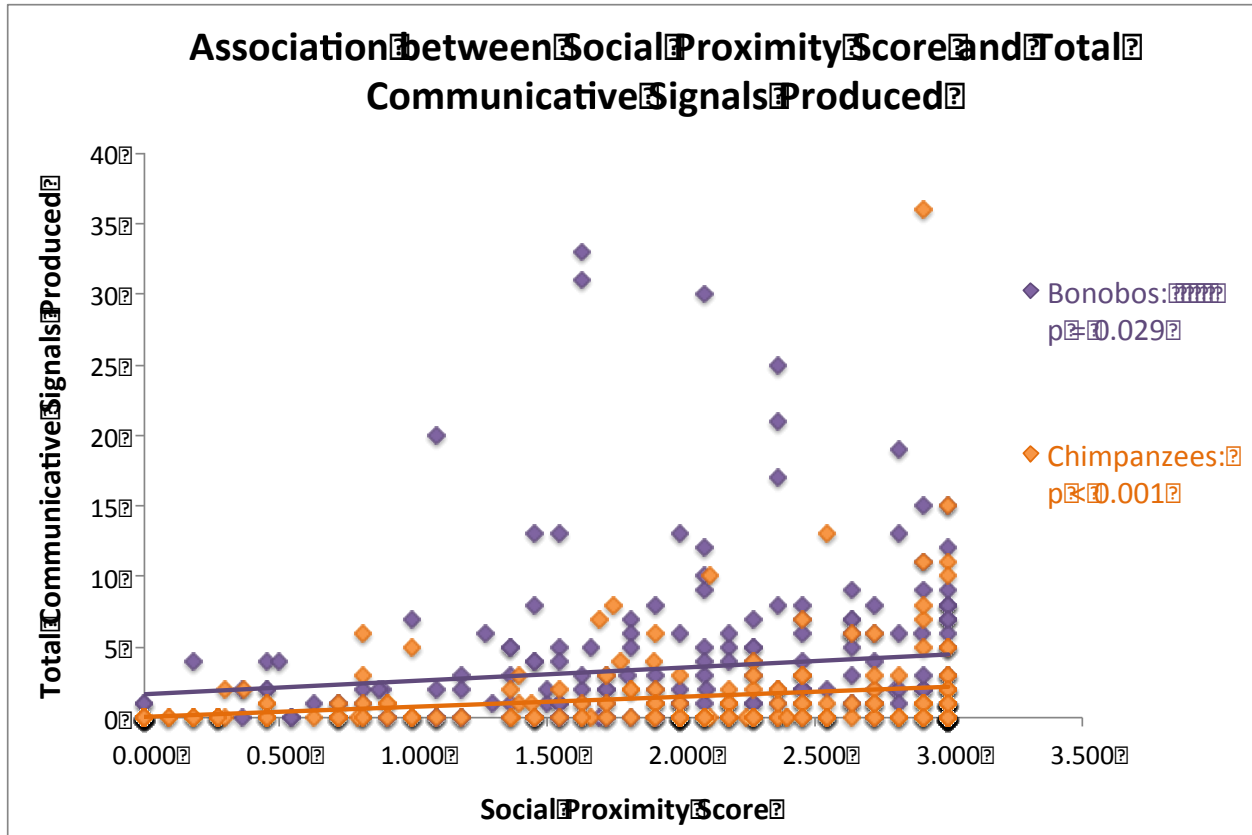
Figure 1: Social proximity score and corresponding total communicative signals produced per focal follow for bonobos (purple) and chimpanzees (orange). Non-transformed data shown for social proximity score.

Figure 2.

Association between Play Proportion and Total Communicative Signals Produced

Bonobos:
p < 0.001

Chimpanzees:
p < 0.001

Total Communicative Signals Produced (y-axis)

Proportion of Time Spent Playing (x-axis)
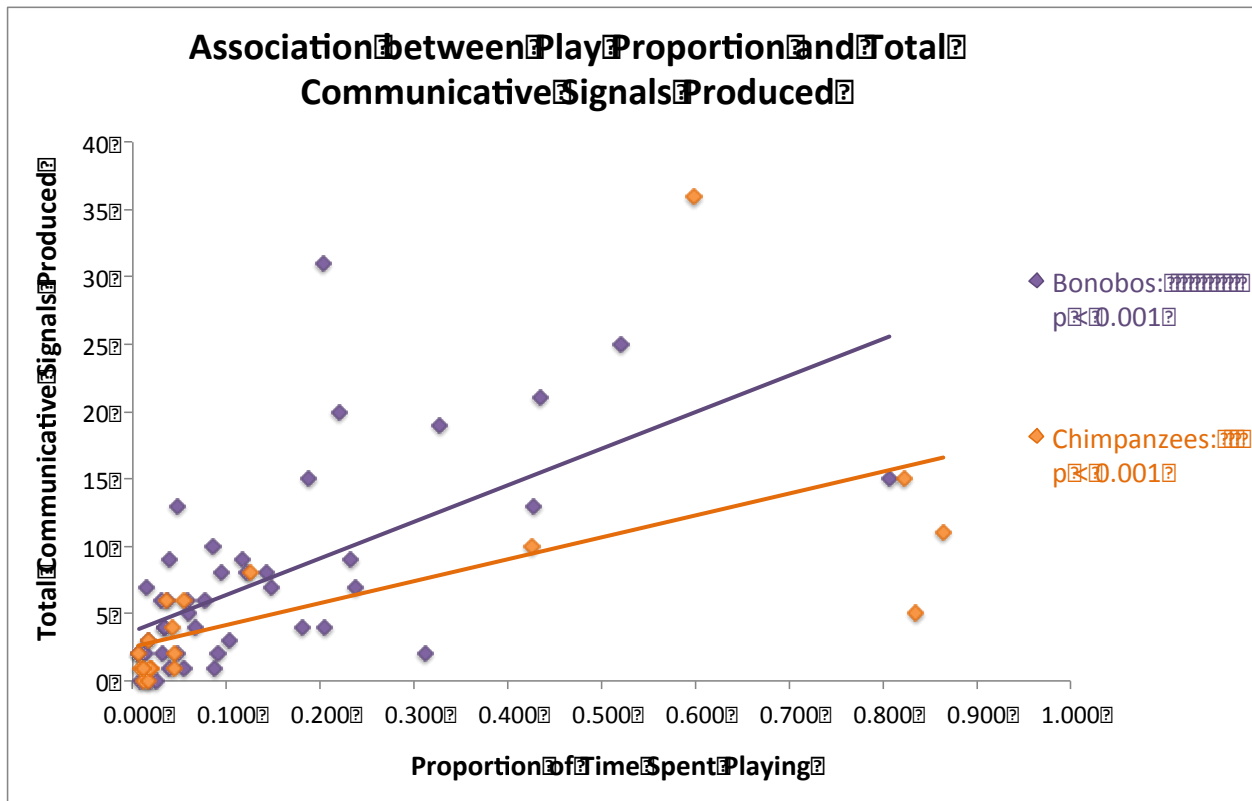
Figure 2: The proportion of time spent playing, and corresponding total communicative signals produced for bonobos and chimpanzees. Only non-zero play proportion values shown (63 follows). Non-transformed data shown for play proportion.
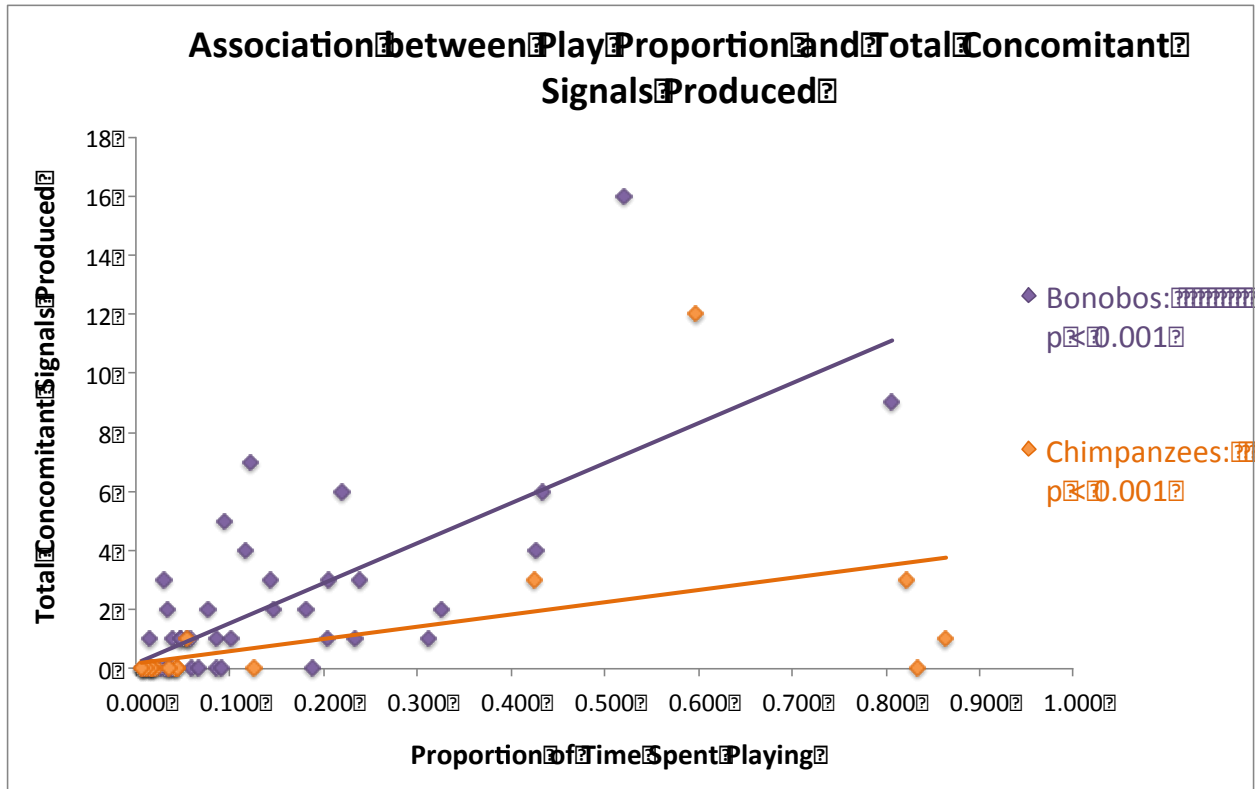
Figure 3A.
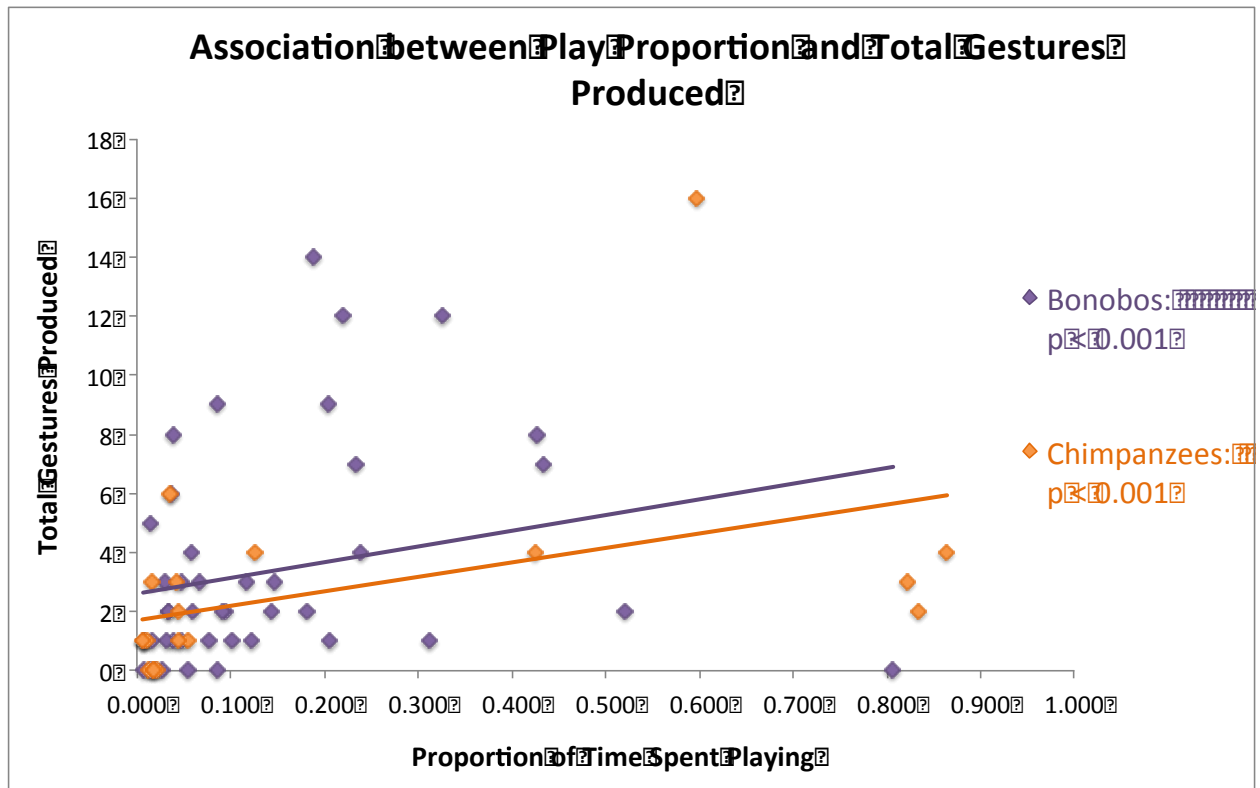
Figure 3B.
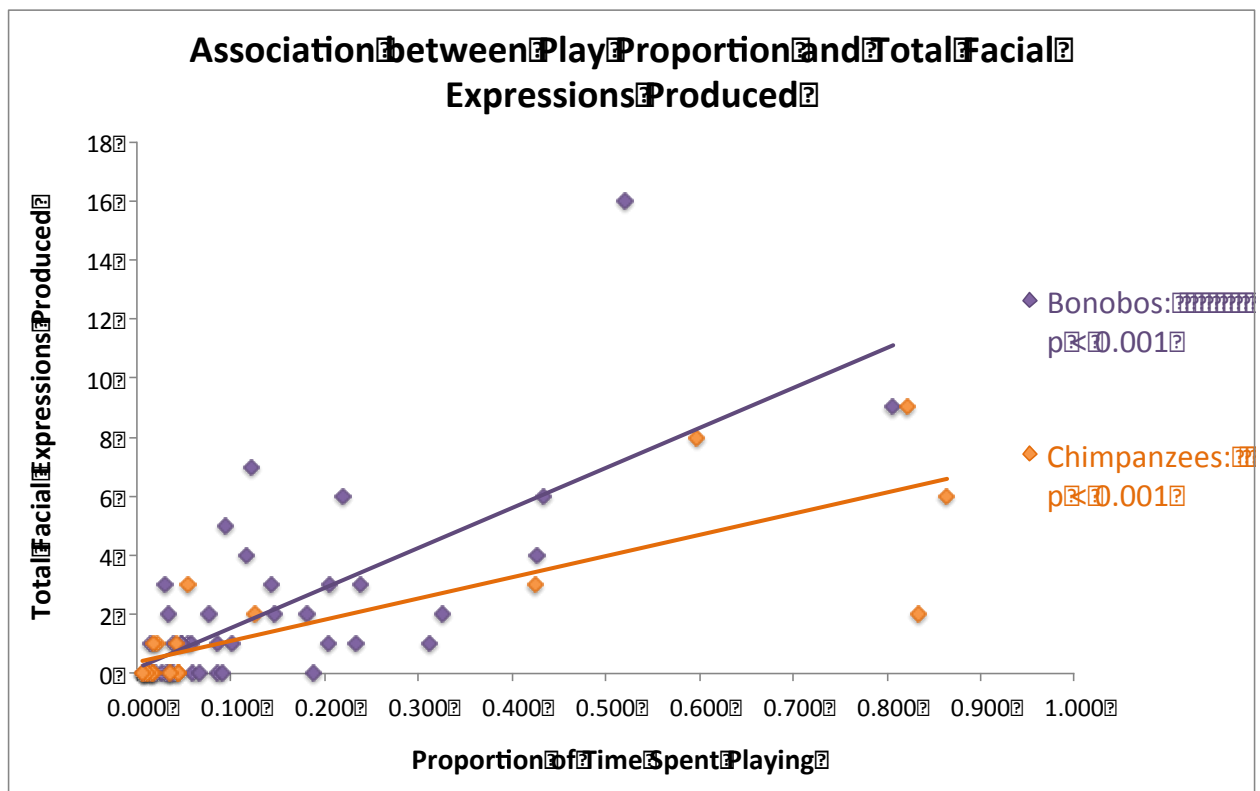
Figure 3C.

Figures 3A, 3B and 3C: The proportion of time spent playing and corresponding total gestures (3A), facial expressions (3B), and concomitant signals (3C) for bonobos (purple) and chimpanzees (orange). Only non-zero play proportion values shown (63 follows). Non-transformed data shown for play proportion.
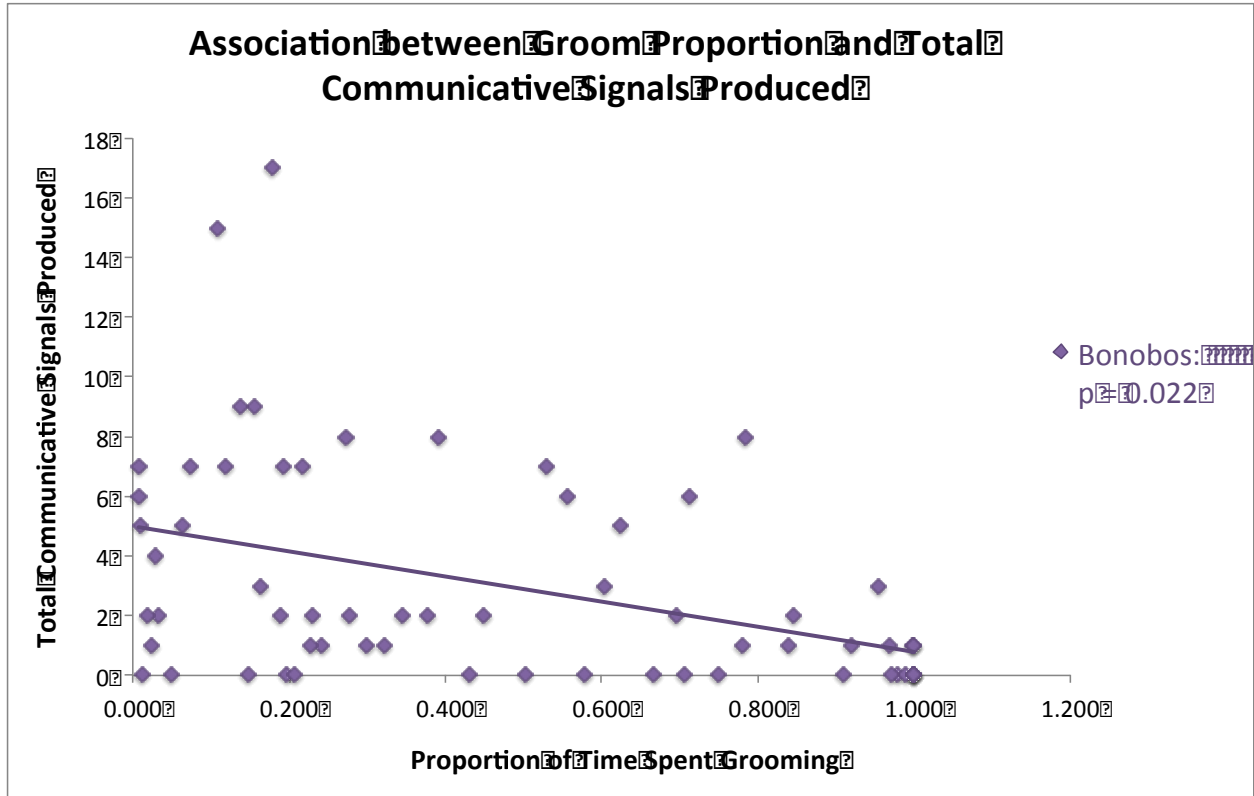
Figure 4.

Figure 4: The proportion of time spent engaged in grooming, and corresponding total communicative signals produced for bonobos. Only non-zero groom proportion values shown (65 follows). Non-transformed data shown for groom proportion.
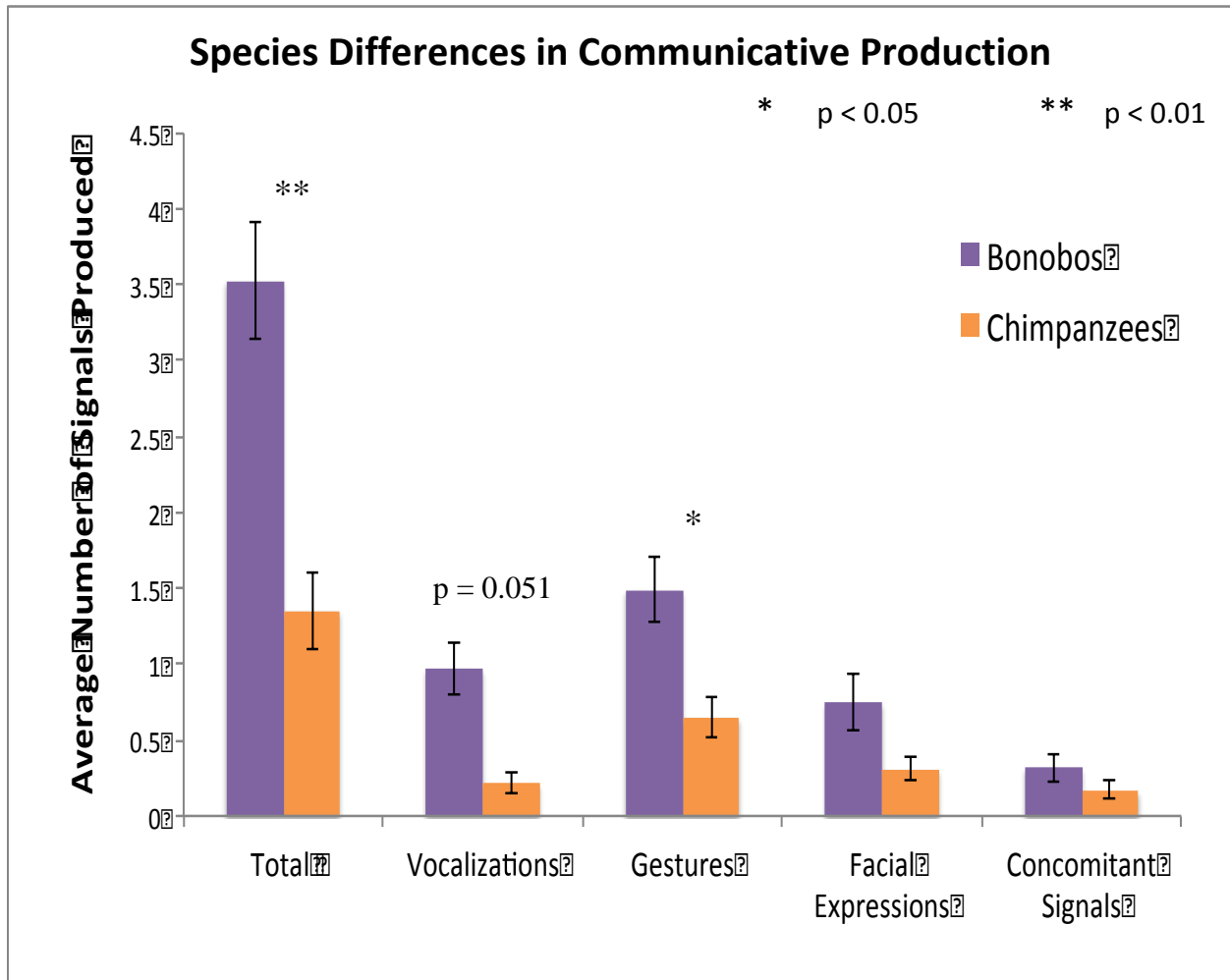
Figure 5

Figure 5: Average number of communicative signals produced for each signal type (total, vocal, gestural, facial, concomitant), separated by species with bonobos in (purple, left bars) and chimpanzees (orange, right bars).
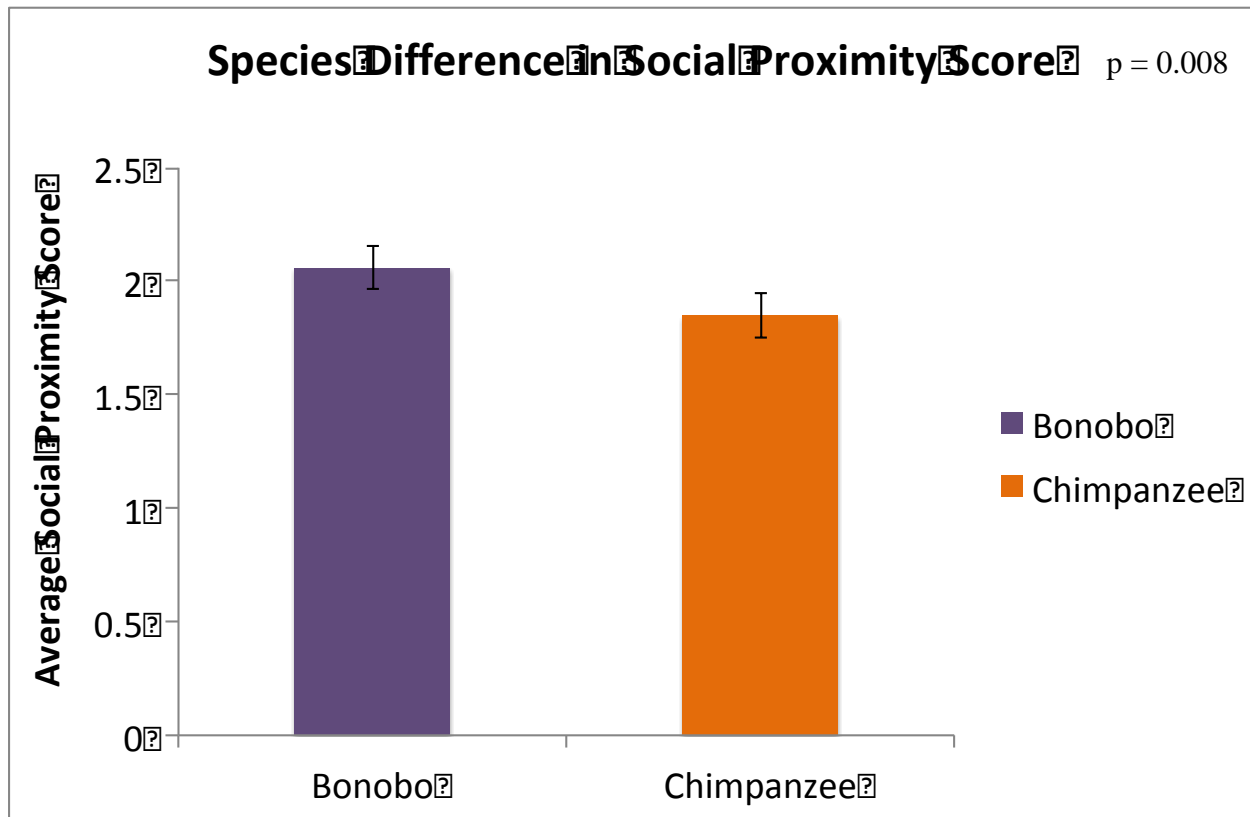
Figure 6.

Figure 6: Average social proximity score for bonobos (left, purple bar) and for chimpanzees (right, orange bar). Error bars represent standard error of the mean. Non-transformed data shown for social proximity score.
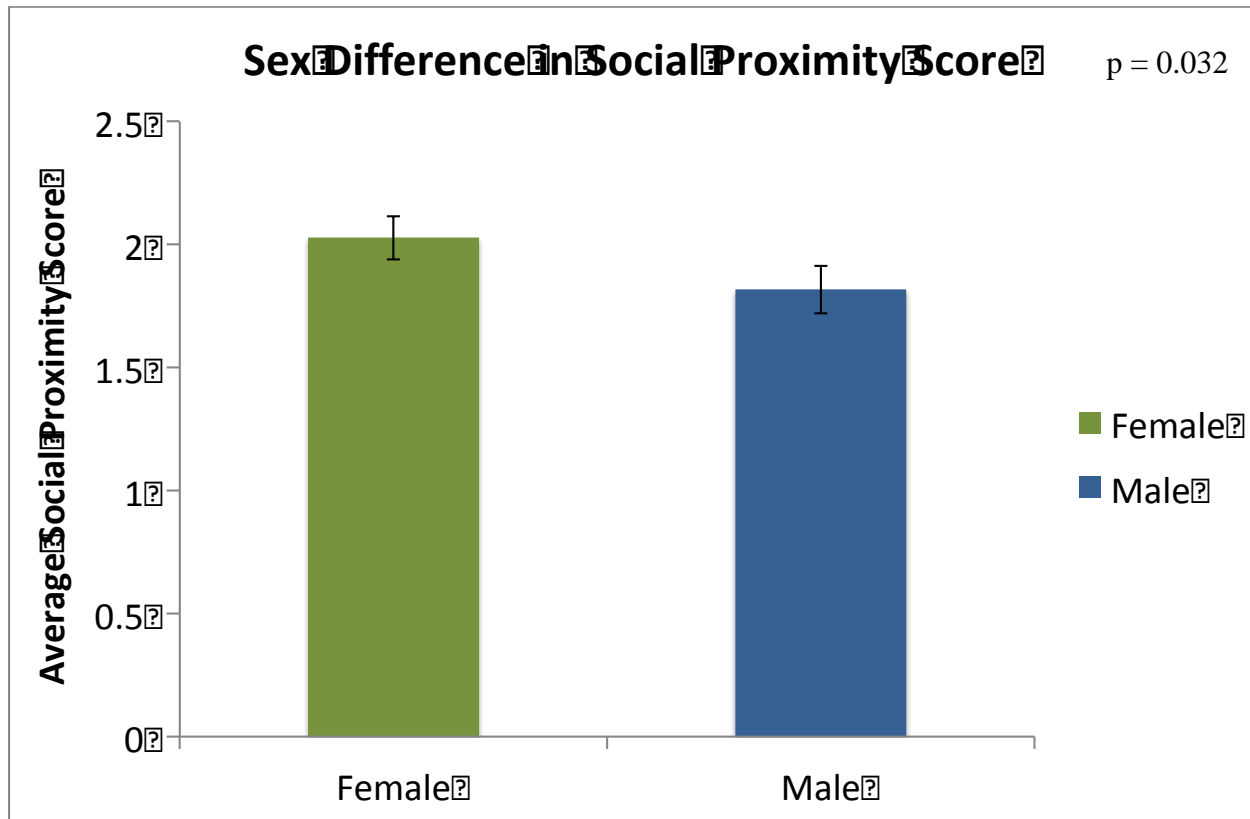
Figure 7.

Figure 7: Average social proximity score for females (left, green bar) and for males (right, blue bar). Error bars represent standard error of the mean. Non-transformed data shown for social proximity score.

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